Ecophysiological responses of marine macroalgae to climate change factors

Yan Ji[1,2] · Zhiguang Xu[3] · Dinghui Zou[4] · Kunshan Gao[1]

Abstract Marine macroalgae are ecologically and economically important primary producers, being adjacent to human living areas and playing key roles in coastal carbon cycles. They are subject to both regional and global environmental changes in coastal waters, where environmental factors fluctuate dramatically due to high biological production and land runoff. Since global ocean changes can influence coastal environments, global warming-induced ocean warming, ocean acidification (OA) caused by atmospheric CO_2 rise and increasing ultraviolet B (UVB) irradiance at the earth's surface are affecting physiology, life cycles, and community structures of macroalgae. Here, we examine recent progress towards understanding the effects of these climate change factors on ecophysiology of macroalgae. Some species tested show enhanced growth and/or photosynthesis under elevated CO_2 levels or ocean acidification conditions, possibly due to increased availability of CO_2 in seawater with neglected influence of pH drop. Nevertheless, OA can harm some macroalgae due to their high sensitivity to the acidic perturbation to intracellular acid–base stability. Mild ocean warming has been shown to benefit most macroalgae examined. Respiration quotient increased due to combined effects of ocean warming and acidification. UVB almost always harms the physiological functions of macroalgae, which develop protective strategies, such as accumulation of UV-absorbing compounds; UVA can drive photosynthesis under moderate levels of solar radiation or when solely exposed to it. However, little has been documented on the interactions of these multiple stressors. Future work requires further investigations to examine the effects of OA under complex environments or under multiple stressors to advance knowledge on macroalgal global change biology.

Keywords CO_2 · Macroalgae · Photosynthesis · Ocean acidification · Ocean warming · UV radiation

Introduction

Continuous emissions and accumulation of greenhouse gases, mainly CO_2, have caused global and ocean warming, which enhances stratification in pelagic waters and expands areas of hypoxia in coastal waters (Goncalves et al. 2010; Beardall et al. 2014). Rapid dissolution of CO_2 into oceans is causing ocean acidification (Connell and Russell 2010; Bates et al. 2012). On the other hand, depletion of the ozone layer enables more harmful UVB (280–315 nm) to reach the earth's surface (Molis and Wahl 2009). Ocean warming, ocean acidification (OA), and ultraviolet B (UVB) radiation may affect marine macroalgae to different extents in different regions.

As an important part of global primary producers, marine macroalgae have received wide attention due to their key roles in the marine biological CO_2 pump and in sustaining natural and sea-farming ecosystems (Gao and McKinley 1994). They are also economically and culturally important for

✉ Kunshan Gao
ksgao@xmu.edu.cn

1 State Key Laboratory of Marine Environmental Science, Xiamen University/College of Ocean and Earth Sciences, Xiamen 361005, China

2 School of Biological and Chemical Engineering, Qingdao Technical College, Qingdao 266555, China

3 Marine Biology Institute of Shandong Province, Qingdao 266104, China

4 College of Environment and Energy, South China University of Technology, Guangzhou 510006, China

providing food, medicine and even storm protection (Rönnbäck et al. 2007).

While there are a number of factors, such as nutrients and currents or waves, which can affect macroalgae, this review mainly focuses on the documented knowledge about the impacts or effects of ocean acidification, warming, and UV radiation, in an effort to enhance the understanding of their eco-physiological responses and subsequently highlights the main questions that need to be addressed in future work.

Effects of increasing CO_2 and ocean acidification

Atmospheric carbon dioxide (CO_2) was maintained at about 280 ± 10 ppm for the last 10,000 years; however, since the industrial revolution, combustion of fossil fuels, cement manufacture and land use are the primary sources of anthropogenic CO_2 released to the atmosphere (Houghton 2008). The concentration of atmospheric CO_2 has been rising steadily up to the recent level of 400 ppmv.

Most of the surface area on the earth is occupied by oceans, and the oceans have many ways of exchange with the atmosphere, including absorbing CO_2 with the help of the so called biological CO_2 pump. A comprehensive survey of inorganic carbon distribution jointly conducted by two international ocean research programs, the World Ocean Circulation Experiment (WOCE) and the Joint Global Ocean Flux Study (JGOFS), showed that the oceans have absorbed more than one third of the anthropogenic CO_2 released to the atmosphere (Sabine et al. 2004), though the capacity to act as a CO_2 sink has diminished (Bates et al. 2012). When CO_2 dissolves into seawater, it acts as follows to alter carbonate chemistry:

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

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

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

Briefly, when CO_2 dissolves in water, it combines with a water molecule to form carbonic acid, which is unstable and disassociates to bicarbonate and hydrogen ions, and then bicarbonate ions further dissociate to carbonate ions. While these equations can be reversible, increasing atmospheric CO_2 concentration moves the 1st and 2nd reactions towards the right side, and the resulting hydrogen ions reverse the 3rd reaction, leading to ocean acidification (OA). Therefore, ocean acidification drops pH, increases pCO_2 and bicarbonate but decreases carbonate ions. This continuous oceanic uptake of CO_2 has been predicted to cause a more significant pH decrease over the next several centuries than in the past 300 million years (Caldeira and Wickett 2003), which has critical consequences for marine organisms.

Marine macroalgae have access to both dissolved CO_2 and the ionic form of dissolved inorganic carbon (DIC), i.e., HCO_3^-, to drive photosynthesis. CO_2 is the only direct carbon source that can be assimilated by all photosynthetic organisms. While CO_2 can pass through biological membranes along concentration gradients, utilization of HCO_3^- must be facilitated by special mechanisms. While most macroalgae are known to utilize both these carbon sources, a few red algae can only take up CO_2 (Hepburn et al. 2011). Photosynthesis of these macroalgae might be severely limited, if it is dependent solely on diffusional entry of CO_2 from the medium to the site of carboxylation, due to the Rubisco's relatively low affinity for CO_2, and the CO_2 binding site of this enzyme can easily be replaced by O_2 when CO_2 concentration is low since marine macroalgae have high K_m values (40–70 μM) of the carbon assimilating enzyme Rubisco. Additionally, both the dissolved CO_2 concentration and the spontaneous formation of CO_2 from HCO_3^- dehydration are rather low. Therefore, marine macroalgae have CO_2 concentrating mechanisms (CCMs), which enable the algae to efficiently utilize the bulk HCO_3^- pool in seawater, to avoid the severe C-limitation of photosynthesis under current atmospheric conditions if they were dependent only on diffusional entry of CO_2 from the medium to the site of fixation via Rubisco, though some low light living species can also survive without the help of CCM (Kübler and Raven 1994).

