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The future of seaweed aquaculture in a rapidly changing world

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ABSTRACT
Human activities are having increasingly negative impacts on the natural environment. The rapidly expanding human population has led to a shortage of resources and the ability to support the growing population sustainably is a major challenge for the future. Coastal environments, including natural seaweed communities, provide a range of important ecosystem services. Since seaweed aquaculture beds (SABs) provide many of the services associated with natural seaweed communities they have a potential role in providing solutions such as CO_2 sequestration, provision of food and the supply of useful chemicals. However, the productivity of natural seaweed communities and SABs is under threat from the rapid changes in climate that the planet is experiencing. Here we examine the likely effects of global change, in particular elevated CO_2 and ocean acidification, increased temperatures and elevated levels of UVB, on the performance of seaweeds. While it is clear that rising temperatures and elevated CO_2 and their interactions with other environmental factors are likely to have profound effects on macroalgal production, such effects are likely to be species dependent. We also examine the fate of organic matter from seaweeds and the potential for using SAB productivity as a contributor to blue carbon as a strategy for amelioration of increases in anthropogenic CO_2 emissions. There is considerable potential for increased drawdown of CO_2 by SABs, though its effectiveness in amelioration of atmospheric CO_2 increase will depend on the fate of the resulting biomass.

Introduction

The aquaculture industry has grown at an impressive rate in recent years. The combined effects of improved productivity and market growth have made aquaculture the world's fastest growing animal-based food sector of the last few decades (FAO, 2010, 2016).

Global aquaculture seaweed production has also increased markedly, having nearly tripled between 2000 and 2014, from 9.3 to nearly 27 million tonnes (Table 1), and the value of world seaweed production has doubled over this period, from about US$3 to US$6 billion (FAO, 2016) with more than 95% of this production being from Asian countries. Seaweeds are used for a wide range of products from food to bioactive compounds for medicine and these uses are reviewed in detail by several authors in this issue (Buschmann et al., in press; Busetti et al., in press; Mac Monagail et al., in press). Recently there has been increasing recognition of seaweed aquaculture and the many positive benefits it supplies, though as the production of seaweeds is limited within several Asian countries and its coverage is also restricted in those areas, the role of seaweed aquaculture has not been properly evaluated (Sondak et al., 2016).

Nonetheless, natural seaweed communities and seaweed aquaculture represent a significant sink for atmospheric CO_2. Carbon sequestered in both living and non-living biomass in the ocean and coastal habitats has been termed 'Blue Carbon' by the United Nations Environment Programme (UNEP) (Nellemann et al., 2009; Vierros, 2013; Howard et al., 2014) and such blue carbon environments provide many ecosystem services (Table 2). Krause-Jensen & Duarte (2016) estimate that seaweeds could potentially assimilate about 173 Tg C year^{-1}, which compares favourably with estimates for carbon burial rates for salt marshes, mangroves and seagrasses of up to 87.3, 24.9 and 112 Tg C year^{-1}, respectively (Duarte et al., 2013), though how much of the carbon assimilated by seaweeds is sequestered over the long term is debatable (Trevathan-Tackett et al., 2015).

Natural seaweed communities provide a range of ecosystem services (Smale et al., 2013; Cabral et al., 2016), and similar roles can be ascribed to artificial seaweed aquaculture beds (SABs) (MEA, 2005). Even though SABs are artificial ecosystems, they fulfil many of the functions exhibited by natural kelp forests and seaweed beds (Table 2). Those functions can be categorized as (1) Provisioning, i.e. food production (Sohn, 1993; FAO, 2003), raw materials (MacArtain et al., 2007) and biofuels (Roesijadi et al., 2010); (2) Regulating, i.e. potential CO_2 sequestration (Chung et al., 2011, 2013; Tang et al., 2011; N'Yeurt et al., 2012), coastal protection (Jackson & Winant, 1983), nutrient removal (Chopin et al., 1999;

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Table 1. World Seaweed Aquaculture Production 2005–2014. Source: FAO (2016).

Seaweed species	2005 (Thousand tonnes)	2010 (Thousand tonnes)	2013 (Thousand tonnes)	2014 (Thousand tonnes)
Kappaphycus alvarezii and *Eucheuma* spp.	2444	5629	10 394	10 992
Saccharina japonica	4371	5147	5942	7655
Gracilaria sp.	936	1696	3463	3752
Undaria pinnatifida	2440	1537	2079	2359
Porphyra (*Pyropia*) sp.	1287	1637	1861	1806
Sargassum fusiforme	86	78	152	175
Total	11 564	15 724	23 891	26 739

Table 2. Comparisons of services derived from mangroves, seagrasses, saltmarshes and SAB ecosystems (see text for details of service types).

	Mangroves[a]	Salt marshes[b]	Seagrasses[c]	SABs[d]
Provisioning	Food	Food	Food	Food
	Water supply		Fibres	Raw materials
	Raw materials		Industrial products	Industrial products
Regulating	Climate regulation (CO$_2$ drawdown)	Climate regulation (CO$_2$ drawdown)	Climate regulation (CO$_2$ drawdown)	Climate regulation (CO$_2$ drawdown)
	Coastal protection	Coastal Protection	Coastal protection	Coastal protection
	Improving air quality	Improving water quality	Improving water quality	Improving water quality
Supporting	Nutrient cycling	Nutrient cycling	Nutrient cycling	Nutrient cycling
	Refugia	Refugia	Refugia	Refugia
	Primary production	Primary production	Primary production	Primary production
Cultural	Recreation and ecotourism	Recreation and ecotourism	Recreation	Recreation and ecotourism
	Aesthetic	Aesthetic	Aesthetic	Aesthetic
	Education	Education	Education	Education

[a]Barbier *et al.*, 2011; Nellemann *et al.*, 2009; Mumby *et al.*, 2004. [b]Barbier *et al.*, 2011; Nellemann *et al.*, 2009; Waycott *et al.*, 2009; Saintilan *et al.*, 2007. [c]Barbier *et al.*, 2011; Nellemann *et al.*, 2009. [d]Jackson & Winant, 1983; Duggins *et al.*, 1989; Sohn, 1993; Chopin *et al.*, 1999; Levinton *et al.*, 2002; Norderhaug *et al.*, 2002; FAO, 2003; Fei, 2004; Graham, 2004; Go, 2010; O'Connor & Anderson, 2010; Chung *et al.*, 2011, 2013; Tang *et al.*, 2011; N'Yeurt *et al.*, 2012.

Fei, 2004) and nursery grounds (Norderhaug *et al.*, 2002; O'Connor & Anderson, 2010); (3) Supporting, i.e. primary production (photosynthesis), nutrient cycling and biodiversity (Duggins *et al.*, 1989; Levinton *et al.*, 2002; Graham, 2004); and (4) Cultural, i.e. recreational, educational, spiritual/aesthetic and scientific properties (Go, 2010).