Intertidal macroalgae during low tide and those floating at the sea surface with canopies are casually exposed to the air. They can access to atmospheric CO_2 in an easier way during exposure, since the diffusion rates of CO_2 are about 10,000 times faster in air than that in seawater (Beardall et al. 1998). However, air exposure does not necessarily reduce carbon limitation, since emersion at low tide can impose desiccation stress on photosynthesis, especially for the macroalgae distributed in the upper intertidal zones, where they experience longer emersion. Prolonged desiccation can reduce physiological activities such as dark respiration, photosynthetic efficiency, apparent carboxylating efficiency, light saturation point (Gao et al. 1999; Ji and Tanaka 2002; Zou and Gao 2002a), and rates of carbon acquisition (Williams and Dethier 2005), causing significant photoinhibition (Henley et al. 1992). Nevertheless, macroalgae experiencing periodical emersion may benefit from increasing atmospheric CO_2 concentrations (Gao et al. 1999; Zou and Gao 2002a). Elevated atmospheric CO_2 concentrations significantly enhance the emersed photosynthetic rates and the primary productivity, as emersed photosynthesis is CO_2 limited at ambient atmospheric CO_2 levels (Zou and Gao 2002a, c, 2005; Zou et al. 2007), although photosynthetic CO_2 affinity decreases (Johnston and Raven 1990). With the advance of water loss during emersion, photosynthesis of marine intertidal macroalgae can reach its maximal rate with disappearance of the water/membrane barrier shortly after desiccation and then declines due to dehydration.

Nevertheless, enriched CO_2 levels always stimulate intertidal macroalgal photosynthesis even at high levels of dehydration (Fig. 1).

In the marine brown alga, *Sargassum fusiforme*, short-term exposure to elevated CO_2 stimulates its photosynthesis when submersed in seawater (Zou et al. 2011a). Similarly, elevated CO_2 levels increase growth rate and maximum photosynthetic rates in some other macroalgal species (Suárez-Álvarez et al. 2012). On the other hand, inorganic carbon in seawater is known to saturate photosynthesis in some macroalgal species (Zou and Gao 2002b, c). CO_2 enrichment and associated chemistry changes decrease gross photosynthesis and net photosynthesis in *Ulva rigida* (Gordillo et al. 2001) or have no effects on some marine canopy-forming kelp species (Falkenberg et al. 2013). It appears that whether the photosynthetic rates of marine macroalgae are saturated by ambient DIC in seawater or not is likely to be species specific (Beer and Koch 1996; Zou and Gao 2010) and may be dependent on the thickness of the diffusion boundary layer around the thalli. In contrast, elevated CO_2 has no obvious effect on mitochondrial respiration in short-term and long-term exposures (Zou

et al. 2011a, b). However, the temperature quotient for respiration (Q_{10}) value (the change in respiration per 10 °C rise) of *S. fusiforme* in CO_2 enriched seawater under extra supplied N conditions is significantly elevated (Fig. 2), implying that a future high CO_2 scenario may stimulate respiratory carbon loss under eutrophic conditions, especially in coastal waters where most macroalgae are distributed.

Most green, brown, and red macroalgae examined so far can utilize bicarbonate, which is the predominant form of carbon sources in seawater. Bicarbonate increases with increased dissolution of CO_2, and it can be transported into cells in different ways and converted to CO_2 intracellularly via CO_2 concentrating mechanisms (CCMs) (Axelsson et al. 2000; Raven et al. 2012). HCO_3^- is usually dehydrated extracellularly by a periplasmic carbonic anhydrase (CA) to release CO_2, which is then taken up into the cell. Another important method for inorganic carbon utilization is the direct uptake of HCO_3^- through the plasma membrane facilitated by an anion exchange protein. Additionally, H^+-ATPase-driven HCO_3^- uptake has also been recognized in several marine seaweeds. CCMs can be affected by exposure to elevated CO_2 concentrations, as the
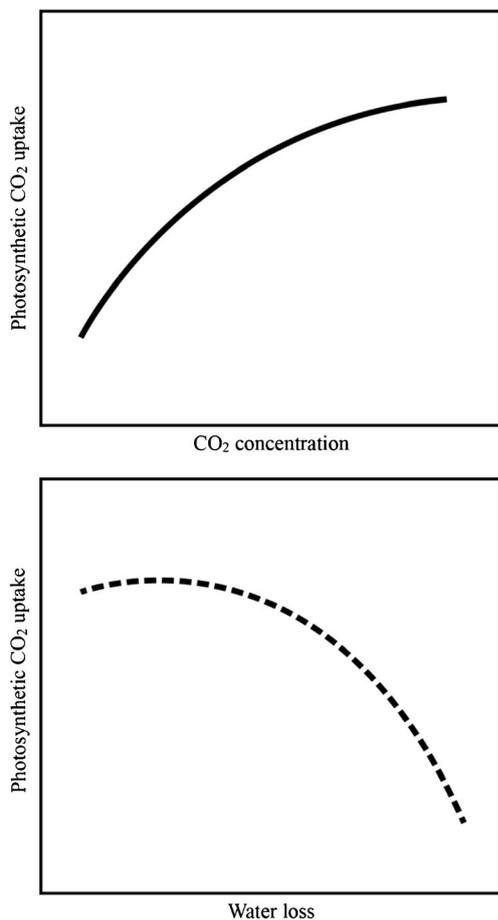
Fig. 1 The conceptual effects of enriched CO_2 (*solid line*) and water loss (*dotted line*) on the photosynthesis during emersion for intertidal macroalgae respectively
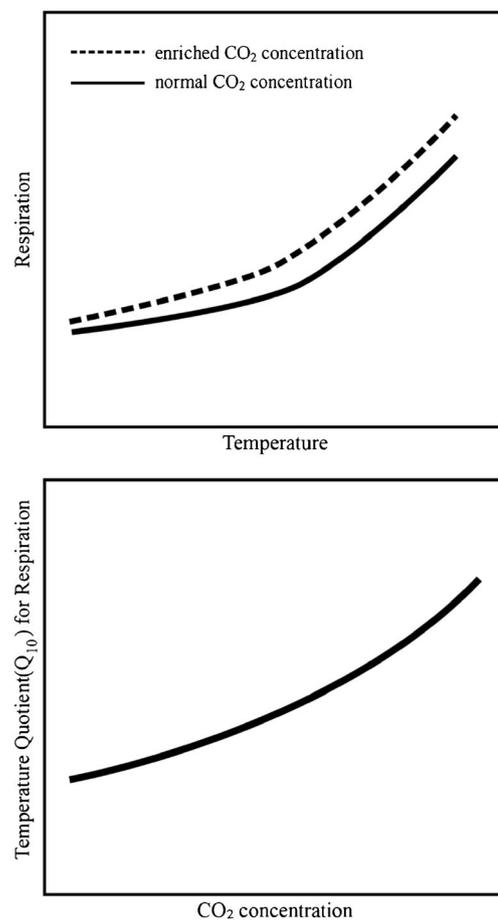
Fig. 2 The conceptual effect of enriched CO_2 on the response of respiration to elevated temperature (Q_{10}) under ample N conditions (data re-drawn from Zou et al. 2011a, b)