SABs, in contrast to natural seaweed communities, are artificial systems in which seaweeds are attached as germlings to cultivation lines attached to buoys or poles and then allowed to grow until they are of harvestable size. Seaweed aquaculture beds cover extensive shallow coastal areas, particularly in the Asia-Pacific region, and although still accounting for only a small portion of global agriculture, seaweed aquaculture is growing more rapidly than other components of production (Sondak *et al.*, 2016; Duarte *et al.*, 2017). The future of seaweed aquaculture is likely to see an increase in the total harvest production following an increase in the number of cultivation areas around the world. In 2012 only 33 countries and territories worldwide cultivated seaweed, but in 2015 50 countries reported the practice of seaweed aquaculture (FAO, 2014, 2016).

However, our planet has entered a new era, the Anthropocene (Monastersky, 2015), where human activity has become one of the major agents of environmental change (IPCC, 2013). Human activities have been, and continue to be, affecting natural and social environments and, as a result, global systems

are facing many problems (Muraoka, 2004; Dearing, 2006; Regnier *et al.*, 2013; Gao *et al.*, 2016).

Among the anthropogenic effects, the greatest threats result from human population growth. Our rapidly expanding population has led to a shortage of resources, and thus sustainable growth is a critical issue that the planet and humankind are facing. In addition to restricted resources, increased carbon dioxide in the atmosphere, mostly due to fossil fuel combustion and deforestation of terrestrial environments, is driving rapid climate change (Chapin *et al.*, 2000; Le Quere, 2010). As atmospheric CO$_2$ increases, so does CO$_2$ dissolved in seawater (Sabine *et al.*, 2004) and this is bringing about major changes in the oceans. In marine ecosystems, the rising atmospheric CO$_2$ is associated with concurrent changes in the environment (details of which are provided below), including alterations in temperature, circulation, stratification, nutrient supply, oxygen content and ocean acidification, with potentially wide-ranging biological effects (Doney *et al.*, 2012). All these changes in climate have the potential to affect the physiological performance of seaweeds and hence the productivity of seaweed aquaculture.

Furthermore, human population distribution is heterogeneous, with just over half the world's population occupying a coastal strip 200 km wide (Small & Nicholls, 2003; Neumann *et al.*, 2015). These populations have a tremendous impact on the quality of coastal and oceanic environments, and coastal

environments are vulnerable to water pollution and eutrophication caused by human activities, climate change and other stresses. Coastal areas are diverse in function and important in terms of transportation, trade, settlement, tourism/recreation, resource extraction including aquaculture, wildlife habitats, industry and defence (Clark, 1992).

As the world's environment is changing, we may need a new paradigm to evaluate our environment and activities in terms of maintaining ecosystem sustainability and services. In this review, we discuss the role of natural macroalgal communities and SABs, and the ecosystem services that they provide, in the context of global change. Other important aspects of algal-based industries, such as the uses of algae for biofuels, high value biochemicals and bioactive substances, the importance of Integrated Multi-trophic Aquaculture (IMTA) and the impacts of diseases are considered elsewhere in this issue (Busetti et al., in press; Buschmann et al., in press; MacMonagail et al., in press).

Seaweed physiological performance is likely to be affected by global environmental change

Anthropogenic CO_2 emissions have resulted in a range of changes to the marine environment. These include the effects of elevated CO_2, changes in carbonate chemistry (Feely et al., 2004), particularly a decrease in oceanic pH (Ocean Acidification, OA), and an increase in sea surface temperatures (Meehl et al., 2007). In turn these have led to alterations in stratification, resulting in impaired nutrient supply from deep to surface waters (Doney et al., 2012). At the same time damage to the stratospheric ozone layer is continuing to cause elevated levels of UVB radiation, especially, but not exclusively, at high latitudes (Hegglin & Shepherd, 2009). The impacts of global change on microalgae have been dealt with extensively elsewhere (Beardall & Raven, 2004; Beardall et al., 2009, 2014; Gao et al., 2012; Johnson et al., 2013), so here we concentrate on the impacts on seaweeds, especially those of potential importance for the aquaculture industry, such as the kelps at higher latitudes and the range of species (dominated by red algae) that are used extensively in the tropics.

Effects of CO_2 levels and ocean acidification (OA)

CO_2 concentrations in the atmosphere are expected to reach 1000 ppm by the end of this century (IPCC, 2013). This will cause dissolved CO_2 concentrations to rise by ~2.5-fold but because of the resulting drop in pH (~0.4 units), bicarbonate concentrations will only increase by ~10% and carbonate levels will approximately halve (Feely et al., 2004; Raven et al., 2005).

The extent to which increasing CO_2 concentrations in seawater will impact seaweed productivity is dependent on the inorganic carbon acquisition kinetics of different species. For example, some species are already CO_2-saturated under present-day CO_2 levels (Beardall et al., 1998; Cornwall et al., 2012) as they generally express active CO_2 concentrating mechanisms (CCMs) (Giordano et al., 2005). Nonetheless some sub-tidal species have been shown to have no, or limited, CCM activity and thus show increases in photosynthetic rate when supplied with additional CO_2 (Holbrook et al., 1988; Johnston et al., 1992; Kübler et al., 1999). Even species that have been demonstrated to have CCMs can show stimulated growth rates under elevated CO_2. Thus Zou & Gao (2009) demonstrated increased growth of Gracilaria lemaneiformis when supplied with 700 ppm CO_2 and saturating irradiance (but not when light was low). Suárez-Álvarez et al. (2012) and Sarker et al. (2013) also showed stimulation of growth of Hypnea spirella and Chondrus crispus, respectively, by elevated CO_2, though in C. crispus the effects of CO_2 were only significant under elevated temperature or low irradiance. Likewise Celis-Plá et al. (2015) have shown that elevated CO_2 had positive effects on the physiological performance of the brown algae Cystoseira compressa and Padina pavonica, though the nature of the changes was also modulated by nitrogen and light availability. It is possible that under elevated CO_2 levels, operation of the energetically expensive CCMs is down-regulated, freeing up extra energy which can then be diverted into investment in growth processes (Israel & Hophy, 2002; Cornwall et al., 2012). This might be especially advantageous under conditions of limited energy supply (light).

However, Zou et al. (2007) showed that elevated CO_2 increased photosynthetic rates of Ulva lactuca, but rendered the alga more susceptible to photoinhibition, possibly because of the down-regulation of the CCM removing a possible mechanism for dissipation of excess energy. Young & Gobler (2016) showed that in situ growth of Gracilaria and Ulva in an estuary was stimulated by elevated CO_2, though in the case of Ulva this was also related to nutrient levels. An excellent summary of the effects of elevated CO_2 on a range of processes in seaweeds is given by Ji et al. (2016), though more work is needed to explore the effects of elevated CO_2 on commercially used seaweed species to get a better picture of what the future of SABS might be in relation to CO_2 and OA, as these are poorly covered in the climate change literature. One effect of elevated CO_2 on C. compressa in the presence of additional N reported by Celis-Plá et al. (2015) was a stimulation of phenolic content, an effect also noticed in the microalga Phaeodactylum (Jin et al., 2015) though Arnold et al. (2012) have reported the opposite effect in seagrasses. While an increase in phenolics

would increase antioxidant capacity, these compounds taste bitter and can act as a deterrent to herbivory (Steinberg, 1988; Van Alstyne, 1988; Salimen & Karonen, 2011; Sarojini et al., 2016). In microalgae at least, changes in CO_2 levels affect fatty acid composition (Riebesell et al., 2000; Rossol et al., 2012; Bermúdez et al., 2016) and this change in nutritional quality can have flow-on effects to copepod grazers, but it is not known at present whether similar flow-on of macromolecular composition to herbivores occurs in the case of seaweeds.

Some effects of elevated CO_2/OA can be indirect. Connell & Russell (2010), for instance, have shown in systems in South Australia that elevated CO_2 favours turf-forming algae which outcompete the kelp species Ecklonia radiata. Recruitment of non-calcifying seaweeds in tropical seas has been shown to be positively influenced by elevated CO_2 as the accompanying OA inhibits the recruitment of coralline species that would normally compete (Kuffner et al., 2008). Harley et al. (2012) pointed out scenarios whereby although temperate kelp species might be negatively impacted by increases in herbivore (e.g. urchin) numbers under warmer future conditions, concomitant OA would overcome this by inhibiting growth of urchins and competing coralline algae and thereby promote kelp growth. In the case of tropical seaweeds, the final impact of warming and OA would depend on the extent of fisheries exploitation and thus top-down pressure on the algae (Harley et al., 2012).

Effects of rising sea surface temperature

Sea surface temperatures are expected to rise on average by ~4°C (range 2.4–6.4) under the A_1F_1 scenario by 2100 (Meehl et al., 2007), though the changes will be heterogeneous across the world's oceans with high latitude regions likely to show greater warming. Increasing sea surface temperatures may have significant direct impacts on the biology of seaweeds used in aquaculture (Stévant et al., 2017). Consequently, the responses to temperature by the algae used in SABs will need to be taken into account as they may determine where establishment of new SABs is best directed, or may dictate that established SABs are relocated to areas where temperature is more amenable to productivity. Natural populations used for harvest may also exceed their temperature optimum and thus become stressed, with subsequent declines in harvest (Steneck et al., 2002; Israel et al., 2010). Thus an understanding of the responses of commercially important seaweeds to temperature is an important issue for management of naturally occurring seaweeds and SABs into the future.

Increased temperature will reduce solubility of O_2 and CO_2 and affect the kinetics of carbon fixation by Rubisco, slightly in favour of the oxygenase activity, though CCM activity in those species that possess one is likely to continue to suppress photorespiration (Raven et al., 2017). Elevated temperature is likely to have the usual effects on metabolism and growth, increasing these properties up to an optimum but causing a decrease as the optimum temperature is exceeded. This may be especially important in South East Asia as this region is predicted to show very significant temperature rises by 2065 (Guinotte et al., 2003).

Terada et al. (2016) showed optimum growth of Kappaphycus alvarezii at 30.5°C, but reported 100% mortality at 36°C. In contrast, optimal temperature for growth of Pyropia yezoensis (as Porphyra yezoensis) was reported as 12–15°C (Yamamoto et al., 1991). For Gracilaria, Raikar et al. (2001) reported that species from Malaysia, Japan and India showed slightly different temperature optima, with maximal growth for the Japanese species being ~20–25°C, while those from India and Malaysia had optima around 25–35°C, though most species examined showed damage as temperatures increased from 30 to between 32.5 and 35°C. Thus for many algae, even small shifts in temperature can have deleterious effects on growth and survival.

In natural ecosystems, such alterations in temperature can result in changes in populations. Barry et al. (1995) reported that over a 60-year period the temperature of their study zone on the Californian coast had increased by 2.2°C and showed increased dominance of warm temperate, low growing, turf algal species such as Gelidium coulteri, Gigartina canaliculata, Endocladia muricata and Mastocarpus papillatus at the expense of larger, colder water preferring species such as Fucus distichus and Pelvetia fastigata. Brodie et al. (2014) have predicted that rising temperatures in the north-east Atlantic will have major negative impacts on the highly productive kelp forests, particularly in the southern reaches (Yesson et al., 2015), while OA will impact badly on maerl (rhodolith-forming free-living coralline algae) in the northern regions. In the 1990s, Breeman (1988, 1990) carried out elegant work on the effects of temperature on reproductive biology and biogeography of canopy-forming kelp species, predicting a northward shift in the southern boundaries of species such as Laminaria hyperborea, Saccharina latissima (as L. saccharina) and L. digitata. Fernández (2011) has shown that population retreats of L. hyperborea, L. ochroleuca and Saccorhiza polyschides from the northern Spanish coast were related to increases in temperature from the 1980s to the 2000s.

Temperature increases in the surface waters of the open ocean will lead to more marked stratification of the water column and this will lead to a diminished supply of nutrients from cold, nutrient-rich water below the thermocline into surface water (Doney, 2006; Doney et al., 2012). Such restriction in nutrient

supply is likely to have a big impact on productivity of phytoplankton in the open ocean, though is likely to be less important in near-shore coastal systems where increased storm activity in future is likely to initiate greater mixing and increased run-off from land, thereby enhancing nutrient availability (Meier, 2006; Beardall et al., 2009). However, SABs deployed in deep water might be affected by the increased stratification and restriction on nutrient supply that would impose.