activity of intracellular and extracellular carbonic anhydrase is decreased in CO_2 enriched environments (Xia and Gao 2005; Hofmann et al. 2013) and so is the photosynthetic CO_2 or HCO_3^- affinity (Xu and Gao 2012). Conversely, lowered CO_2 concentration increases the intracellular carbonic anhydrase (CA) activity (Zou et al. 2003).

Marine macroalgae with lower levels or absence of CCMs are usually carbon limited and more likely benefit from anthropogenic CO_2 increase to different extents, while the CCM-possessing species may be light dependent in response to CO_2 increase (Harley et al. 2012; Xu and Gao 2012). It has been shown that CO_2 enrichment increases the growth rate of *Pyropia yezoensis* juveniles (Gao et al. 1991), *U. rigida* (Gordillo et al. 2001), and *Lomentaria articulata* (Kübler et al. 1999). Similar results are reported for *Gracilaria chilensis* and *Gracilariopsis lemaneiformis* (Gao et al. 1993b; Zou and Gao 2009) and *Ulva prolifera* (Xu and Gao 2012), but the photosynthetic rates of the species with CCMs or non-bicarbonate using species that are not carbon limited do not increase (Cornwall et al. 2012). However, some species with CCMs choose to use CO_2 instead of bicarbonate under CO_2 enriched conditions, which may benefit the species by avoiding or reducing the extra energy expenditure that CCMs may require (Israel and HopHy 2002; Cornwall et al. 2012).

Enriched CO_2 may decrease photosynthetic pigments such as chlorophyll *a* (Garcíá-Sánchez et al. 1994; Andríá et al. 2001; Gao and Zheng 2010) and phycobiliprotein (Zou and Gao 2009). The reason for this may be that CO_2 enrichment may lower the energy expenditure of bicarbonate utilization mechanisms and thereby causes the down-regulation of pigmentation. CO_2 enrichment can increase photorespiration and the contents of carotenoids in some green algae (Xu and Gao 2012). Considering down-regulation of CCMs under high CO_2, some species may take special measures such as an increase in the electron transport rate (ETR) against CO_2 induced OA at the cost of net photosynthesis. Concentrated intracellular CO_2 may acidify the thylakoid lumen, an important component of CCMs (Raven 1997), causing the decline of intracellular CO_2 levels. Under stressful intensified light levels, enriched CO_2 leads to increased nonphotochemical quenching (NPQ), reflecting an additional light stress. For some macroalgae, CO_2-induced OA acts as a stressor, although it may contribute to energy-saving under limited light conditions (Gao et al. 2012).

Increased CO_2 concentration does not necessarily mean elevated supply of CO_2 into cells, especially for the CCM-possessing species, because down-regulated CCMs and intracellular CO_2 concentration can be altered (Raven et al. 2012). At the same time, algae tend to maintain a relatively stable pH of 7.0–7.5 within cells, and increased acidity due to OA appears to affect intracellular acid–base stability (Gao et al. 2012), although the pH in the milieu is still higher than that within the cells. Increased inorganic

carbon supply under OA may benefit algae with less efficient CCMs or under light-limited conditions. When light intensity is too high, OA stimulates photoprotective processes and causes the decline of photosynthetic carbon fixation and growth rate for some diatom species (Gao and Campbell 2014). In macroalgae, little has been documented on this aspect. While increased availability of carbon and increased acidity in seawater with atmospheric CO_2 rise may have counteractive effects on the physiological activities and growth of macroalgae, and altered chemistry under OA may reduce growth, photosynthesis and even lead to death of some macroalgal species (Israel and Hophy 2002; Aline et al. 2006; Martin and Gattuso 2009). The discrepant effects of OA on macroalgae can be species specific and region specific (Table 1).

OA increases the cost of calcification in calcifying macroalgae, since the lowered pH causes dissolution of $CaCO_3$ and decreases the percentage of inorganic carbon in the algal skeleton (Hofmann et al. 2013). It is also known to reduce growth rate or photosynthetic efficiency in these algal calcifiers (Guinotte and Fabry 2008; Martin and Gattuso 2009; Kroeker et al. 2010; Hofmann et al. 2012; Cornwall et al. 2013a), and the diurnal fluctuation of pH can decrease the growth rates of the coralline alga *Arthrocardia corymbosa* further (Cornwall et al. 2013a), although the daytime rise of pH due to photosynthesis alleviates the OA's negative effect to some degree (Cornwall et al. 2013b). Reduced calcification rates under elevated pCO_2 levels have been demonstrated in crustose and coralline red algae as well as the green calcifying algae, *Halimeda* spp. (Gao et al. 1993a; Büdenbender et al. 2011; Price et al. 2011). However, higher pCO_2 does not always lead to reduced calcification (Kroeker et al. 2010), since different species have different calcification strategies (Borowitzka 1987; 1989; Price et al. 2011) and coralline red algae and most calcareous green algae calcify within an intracellular compartment separated from the external seawater (Borowitzka 1982; Ries et al. 2009). Some species can create microclimates favorable for calcification despite ambient pH conditions (Borowitzka and Larkum 1976). OA may cause increased dissolution rather than reduced production of calcium carbonate (Roleda et al. 2012a), so that net dissolution may exceed net calcification for coralline algae with progressive OA (Martin and Gattuso 2009). Under OA, with less calcification, algae lose protective calcified layers against solar UV radiation and other natural stresses such as water movement, overgrowth or grazing (Büdenbender et al. 2011), and their photosynthetic carbon fixation or daily primary production becomes less (Gao and Zheng 2010). Collectively, OA is mostly unfavorable for marine calcifying macroalgae, especially with the help of local stressors such as elevated nutrients, it stimulates the expansion of filamentous turfs at the expense of calcified algae (Russell et al. 2009), drive community shift towards non-calcifying species, albeit