Other global change factors

Levels of UVB radiation reaching the Earth's surface are still increasing, due to complex interactions between breakdown of stratospheric ozone and global warming and, although ozone 'holes' are still occurring annually over the Poles, increases in UVB fluxes to the Earth's surface are not restricted to high latitudes, though changes at the tropics are minimal (Hegglin & Shepherd, 2009; Herman, 2010). Increased UVB has a range of deleterious effects on algae (see Beardall et al., 2014, and references therein) so increased UVB would pose problems for seaweeds, though many can modulate levels of reactive oxygen scavenging compounds and UVB-screening compounds such as mycosporine amino acids (MAAs) (Richa et al., 2016). Studies of the effects of UVB on seaweeds have focused more on early developmental stages than on mature thalli (Beardall et al., 2014) and the effects of UV radiation appear to be very species-specific, even within a genus (see for instance the work of Altamirano et al. (2003) on Fucus species). As described in the recent review by Beardall et al. (2014), UVB effects are modulated by other environmental factors such as temperature (which appears to promote repair and reduce the overall UVB damage), CO_2 (both positive and negative effects on UVB sensitivity have been recorded) and nutrient limitation (which generally increases UVB sensitivity). However, it is noteworthy that although UVB levels are higher in tropical regions than at higher latitudes, UVB levels are not rising significantly in the tropics and therefore may not adversely affect seaweed performance in the Asia-Pacific as the algae in this region may be better evolved to cope with the existing, high, UVB fluxes.

One of the consequences of global warming will be increased storm activity (Meier, 2006) and this has the potential to affect seaweed aquaculture by (a) increasing turbidity and decreasing productivity through light limitation, (b) physical damage to macroalgal beds and SABs by increased wave action (Pickering et al., 2011), and (c) decreased water quality though increased runoff of nutrients and pollutants from terrestrial and riverine systems (Eng et al., 1987; Fei, 2004). Given the predictions (IPCC, 2013) that storm activity is likely to be enhanced in future, due to increased temperature differences between the land and sea, it is very likely that SABs will be more prone to storm damage in a future climate and consequently more attention will need to be paid to constructing systems that will withstand greater wave and wind forces.

Although many stressors are known to affect seaweeds, few studies have addressed interactions between the various components of global change. The data available in the literature are largely from single-stressor physiology, ecotoxicology and global change studies (Israel et al., 2010). A few studies (touched on above) have investigated the interactive effects of warming, UVB and CO_2-driven acidification on marine organisms. Our limited knowledge of the interactive effects of climate change stressors is a major knowledge gap and some progress is being made with phytoplankton (Boyd et al., 2015). However, similar studies on seaweeds are few and far between and if we are to truly understand how seaweeds in SABs are going to respond in the future then more work on interactive effects of climate change components is necessary.

Adaptation in a changing ocean is crucial to identify potential 'winners' and 'losers' in the climate change stakes (Somero, 2010). Physiological responses to temperature are known to be a major determinant of species distributions and can dictate the sensitivity of populations to global warming (Southward et al., 1995; Pearson & Dawson, 2003; Harley et al., 2012; Jueterbock et al., 2013; Wernberg et al., 2013). However, if species can adapt to become more tolerant to climate change related stressors, or if active selection for tolerant strains is encouraged, then the potential damage to SABs from a changing climate will be minimized. Again, although some advances in considering evolutionary adaptations to climate change-related changes are being made with phytoplankton, work with seaweeds in this respect is lagging far behind (see Reusch, 2014).

The potential of seaweeds as one solution to ameliorating climate change

The potential of seaweeds as a mitigation measure for increasing CO_2 emissions has also been considered. There have been several reports which demonstrate the capacity for seaweeds to draw down and fix anthropogenic CO_2 into organic matter (N'Yeurt et al., 2012; Chung et al., 2013; Duarte et al., 2017). There is also evidence that some of this organic carbon is in refractory forms that would resist decomposition and thus would not be released as CO_2 back into the atmosphere (Trevathan-Tackett et al., 2015) and seaweeds could therefore act as a "blue carbon" sink (Hill et al., 2015).

Chung et al. (2013) proposed the concept of a coastal CO_2 removal belt (CCRB) and reported a potential sequestration capability of about 10 ton CO_{2eq} ha^{-1}

year^{-1} for a project in Korea. In addition to drawdown by natural macroalgal communities, artificial seaweed aquaculture beds (SABs) could also provide the same potential CO_2 removal capability. The potential use of seaweed aquaculture beds in CO_2 mitigation efforts has been proposed for commercial seaweed production in Asian countries (Sondak et al., 2016). SABs and natural seaweed beds and kelp forests represent very significant pools of aquatic vegetation and C sinks and they could thus enhance carbon sequestration in coastal waters like other blue carbon systems (Nellemann et al., 2009; Vierros, 2013; Howard et al., 2014).

However, it is difficult for seaweeds to be recognized as carbon sink agents under the current concept of CO_2 sequestration as conceived by the UN Framework Convention on Climate Change (UNFCCC). There has been considerable debate about considering seaweeds as a CO_2 sink, particularly with respect to the time period of sequestration of the carbon in their organic matter. It is obvious that seaweeds draw down CO_2 from seawater through photosynthesis in the water column, but a good proportion of this carbon is easily decomposed back to CO_2 (see Hill et al., 2015; Trevathan-Tackett et al., 2015).

The current definition of a carbon sink in terms of turnover time has been set up for trees and forests, including mangroves, in the terrestrial environment and the afforestation and reforestation process of the clean development mechanism (A/R CDM) is based on this concept (Wylie et al., 2016). When we consider seaweeds as CO_2 sink agents, we have to apply a different time frame, applicable to the oceanic life cycle. Thus, when we consider the time frame for the oceanic environment we need to develop two different time frame strategies. One is based on the time to reach the climax condition and the other is related to the displacement of organic carbon to specific regions of the oceans for sequestration.

Compared to the time scale of decades, used when the A/R CDM is applied to terrestrial environments, turnover in the coastal environment occurs on quite short time scales, less than 10 years (Chung et al., 2013). It is, however, unreasonable to apply the terrestrial time scale, for example a period of at least 50 years required for afforestation, to those of oceanic blue carbon (UNFCC, 2016). Therefore, we need to develop a new concept encompassing different time scales and a new paradigm for oceanic carbon sequestration.

Alternatively, we could apply the same time frame used for terrestrial CDMs if we consider draw-down of CO_2 in one place (based on SABs or natural macroalgal beds in coastal regions) and displacement of the biomass to another place for sequestration purpose – such as sinking them into the deep sea. If we use the same 'terrestrial clock', we could develop appropriate solutions to keep the biomass from SABs for more than 1000 years if introduced into deep water, this being the approximate time scale for deep-sea circulation and the biological carbon pump (Maier-Reimer & Hasselmann, 1987; Sabine et al., 2004).

The importance of blue carbon has been ever increasing and it is now recognized as an important agent in the new era of climate change. Seaweeds are quite different from other blue carbon systems as they almost all grow on hard substrata and therefore are not associated with sediments in which organic carbon could be buried. However, because of seaweeds' capability for attachment to hard structures, SABs could be developed in offshore waters and therefore have a strong potential for expansion, beyond what is possible within coastal waters. The concept of open-ocean aquaculture of seaweeds using structures, such as 'the offshore-ring', was introduced in combination with offshore wind parks and harvesting and conversion of seaweed biomass to renewable energy carriers and chemicals (Buck & Buchholz, 2004). Considerable system development is required, however, to enable large-scale, economically attractive cultivation of seaweeds combined with offshore wind parks (Buck et al., 2008).