Table 1 Representative effects of elevated CO_2 concentrations on algae

Species	Variables (growth, Pn, calcification)	Study type	Stressors	Effect	Source
Ulva linza	Photosynthesis in emersed conditions	Lab	CO_2-enriched air	Positive	Gao et al. (1999)
Ulva linza	Submerged net photosynthetic rates	Lab	Additions of Ci	Positive	Beer and Koch (1996)
Ulva rigida	Growth rate	Lab	CO_2-enriched aeration	Positive	Gordillo et al. (2001)
	Net and gross photosynthesis			Negative	
Ulva prolifera	Growth rate	Lab	CO_2-enriched aeration	Positive	Xu and Gao (2012)
	Net photosynthetic rates			Negative	
Auxenochlorella pyrenoidosa	Carbonic anhydrase activity	Lab	CO_2-enriched seawater	Negative	Xia and Gao (2005)
Chloromonas lateovalis	Carbonic anhydrase activity	Lab	CO_2-enriched seawater	Negative	Xia and Gao (2005)
Halimeda opuntia (coral reef green alga)	Photosynthetic capacity	Lab	CO_2-enriched aeration	Negative	Price et al. (2011)
	Dissolution of existing skeletal structure				
Halimeda taenicola (coral reef green alga)	Calcification	Lab	CO_2-enriched aeration	Negative	
Ishige okamurae	Photosynthesis in emersed conditions	Lab	CO_2-enriched air	Positive	Gao et al. (1999)
Petalonia binghamiae	Emersed photosynthetic rates	Lab	Ci concentration	Positive	Zou and Gao (2010)
Sargassum fusiforme	Net photosynthetic rates	Lab	CO_2-enriched aeration	Positive	Zou et al. (2011a, b)
	growth rate				
Sargassum fusiforme	Extracellular and total CA	Lab	CO_2-enriched aeration	Negative	Zou et al. (2003)
	Photosynthesis				
Saccharina latissima	Submerged net photosynthetic rates	Lab	Additions of Ci	Positive	Beer and Koch (1996)
Fucus serratus	Emersed photosynthetic CO_2 assimilation	Lab	CO_2-enriched air	Positive	Johnston and Raven (1990)
	Affinity for CO_2	Lab	CO_2-enriched air	Negative	
Gloiopeltis furcata	Photosynthesis in emersed conditions	Lab	CO_2-enriched air	Positive	Gao et al. (1999)
Pyropia haitanensis	Net photosynthesis in emersed conditions	Lab	CO_2-enriched air	Positive	Zou and Gao (2002a, b, c)
Palmaria palmata	Submerged net photosynthetic rates	Lab	Additions of Ci	Positive	Beer and Koch (1996)
Hypnea spinella	Growth rate	Lab	CO_2-enriched aeration	Positive	Suárez-Álvarez et al. (2012)
	Maximal photosynthesis				
Corallina officinalis (calcifying rhodophyte)	External carbonic anhydrase activity after long-term exposure	Mesocosm	CO_2-enriched aeration	Negative	Hofmann et al. (2013)
Corallina pilulifera	Net photosynthetic rates	Lab	CO_2-enriched aeration	Negative	Gao and Zheng (2010)
	Calcification				
	Growth rate				
Pyropia yezoensis	Growth rate	Lab	CO_2-enriched aeration	Positive	Gao et al. (1991)
Lomentaria articulata	Growth rate	Lab	CO_2-enriched aeration	Positive	Kübler et al. (1999)
Gracilaria chilensis	Growth rate	Lab	CO_2-enriched aeration	Positive	Gao et al. (1993a, b)
Gracilariopsis lemaneiformis	Growth rate	Lab	CO_2-enriched aeration	Positive	Zou and Gao (2009)
Lithophyllum cabiochae (coralline alga)	Calcification	Lab	CO_2-enriched aeration	Negative	Martin and Gattuso (2009)
Lithothamnion glaciale (crustose coralline red algae)	calcification	Lab	CO_2-enriched aeration	Negative	Büdenbender et al.(2011)

OA's effects can be diversified (Kuffner et al. 2008; Connell and Russell 2010; Roleda et al. 2012b).

Impacts of UV radiation

As a part of solar radiation, the two types of ultraviolet radiation (UVR) that can penetrate the atmosphere are classified as UVA (315~400 nm) and UVB (280~315 nm) according to their respective wavelengths. The stratospheric ozone layer is a major shield that protects all organisms from the UVR (Madronich 1992), especially UVB. However, the anthropogenic pollutants such as chlorofluorocarbons (CFCs) have caused significant reduction in the thickness of this natural barrier, enabling more UVB to reach the earth's surface. Although CFCs emission has slowed down since the execution of the Montreal Protocol, the time needed for the full recovery of ozone layer remains unclear (Weatherhead and Andersen 2006), and the interaction between global warming and ozone decreases may delay this recovery (Häder et al. 2007; McKenzie et al. 2003).

UVR can affect ocean plants in variable ways, mainly acts as an inhibitory factor to harm macroalgae, causing decreased effective quantum yield and CO_2 fixation (Jiang and Gao

2008). UVA has ambiguous effects on macroalgae. It can be used as light source for photosynthesis, driving photosynthetic utilization of bicarbonate (Xu and Gao 2010a), and have positive effect on morphogenesis (Jiang et al. 2007) and growth for some macroalgal species (Xu and Gao 2010b; Beardall et al. 2014). However, moderate to high levels of UVA can cause decrease of maximum quantum yield (Xu and Gao 2010b) and photosynthesis inhibition (Zheng and Gao 2009), and alter diversity and biomass of marine benthic community (Wahl et al. 2004), which imposes greater inhibition than UVB since its dosage is more than ten times larger than that of UVB.

UVB has rarely been found to show positive effect. Prior exposure to it may help recovery of photochemical quantum yield (Xu and Gao 2010b). UVB, with its energy only accounting for less than 1 % of solar radiation, can cause changes in mitochondria, chloroplasts and other organelles (Poppe et al. 2003), increase thickness of cell wall (Schmidt et al. 2010), reduce intracellular space, even change cell contours and morphologies (Éder et al. 2012) and delay the formation of sporelings (Jiang et al. 2007).

UVB exposure causes a decline of growth rate in marine macroalgae (Grobe and Murphy 1994; Zheng and Gao 2009; Schmidt et al. 2010; Xu and Gao 2010b; Éder et al. 2012). The decrease of growth rate is related to the extra energy required for activation of repairing processes following UVB damage (van de Poll et al. 2001). The capability of repairing or even preventing damage determines the extent of UV tolerance, although these repairing processes may consume extra energy and thereby decrease growth.

UVB can also cause photoinhibition (Figueroa and Gómez 2001), decrease net photosynthetic rates (Xu and Gao 2012), quantum yield (Xu and Gao 2010b), ETR (Schmidt et al. 2012), and photosynthetic activities (Jiang et al. 2009; Zheng and Gao 2009). UVB mainly targets photosystem II (PSII) and strongly decreases its photochemical efficiency (Vass 1997; Holzinger et al. 2004). UVB increases the difficulty of establishing a proton gradient across the thylakoid membrane, thus impairing photosynthetic reactions (Poppe et al. 2002). The repair process following damage to membranes and electron transport components increases enzymatic activities with higher nitrogen requirements (Poppe et al. 2002).

UVB exposure can have ambiguous effects on photosynthetic pigments such as chlorophyll *a*. It has been reported that UVB exposure causes the decrease in chlorophyll *a* in *Corallina pilulifera* (Gao and Zheng 2010), *Kappaphycus alvarezii* (Schmidt et al. 2010), *Kappaphycus striatus* (Wood 1989) and phycobiliproteins in *K. alvarezii* (Eswaran et al. 2001; Schmidt et al. 2010) and *Hypnea musciformis* (Schmidt et al. 2012). However, in contrast, it also has been reported that UVB may stimulate the synthesis of chlorophyll *a* in *Mastocarpus stellatus* and *Chondrus crispus* (Roleda et al. 2004), while some other species such as *H. musciformis* showed resistance to UVB with no significant changes in chlorophyll *a*

between photosynthetically active radiation (PAR) only exposure and esposure to PAR + UVB (Éder et al. 2012).

Synthesis of carotenoids also responds to UVB exposure. For example, esterified zeaxanthin decreases significantly with a slight increase of *trans-ß*-carotene, *cis-ß*-carotene as well as increase of free zeaxanthin in response to UVB exposure (Éder et al. 2012). This can be explained as a protective pigmentation mechanism (Altamirano et al. 2000). The increase of free zeaxanthin can be attributed to the effects of UVB breaking the ester bonds of esterified zeaxanthin. The finding of reduced lutein and zeaxanthin levels in the red macroalga, *Palmaria decipiens*, exposed to UVB (Döhler 1998), supports this explanation.

UVB can induce the production of reactive oxygen species (ROS) (Costa et al. 2002). ROS are harmful for all organisms including oxidative damage to lipids of membranes, proteins, enzymes, DNA and other biomolecules (Ruhland et al. 2007). NADH dehydrogenase activity increases in *H. musciformis* exposed to UVB, which stimulates oxygen consumption and finally causes more ROS formation. Meanwhile, the increase of NADH dehydrogenase activity can be attributed to extra energy production that is used for potential membrane loss and energy deficit. To prevent the damage caused by ROS, some macroalgae exposed to UVB increase the production of UV-absorbing compounds (UVACs) (Häder and Figueroa 1997; Han and Han 2005; Zheng and Gao 2009; Xu and Gao 2010b), which are mainly mycosporine-like amino acids (MAA), although phenolic compounds and carotenoids also play screening roles. UVACs are produced as a photoprotective mechanism against UVB, and serve as a sunscreen against UVB and ameliorate damage caused by increased ROS (Ruhland et al. 2007). The phenolic compounds can absorb incident photons or can be created as a by-product of antioxidant activity (Abdala-Díaz et al. 2006). Therefore, the capability of synthesizing UVAC provides macroalgae the advantage of enhancing their photosynthetic tolerance of UVR (Jiang and Gao 2008) and enables them to survive in the presence of UVB. Therefore, UVB has the effect to induce the activation of antioxidant cell defense.

The negative effects mentioned above can be minor or none for macroalgal species armed with certain protective mechanisms, such as extremely thick cell walls covered with mucilage sheath, a dense layer of mineral depositions or calcareous matrix covers (Jiang et al. 2009; Roleda et al. 2010), and its effects on shallow-water macrobenthic communities can be transitory and vanish totally in a short period (Molis and Wahl 2009), which is supported by a global comparison of how UV impacts marine benthic community (Wahl et al. 2004). In this study, UV doses around the world were measured, but no UV dosage effects were found, although UV may have long-term effects on the species composition of marine benthic communities (Molis et al. 2003). However, a positive relation was acknowledged for some polar

macroalgal species between the natural vertical distribution in the field and the individual sensitivity towards UV radiation (Michler et al. 2002).

Effects of ocean warming

Climatic changes predicted for the end of this century include a continuous warming of near-surface air temperature, at the order of 2–7 °C with regional, seasonal and diurnal variations (Christensen et al. 2007), causing continuing temperature rise in surface oceans.

Temperature is an important factor that determines biogeographical distribution and rates of metabolism of marine macrophytes (Van den Hoek et al. 1990; Wernberg et al. 2003; Martínez et al. 2012) and different macroalgal species may have different temperature tolerance due to their local temperature ranges (Pakker et al. 1996). Ocean warming may result in extinction of several hundred species of macroalgae (Wernberg et al. 2011) or may reduce the physiological responsiveness of kelps to perturbation (Wernberg et al. 2010); certainly, those species with higher temperature tolerance will be better prepared to cope with a warmer seawater environment. The observed decrease of some cold and temperate intertidal macroalgae has been attributed to the rise of ocean temperature (Martínez et al. 2012). Consequently, ocean warming will expand warm water species to formerly colder regions, while cold water species will be driven to formerly even colder regions, a conclusion which is supported by North-Atlantic rocky intertidal model predictions (Jueterbock et al. 2013).

Temperature changes affect photosynthesis and respiration instantly, since a temperature change can bring about immediate changes in biochemical reactions. Marine macroalgae distributed in subtropical or temperate regions usually have an optimal temperature of normally between 25 and 30 °C for net photosynthesis (Pn) and gross photosynthesis (Pg), which then decline with increasing temperature. For the species that are found in cold regions, the optimal temperature for their photosynthesis and growth, can be much lower (Müller et al. 2008). Extreme high temperature up to 35 °C causes a decrease in ETR and maximal photochemical yield in the marine green macroalga, *Ulva conglobata* (Zou and Gao 2014b) and death for even the tropical seaweeds (Pakker and Breeman 1996). In contrast, mitochondrial respiration usually shows a linear correlation with temperature rise. The different responses to short-term temperature changes between photosynthesis and respiration can be explained by the observation that photosynthetic light reactions are usually less affected by temperature than respiration enzymatic reactions (Davison 1991).