Krause-Jensen & Duarte (2016) proposed a role for macroalgal carbon sequestration which accounts for accumulation of a large stock of organic carbon with two modes for the transport of organic carbon to the deep ocean and sediments: (1) macroalgal material drifting through submarine canyons, and (2) the sinking of negatively buoyant macroalgal detritus. Their estimations suggested that seaweeds could sequester about 173 Tg C year^{-1} (with a range of 61–268 Tg C year^{-1}) globally. About 90% of this sequestration occurs through export to the deep sea, and the rest through burial in coastal sediments. This estimate exceeds that for carbon sequestered in angiosperm-based coastal habitats (Krause-Jensen & Duarte, 2016).

It is critical to provide accurate methodology to estimate the amount of carbon sequestered by SABs and establish the measurement, reporting and verification (MRV) methodology. The general techniques and biology of seaweed culture are well known. It should therefore be easy to apply this information to projects involving mass growth of seaweeds and establish the MRV system as well. When the MRV is provided, this can then be adopted and implemented as a measure of mitigation in the Nationally Determined Contribution (NDC) and/or Nationally Appropriate Mitigation Action (NAMA) registry (http://unfccc.int/coopera tion_support/nama/items/7476.php).

This is especially significant where SABs are located in shallow waters where the natural standing biomass of other vegetation is absent or low (Mitra et al., 2014). Moreover, the services that natural seaweeds and SABs provide fulfil some strategies for climate change adaptation. The ecosystem services

Table 3. The main steps to consider when planning, conducting, or evaluating seaweed farming at sea as a blue carbon sink. (Modified from Radulovich et al., 2015).

1. Evaluating the main characteristics of each coastal-marine environment where farming is intended, including water and climate, environmental quality and biodiversity, other uses of water, access and facilities, manpower availability, socioeconomic, cultural, and legal characteristics;
2. Selecting the right seaweed species to farm in each environment for the purposes of bioenergy, ecosystem services and carbon sequestration;
3. Selecting the right site(s) within each environment, emphasizing local conditions in relation to the seaweed species selected;
4. Selecting and implementing reproduction/propagation techniques to secure sufficient numbers and quality of propagules with reliable timing;
5. Selecting and implementing cultivation technique (planting), populating the farmed area in optimal spatial arrangement and density of propagules;
6. Following up during grow-out, making sure that the crop stays in place in the desired spatial arrangement during the entire project period;
7. Quantification of C_{org} and transport offshore to sink for sequestration or harvest for biofuel conversion.

that natural seaweed beds and SABs provide have been well documented (Table 1). In addition, coastal eutrophication, deoxygenation and ocean acidification could be reduced by seaweeds. The design structure of SABs could also facilitate coastal protection to reduce wave energy as currently occurs e.g. with mangroves (Duarte et al., 2017).

When a novel way of using seaweeds is developed to increase C assimilation as a blue carbon sink for CO_2, this could then be implemented as a new seaweed-based 'carbon capture and storage' project (Chung et al., 2013; Sondak et al., 2016). The amount of C_{org} produced could be easily monitored and quantified. After the project period the total biomass could be taken offshore for sinking into deep waters. The procedures that might be used in such projects are described in Table 3 (modified from Radulovich et al., 2015). However, as pointed out earlier, how successful burial efforts will be in sequestering C will depend, inter alia, on the recalcitrance of the organic matter to decomposition (Hill et al., 2015, Trevathan-Tackett et al., 2015).

The estimate of Krause-Jensen & Duarte (2016) of about 173 Tg C year^{-1} (with a range of 61–268 Tg C year^{-1}) fixed by seaweeds globally is a relatively small proportion of total oceanic primary production (54–59 Pg C year^{-1}) and the increase in atmospheric CO_2 of 4 Pg C year^{-1} (Denman et al., 2007). However, SABs should prove to be expandable to the offshore environment and the open sea, in contrast to the A/R CDM which is limited to land, unlocking a capacity to greatly increase carbon caption in biomass. This approach has been termed Seaweed Carbon Capture and Sink ('Seaweed CCS'; analogous to terrestrial Carbon Capture and Storage) and could also be applied as a measure for mitigation and other adaptation measures against OA in coastal areas in the NDC and as a new CDM method.

There is thus significant potential for increasing the drawdown of CO_2 using macroalgal cultivation, and especially SABs. However, it is clear that many of the seaweeds that are used in aquaculture at present are susceptible to climate change, so further

efforts to identify species for use in SABs in future will need to take into account their physiological tolerance to environmental changes and to OA and warming in particular.

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Disclosure statement

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Author contributions

J. Beardall: planning, drafting and editing the manuscript; I.K. Chung: planning, drafting and editing the manuscript; C.F.A. Sondak contributed important information on ecosystem services and assisted with writing.

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References

Altamirano, M., Flores-Moya, A. & Figueroa, F.L. (2003). Effects of UV radiation and temperature on growth of germlings of three species of *Fucus* (Phaeophyceae). *Aquatic Botany*, **75**: 9–20.
Arnold, T., Mealey, C., Leahey, H., Miller, A.W., Hall-Spencer, J.M., Milazzo, M. & Maers, M. (2012). Ocean acidification and the loss of phenolic substances in marine plants. *PLoS ONE*, **7**(4): e35107.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A. C. & Silliman, B.R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, **81**: 169–193.

Barry, J.P., Baxter, C.H., Sagarin, R.D. & Gilman, S.E. (1995). Climate-related, long term faunal changes in a California rocky intertidal community. *Science*, **267**: 672–675.

Beardall, J. & Raven, J.A. (2004). The potential effects of global climate change on microalgal photosynthesis, growth and ecology. *Phycologia*, **43**: 26–40.

Beardall, J., Beer, S. & Raven, J.A. (1998). Biodiversity of marine plants in an era of climate change: some predictions on the basis of physiological performance. *Botanica Marina*, **41**: 113–123.

Beardall, J., Stojkovic, S., & Larsen, S. (2009). Living in a high CO_2 world: impacts of globalclimate change on marine phytoplankton. *Plant Ecology and Diversity*, **2**: 191–205.

Beardall, J., Stojkovic, S. & Gao, K. (2014). Interactive effects of nutrient supply and other environmental factors on the sensitivity of marine primary producers to ultraviolet radiation: implications for the impacts of global change. *Aquatic Biology*, **22**: 5–23.