Metabolic pathways of macroalgae may acclimate to temperature changes. Species growing under colder environment frequently achieve higher photosynthetic rates at lower temperature compared with those growing under warmer

environments (Davison et al. 1991; Kübler et al. 1991; Kübler and Davison 1995; Eggert et al. 2006; Staehr and Wernberg 2009). Thermal acclimation of photosynthesis and respiration is associated with temperature induced changes in cellular biochemical compositions (Kübler and Davison 1995; Machalek et al. 1996; Staehr and Wernberg 2009), with higher contents of chlorophyll *a*, soluble proteins and soluble carbohydrates in low temperature-grown algae compared with their high-temperature-grown counterparts. These changes are supposed to relieve the constraints of low temperature on metabolic rates (Atkin and Tjoelker 2003; Staehr and Wernberg 2009). Low temperature may slow electron transport, thus down-regulating the ratio of antenna capacity to reaction centers. With gradual ocean warming, this down-regulation may no longer be needed or be as important as before in marine algae. Therefore, ocean warming may benefit some species by increasing the activity of reaction centers, as reflected in *Gracilariopsis lemaneiformis* where photosynthesis is more enhanced than respiration with warming (Zou and Gao 2013). In *G. lemaneiformis*, mitochondrial respiration remains relatively unchanged, while photosynthesis increases significantly with moderate temperature rise, as respiratory processes have acclimated during the 21 days growth under elevated levels of temperature. Therefore, under a long-term gradual seawater temperature rise scenario, photosynthesis will increase faster than respiration, resulting in elevated primary productivity by macroalgae in some regions. However, when temperature rises beyond a certain threshold, photosynthesis begins to decline, whereas respiration remains unchanged or rises only slightly. As a result, net photosynthesis and productivity will decline.

As photosynthesis and respiration show different thermal windows and acclimation tempos to warming, the ratio of dark respiration to gross photosynthesis declines with a moderate rise of temperature (Zou and Gao 2013, 2014b). This corroborates the hypothesis that many macroalgae can benefit from mild ocean warming, as the carbon acquisition and net carbon balance is favored by a moderate rise of seawater temperature. However, the extent of warming influence depends on latitude or the macroalgas niche, as well as the nutrient status in water bodies, as nutrient may act synergistically with temperature to enhance macroalgal recruitment, causing macroalgal blooms in costal ecosystems (Lotze and Worm 2002).

A fluctuation in temperature can result in an immediate change in the rates of photosynthesis and respiration, with the magnitudes of the changes being determined by the short-term sensitivity of each process to temperature. In contrast to instantaneous responses, the effect of prolonged changes in growth temperatures on rates of respiration and photosynthesis relies on the extent to which these processes acclimate. Phenotypic acclimation to seawater temperatures may enable algae to tolerate higher temperatures (Kübler and Davison 1993). Acclimation could eventually result in

complete metabolic homeostasis. The thermal acclimation of photosynthesis and/or respiration is associated with temperature-mediated changes of cellular biochemical composition (Kübler and Davison 1995; Machalek et al. 1996; Staehr and Wernberg 2009). In marine macroalgae, it is well established that many species have a high, genetically fixed potential for photosynthetic acclimation, enabling them to adjust and optimize photosynthesis to the prevailing temperature conditions (Davison et al. 1991; Zou and Gao 2005, 2013; Staehr and Wernberg 2009). The ability of the macroalgae to maintain positive photosynthesis over a broad range of temperatures may play an important role to their wide distribution and success. In the marine red macroalga *G. lemaneiformis*, it was shown that both respiration and photosynthesis acclimate to contrasting growth temperatures irrespective of the N availability under which the algae were grown, but there was difference of the degree of acclimation between the two physiological processes. However, studies on the thermal acclimation potential of photosynthesis and respiration in marine macroalgae are generally limited. Many studies with a range of species are needed to establish whether the degree of acclimation of photosynthesis and respiration differs among different locations and microhabitats.

Interactive effects of multiple climatic factors

There is little documentation on how combined effects of OA, warming, and UVR would affect macroalgae. Since these factors simultaneously influence most marine photosynthetic organisms, macroalgae are supposed to respond to their combined impacts. Although almost all macroalgae are found in coastal waters, where fluctuating pH and temperature are typically obvious, they can still be affected by OA and warming, which alter the diel pH or temperature fluctuation ranges.

UVR inhibits photosynthetic DIC uptake rates, which thereby further decreasing pH, and furthermore it can stimulate respiration, which further contributes to the pH decline (Aguilera et al. 1999). Therefore, UVR may accelerate the progress of ocean acidification. In the coralline alga *C. pilulifera*, CO_2 enrichment/lower pH and UVR act synergistically to inhibit growth, photosynthesis and calcification rates, and photosynthetic pigments such as chlorophyll *a* and phycoerythrin contents also decrease (Gao and Zheng 2010). The presence of UVR in this study did result in lower pH compared with the treatment without UVR, in both low and high CO_2 cultures. It can be seen that high CO_2/lower pH exacerbates the inhibition of photosynthesis and calcification caused by UVB. However, enriched CO_2 treatment was found to increase the absorptivity of UVACs, mainly mycosporine-like amino acids (MAAs) in *C. pilulifera* (Gao and Zheng 2010). Higher concentration of CO_2 caused the increase of acidity, resulting in a thinner calcified layer and less protection from UVR. As

compensation, algae may be forced to enhance the protective mechanism, such as the production of UVACs. In contrast, high CO_2/low pH conditions can lower the concentrations of phenolic protective substances (which are supposed to serve as UV screens) in seagrasses and euryhaline marine plants (Arnold et al. 2012). Therefore, the real effects of UV on the accumulation of UVACs can be complicated and varied among different taxa.

The rise of both CO_2 concentration and temperature can have short-term and long-term effects on photosynthesis and respiration of marine macroalgae (Fig. 3). Photosynthesis has an instant positive responses to CO_2 and temperature rises, and so does the respiration to temperature rises. However, only photosynthesis shows positive responses to long-term temperature rise, while no positive effects or even no effects at all have been shown for respiration, because respiration exhibited significant levels of acclimation to changing temperature, whereas photosynthesis acclimated less (Zou et al. 2011a, b; Zou and Gao 2013, 2014a, b).

The combined effects of elevated CO_2 concentrations and temperature can be greater than the impacts of the CO_2 or temperature alone (Martin and Gattuso 2009; Connell and Russell 2010; Rodolfo-Metalpa et al. 2011). Calcifying macroalgae may be more vulnerable to the effects of ocean acidification in warmer seawater, because the dissolution of calcified structures in acidified seawater is faster in a warmer environment, and calcification can be significantly reduced only when both temperature and pCO_2 are elevated (Martin and Gattuso 2009). Therefore, the effects of CO_2-induced seawater acidification can be aggravated by ocean warming for some crustose coralline and non-calcifying algae (Anthony et al. 2008; Connell and Russell 2010), meanwhile algal death caused by higher temperature is further exacerbated by increased pCO_2 (Martin and Gattuso 2009). Other physiological parameters such as photorespiration, enzyme activites, and carbohydrate production are also significantly affected by the interactions between OA and ocean warming (Koch et al. 2013), though the influence of OA on thermal acclimation of macroalgae is almost unknown. Some macroalgal species, such as those in algal turfs, biomass production can be enhanced due to synergistic effects of increased levels of CO_2 and temperature (Connell and Russell 2010). Therefore, effects of ocean warming and acidification on macroalgae are likely to be species and/or region specific considering the dynamic environments they are living in.

Interactive effects between UVR and ocean warming

An increased level of UVR is supposed to contribute to ocean warming, though only a little, considering it only accounts for a small fraction of solar energy (Mckenzie et al. 2003). In contrast, ocean warming can have contradictory effects on
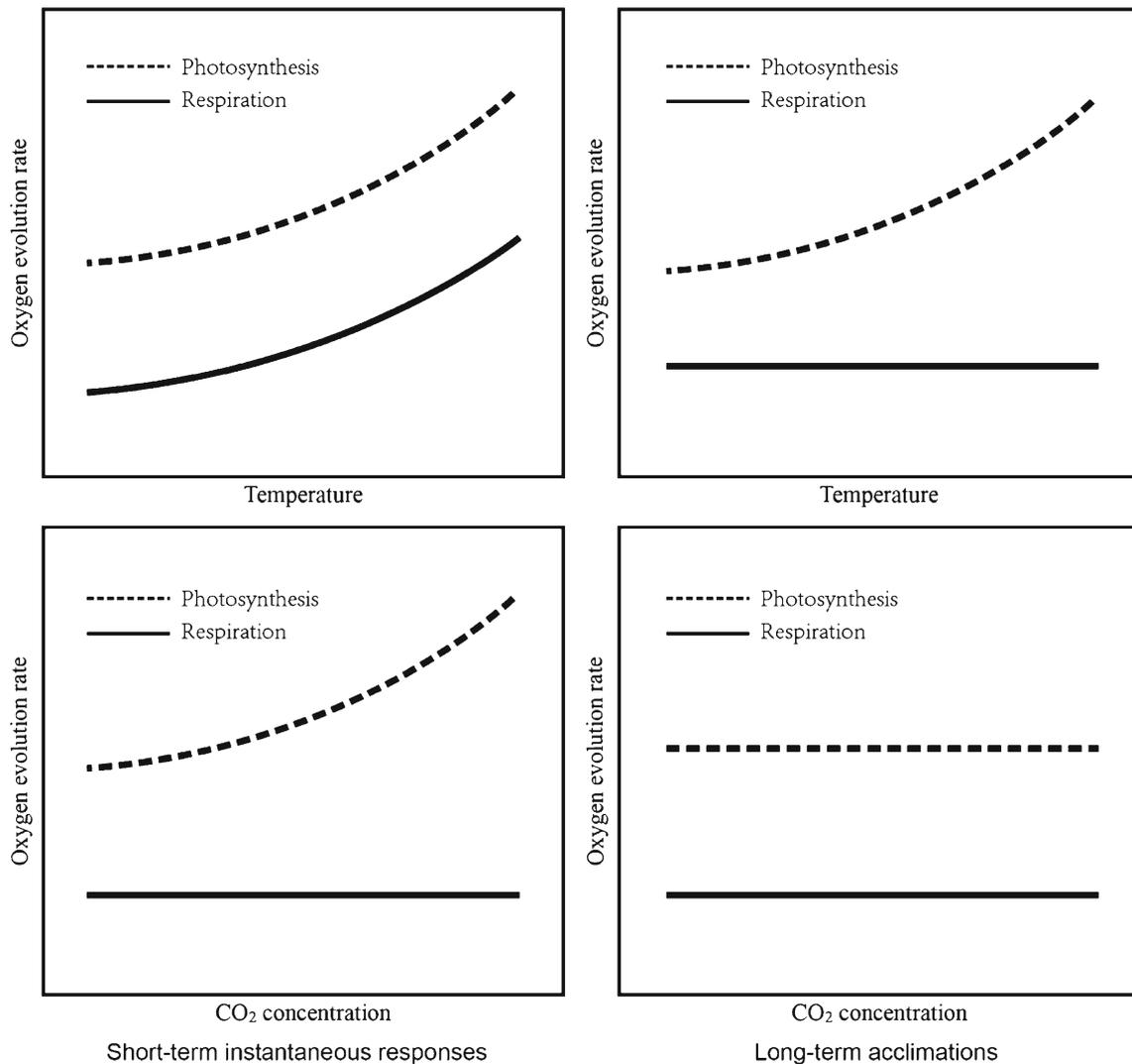
Fig. 3 The conceptual short-term (*upper graph*) and long-term (*lower graph*) effects of enriched CO_2 (*active line*) and temperature rise (*dashed line*) on the photosynthesis (*gray line*) and respiration (*dark line*), respectively

the responses of macroalgae to UVR, since moderately increased temperature can stimulate enzymatic activities and improve physiological functions of algae, such as stimulating the repair rate of photosystems caused by UVR (Li et al. 2012), and relatively higher temperature stimulates the repair processes and favors the recovery after UVR exposure (Gómez et al. 2001; van de Poll et al. 2002). Temperature mediates the biological effects caused by UVR and UVR affects the effects of temperature similarly (Hoffman et al. 2003). On the other hand, however, ocean warming enhances ocean stratification, making the upper mixed layer (UML) thinner. Photosynthetic organisms living within UML, especially phytoplankton will face difficulty to acquire enough nutrients from deeper layers and will be exposed to increasing integrative UV exposures (Helbling et al. 2011; Gao et al. 2012). However, since most macroalgae are distributed in coastal waters that are well mixed due to waves, except the

Sargassum spp. in the Sargasso Sea, they are less affected by enhanced stratification. On the other hand, since organisms in intertidal zones will experience casual heat shock during the period of low tides, intertidal macroalgae are expected to live with increasing heat shocks—especially the small, fragmented edge populations whose adaptive capacity or fitness is reduced compared with larger central populations (Pearson et al. 2009). Nevertheless, the threshold that these algae can tolerate is unknown; further, the tipping point for these species to decrease under combined pressure of heat shock and UVR needs to be examined.