Bermúdez, J.R., Riebesell, U., Larsen, A. & Winder, M. (2016). Ocean acidification reduces transfer of essential biomolecules in a natural plankton community. *Science Reports*, **6**: 27749. doi: 10.1038/srep27749.

Boyd, P.W., Lennartz, S.T., Glover, D.M. & Doney, S. (2015). Biological ramifications of climate-change-mediated oceanic multi-stressors. *Nature Climate Change*, **5**: 71–79.

Breeman, A.M. (1988). Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: experimental and phenological evidence. *Helgolander Meeresuntersuchungen*, **42**: 199–241.

Breeman, A.M. (1990). Expected effects of changing seawater temperatures on the geographic distribution of seaweed species. In *Expected Effects of Climate Change on Marine Coastal Ecosystems* (Beukema, J.J., Wolff, W.J. & Brouns, J. J.W.M., editors), 69–76. Kluwer Academic, Dordrecht.

Brodie, J., Williamson, C.J., Smale, D.A., Kamenos, N.A., Mieszkowska, N., Santos, R., Cunliffe, M., Steinke, M., Yesson, C., Anderson, K.M., Asnaghi, V., Brownlee, C., Burdett, H.L., Burrows, M.T., Collins, S., Donohue, P.J. C., Harvey, B., Foggo, A., Noisette, F., Nunes, J., Ragazzola, F., Raven, J.A., Schmidt, D.N., Suggett, D., Teichberg, M. & Hall-Spencer, J.M. (2014). The future of the northeast Atlantic benthic flora in a high CO_2 world. *Ecology and Evolution*, **4**: 2787–2798.

Buck, B.H. & Buchholz, C.M. (2004). The offshore ring: a new system design for the open ocean aquaculture for macroalgae. *Journal of Applied Phycology*, **16**: 355–368.

Buck, B., Krause, G., Michler-Cieluch, T., Brenner, M., Buchholz, C., Busch, J., Fisch, R., Geisen, M., & Zielinski, O. (2008). Meeting the quest for spatial efficiency: progress and prospects of extensive aquaculture within offshore wind farms. *Helgoland Marine Research*, **62**: 269–281.

Buschmann, A.H., Camus, C., Infante, J., Neori, A., Israel, Á., Hernández-González, M.C., Pereda, S.V., Gomez-Pinchetti, J.L., Golberg, A, Tadmor-Shalev, N. & Critchley, A.T. (in press). Seaweed production: overview of the global state of exploitation, farming and emerging research activity. *European Journal of Phycology*.

Busetti, A., Maggs, C.A., & Gilmore, B. (in press). Marine macroalgae and their associated microbiomes as a source of antimicrobial chemical diversity. *European Journal of Phycology*.

Cabral, P., Levrel, H., Viard, F., Frangoudes, K., Girard, S. & Scemama, P. (2016). Ecosystem services assessment and compensation costs for installing seaweed farms. *Marine Policy*, **71**: 157–165.

Celis-Plá, P.S.M., Hall-Spencer, J.M., Horta, P.A., Milazzo, M., Korbee, N., Cornwall, C.E. & Figueroa, F.L. (2015). Macroalgal responses to ocean acidification depend on nutrient and light levels. *Frontiers of Marine Science*, **2**: 26. doi: 10.3389/fmars.2015.00026.

Chapin, F.S.I, Zavaleta., E.S., Eviner., V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. & Díaz, S. (2000). Consequences of changing biodiversity. *Nature*, **405**: 234–242.

Chopin, T., Yarish, C., Wilkes, R. Belyea E., Lu, S. & Mathieson, A. (1999). Developing *Porphyra*/salmon integrated aquaculture for bioremediation and diversification of the aquaculture industry. *Journal of Applied Phycology*, **11**:463–472.

Chung, I.K., Beardall, J., Mehta, S., Sahoo, D. & Stojkovic, S. (2011). Using marine macroalgae for carbon sequestration: a critical appraisal. *Journal of Applied Phycology*, **23**: 877–886.

Chung, I.K., Oak, J.H., Lee, J.A., Shin, J.A., Kim, J.G. & Park, K.S. (2013). Installing kelp forest/seaweed beds for mitigation and adaptation against global warming: Korean Project overview. *ICES Journal of Marine Science*, doi:10.1093/icesjms/fss206.

Clark, J.R. (1992). *Integrated Management of Coastal Zones*. FAO Fisheries Technical Paper. No. 327. FAO, Rome. 167 pp.

Connell, S.D. & Russell, B.D. (2010). The direct effects of increasing CO_2 and temperature on non-calcifying organisms: increasing the potential for phase shifts in kelp forests. *Proceedings of the Royal Society B: Biological Sciences*, **277**: 1409–1415.

Cornwall, C.E., Hepburn, C.D., Pritchard D., Currie, K.I., McGraw, C.M., Hunter, K.A. & Hurd, C.L. (2012). Carbon use strategies in macroalgae: differential responses to lowered pH and implications for ocean acidification. *Journal of Phycology*, **48**: 137–144.

Dearing, J.A. (2006). Climate-human-environment interactions: resolving our past. Climate of the Past Discussions. *European Geosciences Union (EGU)*, **2**: 563–604.

Denman, K.L., Brasseur, G.P., Chidthaisong, A., Ciais, P., Cox, P., Dickinson, R.E., Hauglustaine, D.A., Heinze, C., Holland, E.A., Jacob, D.J., Lohmann, U., Ramachandran, S., Leite da silva Dias, P., Wofsy, S.C., Zhang, X.Y. & Steffen, W. (2007). Coupling between changes in the climate system and biogeochemistry. *ANU Research Publications*, http://hdl.handle.net/1885/57818.

Doney, S.C. (2006). Plankton in a warmer world. *Nature*, **444**: 695–696.

Doney, S.C., Ruckelshaus, M., Duffy, J.E., Barry, J.P., Chan, F., English, C.A., Galindo, H.M., Grebmeier, J.M., Hollowed, A. B., Knowlton, N., Polovina, J., Rabalais, N.N., Sydeman, W.J. & Talley, L.D. (2012). Climate change impacts on marine ecosystems. *Annual Review of Marine Science*, **4**: 11–37.

Duarte, C.M., Losada, I.J., Hendriks, I.E., Mazarrasa, I., & Marbà, N. (2013). The role of coastal plant communities for climate change mitigation and adaptation. *Nature Climate Change*, **3**: 961-968.

Duarte, C.M., Wu, J., Xiao, X., Bhrun, A. & Krause-Jensen, D. (2017). Can seaweed farming play a role in climate change mitigation and adaptation? *Frontiers in Marine Science*, **4**: 1–8.

Duggins, D.O., Simenstad, C.A. & Estes, J.A. (1989). Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science, New Series*, 245: 170–173.

Eng, C.T., Paw, J.N., & Guarin, F.Y. (1987). The environmental impact of aquaculture and the effects of the pollution on coastal aquaculture development in Southeast Asia. *Marine Pollution Bulletin*, 20: 335–343.

FAO (2003). *A Guide to the Seaweed Industry*. Fisheries Technical Paper 441. Food and Agriculture Organisation of the United Nations, Rome. 118 pp.

FAO (2010). *The State of World Fisheries and Aquaculture*. Food and Agriculture Organisation of the United Nations, Rome. 197 pp.

FAO (2014). *The State of World Fisheries and Aquaculture 2016*. Food and Agriculture Organisation of the United Nations, Rome. 223 pp.

FAO (2016). *The State of Fisheries and Aquaculture 2016*. Contributing to food security and nutrition for all. Food and Agriculture Organisation of the United Nations, Rome. 200 pp.

Feely, R.A., Sabine, C.L., Lee, K., Berelson, W., Kleypas, J.A., Fabry, V.J. & Millero, F.J. (2004). Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. *Science*, 305: 362–366.

Fei, X.G. (2004). Solving the coastal eutrophication problem by large scale seaweed cultivation. *Hydrobiologia*, 512: 145–151. doi:10.1007/978-007-0944-7_19.

Fernández, C. (2011). The retreat of large brown seaweeds on the north coast of Spain: the case of *Sacchoriza polyschides*. *European Journal of Phycology*, 46: 352–360.

Gao, K., Helbling, E.W., Häder, D.P. & Hutchins, D.A. (2012). Responses of marine primary producers to interactions between ocean acidification, solar radiation, and warming. *Marine Ecology Progress Series*, 470: 167–189.

Gao, Y., Yu, G., Yang, T., Jia, Y., He, N. & Zhuang, J. (2016). New insight into global blue carbon estimation under human activity in land-sea interaction area: a case study of China. *Earth-Science Reviews*, 159: 36–46.

Giordano, M., Beardall, J. & Raven, J.A. (2005). CO_2 concentrating mechanisms in algae: mechanisms, environmental modulation and evolution. *Annual Review of Plant Biology*, 56: 99–131.

Go, F. (2010). Rural space as a regional resource for education: a case study of education farm, activities at elementary schools in Saga city. *Geographical Review of Japan Series B*, 82: 137–148.

Graham, M.H. (2004). Effects of local deforestation on the diversity and structure of Southern California giant kelp forest food webs. *Ecosystem*, 7: 341–357.

Guinotte, J.M., Buddemeier, R.W. & Kleypas, J.A. (2003). Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin. *Coral Reefs*, 22: 551–558.

Harley, C.D.G., Anderson, K.M., Demes, K.W., Jorve, J.P., Kordas, R., Coyle, T.A. & Graham, M.H. (2012). Effects of climate change on global seaweed communities. *Journal of Phycology*, 48: 1064–1078.

Hegglin, M.I. & Shepherd, T.G. (2009). Large climate-induced changes in ultraviolet index and stratospheric-to-troposphere ozone flux. *Nature Geoscience*, 2: 687–691.

Herman, J.R. (2010). Global increase in UV irradiance during the last 30 years (1979–2008) estimated from satellite data. *Journal of Geophysical Research*, 115: D04203, doi: 10.102912009/JDOI2219.

Hill, R., Bellgrove, A., Macreadie, P.I., Petrou, K., Beardall, J., Steven, A. & Ralph, P.J. (2015). Can macroalgae contribute to Blue Carbon? An Australian perspective. *Limnology and Oceanography*, 60: 1689–1706.

Holbrook, G.P., Beer, S., Spencer, W.E., Reiskind, J.B., Davis, J.S. & Bowes, G. (1988). Photosynthesis in marine macroalgae: evidence for carbon limitation. *Canadian Journal of Botany*, 66: 577–582.

Howard, J., Hoyt, J., Isensee, K., Pidgeon, E. & Telszewski, M. (2014). *Coastal Blue Carbon: Methods for Conservation*. International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature Factors in Mangroves, Tidal Salt Marshes, and Seagrasses Meadows. Conservation International, Inter-governmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature. Arling-ton, Virginia.

IPCC (2013). *Climate Change 2013*: *The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V. & Midgley, P.M., editors). Cambridge University Press, Cambridge, 1535 pp., doi: 10.1017/CBO9781107415324.

Israel, A. & Hophy, M. (2002). Growth, photosynthetic properties and Rubisco activities and amounts of marine macroalgae grown under current and elevated seawater CO_2 concentrations. *Global Change Biology*, 8: 831–840.

Israel, A., Einav, R. & Seckbach, J. (eds) (2010). *Seaweeds and their Role in Globally Changing Environments*. Cellular Origin, Life in Extreme Habitats and Astrobiology, Volume 15. Springer, Dordrecht, 479 pp., doi 10.1007/978-90-481-8569-6.

Jackson, G.A. & Winant, C.W. (1983). Effect of a kelp forest on coastal currents. *Continental Shelf Research*, 2: 75–80.

Ji, Y., Xu, Z., Zou, D., & Gao, K. (2016). Ecophysiological responses of marine macroalgae to climate change factors. *Journal of Applied Phycology*, 28: 2953–2967.

Jin, P., Wang, T., Liu N., Dupont, S., Beardall, J., Boyd, P W., Riebesell, U. & Gao, K. (2015). Ocean acidification increases accumulation of toxic phenolic compound across trophic levels. *Nature Communications*, 6: 8714. doi: 10.1038/ncomms9714.

Johnson, V.R., Brownlee, C., Rickaby, R.E.M., Graziano, M., Milazzo, M. & Hall-Spencer, J.M. (2013). Responses of marine benthic microalgae to elevated CO_2. *Marine Biology*, 160: 1813–1824.

Johnston, A.M., Maberly, S.C. & Raven, J.A. (1992). The acquisition of inorganic carbon by four red macroalgae. *Oecologia*, 92: 317–326.

Jueterbock, A., Tyberghein, L., Verbruggen, H., Coyer, J.A., Olsen, J.L. & Hoarau, G. (2013). Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal. *Ecology and Evolution*, 3: 1356–1373.

Krause-Jensen, D. & Duarte, C.M. (2016). Substantial role of macroalgae in marine carbon sequestration. *Nature Geoscience*, 9: 737–742.

Kübler, J.E., Johnston, A.M. & Raven, J.A. (1999). The effects of reduced and elevated CO_2 and O_2 on the seaweed *Lomentaria articulata*. *Plant Cell and Environment*, 22: 1303–1310.

Kuffner, I.B., Andersson, A.J., Jokiel, P.L., Rodgers, K.S. & Mackenzie, F.T. (2008). Decreased abundance of crustose coralline algae due to ocean acidification. *Nature Geoscience*, 1: 114–117.