Conclusions and future work suggestions

Ocean acidification induced by anthropogenic CO_2 release is undoubtedly going to have consequences for marine

macroalgae and other organisms. Up-to-date investigations have mostly focused on short-term effects which stimulating photosynthesis and/or growth in some macroalgae tested. However, responses to long-term exposures to OA conditions are almost unknown. Based on the very limited number of studies, OA can impact photosynthesis and respiration differently in some macroalgae. While it is important to look into responses of macroalgae to diel fluctuating pH (common in coastal waters) under OA (Cornwall et al. 2013a, b), impacts of OA would affect productivity of sea-farmed macroalgae, that experience dramatic diel pH variations.

Ocean warming also significantly affects marine macroalgae. While there are possible positive effects of ocean warming for some warm seawater-grown species, for the cold seawater-grown species, rise of temperature may reduce their living space and narrow their available niche. However, the phenomenon of how intertidal species cope with dramatic temperature changes during emersion has been little studied. On the other hand, UVB, which penetrates only several meters in coastal waters, is harmful for macroalgae either in their adult stages or through their life cycles. Nevertheless, little has been documented on microscopic stages or the life cycles of macroalgae. The red alga *Gracilaria* sp. is known to synthesize more MAAs in the presence of UVR, and their contents increased with increased availability of nitrate (Zheng and Gao 2009). Consequently, it is obvious that macroalgae

distributed in waters of different nutrient levels can respond to UV stress to different extents (Xu and Gao 2009).

OA, warming and UVR may have different effects on different life history stages of marine macroalgae (Fig. 4), though most effects are unknown or neutral for elevated temperature and enriched CO_2, implying a huge research blank. Elevated temperature is suggested to set the northern or southern distribution boundaries of macroalgae by impacting their life cycles (Breeman 1990), impact life stages of macroalgae, including spore production and germination (Buschmann et al. 2004), recruitment (Deysher and Dean 1986) and sporophyte growth (Rothäusler et al. 2011). High temperature can even cause mortality of spores, gametophytes, eggs, and sporophytes (Ladah and Zertuche-González 2007) and germlings of some *Fucus* species together with high dose of UVB (Altamirano et al. 2003); therefore, profound effects of ocean warming are expected to be observed in future studies. While the effects of OA have been relatively less documented compared with those of ocean warming, OA may positively affect gametogenesis due to increased availability of CO_2 and may neutrally influence germination due to the counteractive effects of decreased pH (Roleda et al. 2012b). As for UVB, negative effects will be pronounced in microscopic stages and in shallow waters with high transparency.

Studies on global change macroalgal biology are greatly outnumbered by those of phytoplankton. Considering the

Fig. 4 The effects of climatic factors on the life stages of the macroalgae with alternation of generations. *Circles, triangles* and *squares* represent the effects of elevated temperature, enriched CO_2 and UVBR. *Positive symbol* indicates experimental evidence of positive effects; *negative symbol* indicates negative effects; *plus-minus symbol* indicates neutral effects; *question mark* indicates unknown effects
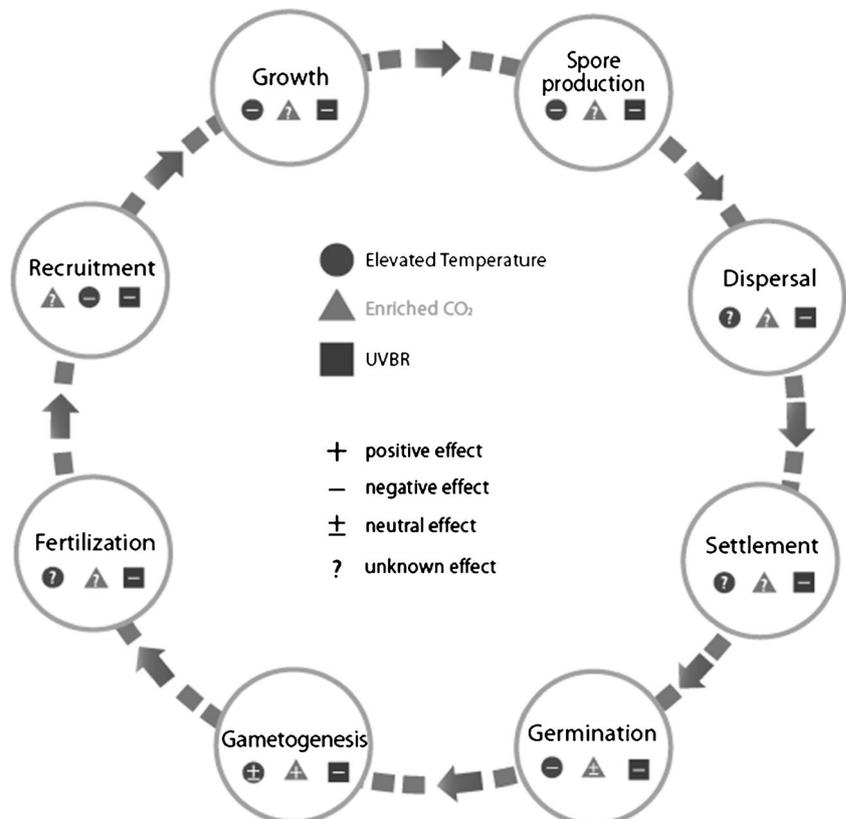
important economic and ecological values of marine macroalgae, we are now suggesting future studies with high priority:

1. Most studies until now have been carried out in the laboratory, however, conditions in natural environments are quite different. With progressive climate change, marine macroalgae in situ have to cope with multifarious stressors, such as pH drop or basification, carbon limitation, warming and UVR. These factors are intertwined, which makes it more complicated to determine how algae respond to climate change. Therefore, to assess the effects of climate change on marine macroalgae, in situ experiments or mesocosm tests to enlarge scales and incorporate multiple stressors are strongly recommended.

2. In terms of the combined effects of OA, UVB, and warming, few studies have been performed to look into their interactive effects, and the mechanism study under these seeming correlations is almost blank. Mechanisms involved in the interactions need to be revealed. Certainly, other environmental factors, such as light and nutrient conditions, should also be taken into consideration. The lack of studies on interactions between these factors hinders biologists, ecologists and modelers to predict reasonable effects of global climate change on macroalgae. As all of these factors do not act alone on macroalgae in nature, the combined effects between two or among multi-factors remain unexplored and thereby are in urgent need to be examined more closely and widely.

3. Macroalgal species have different adaptation mechanisms to climate change and respond differently in different regions or waters. Therefore, with development of regional monitoring of ocean acidification, macroalgal ecological responses and productivity should be observed in different areas. Laboratory studies should be paralleled with in situ observations to understand how macroalgae adapt to or evolve in changing environments.

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