Le Quere, C. (2010). Trends in the land and ocean carbon uptake. *Environment Sustainability*, **2**: 219–224.

Levinton, J.S., Ward, J.E. & Shumway, S.E. (2002). Feeding responses of the bivalves *Crassostrea gigas* and *Mytilus trossulus* to chemical composition of fresh and aged kelp detritus. *Marine Biology*, **141**: 367–376.

Mac Monagail, M., Cornish, L., Morrison, L, Araújo, R., & Critchley, A.T. (in press). Sustainable harvesting of wild seaweed resources. *European Journal of Phycology*.

MacArtain, P., Gil, C.I.R., Brooks, M., Campbell, R. & Rowland, I.R. (2007). Nutritional value of edible seaweeds. *Nutrition Review*, **65**: 535–543.

Maier-Reimer, E., & Hasselmann, K. (1987). Transport and storage of CO_2 in the ocean – an inorganic ocean-circulation carbon cycle model. *Climate Dynamics*, **2**: 63–90.

MEA (2005). *Millennium Ecosystem Assessment. Ecosystems and Human Well-being: Current State and Trends, Findings of the Condition and Trends Working Group.* Millennium Ecosystem Assessment Series, Island Press, Washington, DC. 47 pp.

Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., *et al.* (2007). Global climate projections. In *Climate Change 2007: The Physical Science Basis.* Contribution of Working Group I *to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. & Miller, H. L., editors), 749–845. Cambridge University Press, Cambridge.

Meier, H.E.M. (2006). Baltic Sea climate in the late twenty-first century: a dynamical downscaling approach using two global models and two emission scenarios. *Climate Dynamics*, **27**: 39–68.

Mitra, A., Zaman, S., Pramanick, P., Bhattacharyya, S.B. & Raha, A.K. (2014). Stored carbon in dominant seaweeds of Indian Sundarbans. *Pertanika Journal of Tropical Agricultural Science*, **37**: 263–274.

Monastersky, R. (2015). Anthropocene: the human age. *Nature*, **519**: 144–147.

Mumby, P., Edwards, A., Aria-Gonzalez, J.E., Lindeman, K. C., Blackwell, P.G., Gail, A., Gorczynska, M.I., Harborne, A., Pescod, C.L., Renken, H., Wabnitz, C.C.C. & Llewellyn, G. (2004). Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature*, **427**: 533–536.

Muraoka, D. (2004). Seaweed resources as a source of carbon fixation. *Bulletin of Fisheries Research Agency*, **Supplement No. 1**: 59–63

Nellemann, C., Corcoran, E., Duarte, C.M., Valdes, L., De Young, C., Fonseca, L. & Grimsditch, G. (2009). *Blue Carbon. A Rapid Response Assessment.* GRID-Arendal: United Nations Environment Programme.

Neumann, B., Vafeidis, A.T., Zimmermann, J. & Nicholls, R.J. (2015). Future coastal population growth and exposure to sea-level rise and coastal flooding – a global assessment. *PLoS ONE*, **10**: e0118571. https://doi.org/10.1371/journal.pone.0118571.

Norderhaug, K.M., Christie, H. & Rinde, E. (2002). Colonization of kelp imitations by epiphyte and a holdfast fauna; a study of mobility patterns. *Marine Biology*, **141**: 965–973.

N'Yeurt, A., Chynoweth, D., Capron, M.E., Stewart, J. & Hasan, M. (2012). Negative carbon via ocean afforestation. *Process Safety and Environmental Protection*, **90**: 467–474.

O'Connor, K.C. & Anderson, T.W. (2010). Consequences of habitat disturbance and recovery to recruitment and the abundance of kelp forest fishes. *Journal of Experimental Marine Biology and Ecology*, **386**: 1–10.

Pearson, R.G., & Dawson, T.P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**: 361–371.

Pickering, T.D., Ponia, B., Hair, C.A., Southgate, P.C., Poloczanska, E.S., Della Patrona, L., Teitelbaum, A., Mohan, C.V., Phillips, M.J., Bell, J.D. & De Silva, S. (2011). Vulnerability of aquaculture in the tropical Pacific to climate change. In *Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change* (Bell, J.D., Johnson, J.E. & Hobday, A.J., editors), 647–731. Secretariat of the Pacific Community, Noumea, New Caledonia.

Radulovich, R., Umanzor S., Cabrera, R. & Mata, R. (2015). Tropical seaweeds for human food, their cultivation and its effect on biodiversity enrichment. *Aquaculture*, **436**: 40–46.

Raikar, S.V., Iima, M. & Fujita, Y. (2001). Effect of temperature, salinity and light intensity on the growth of *Gracilaria* spp. (Gracilariales, Rhodophyta) from Japan, Malaysia and India. *Indian Journal of Marine Sciences*, **30**: 98–104.

Raven, J.A., Beardall, J. & Sánchez-Baracaldo, P. (2017). The possible evolution and future of CO_2 concentrating mechanisms. *Journal of Experimental Botany*, 68: doi: 10.1093/jxb/erx110.

Raven, J.A., Caldeira, K., Elderfield, H., Hoegh-Guldberg, O., Liss, P.S., Riebesell, U., Shepherd, J., Turley, C. & Watson, A. (2005). *Ocean Acidification due to Increasing Atmospheric Carbon Dioxide.* Royal Society Policy Document 12/05. The Royal Society, London.

Regnier, P., Friedlingstein, P., Ciais, P., Mackenzie, F.T., Gruber, N., Janssens, I.A., Laruelle, G.G., Lauerwald, R., Luyssaert, S., Andersson, A.J., Arndt, S., Arnosti, C., Borges, A.V., Dale, A.W., *et al.* (2013). Anthropogenic perturbation of the carbon fluxes from land to ocean. *Nature Geoscience*, **6**: 597–607.

Reusch, T.B.H. (2014). Climate change in the oceans: evolutionary versus phenotypically plastic responses of marine animals and plants. *Evolutionary Applications*, **7**: 104–122.

Richa, Sinha, R.P. & Häder, D.-P. (2016). Effects of global change, including UV and UV screening compounds. In *The Physiology of Microalgae* (Borowitzka, M., Beardall, J. & Raven, J.A., editors), 373–409. Springer, Dordrecht.

Riebesell, U., Revill, A., Holdsworth, D. & Volkman, J. (2000). The effects of varying CO_2 concentration on lipid composition and carbon isotope fractionation in *Emiliania huxleyi*. *Geochimica et Cosmochimica Acta*, **64**: 4179–4192.

Roesijadi, G., Jones, S.B., Snowden-Swan, L.J. & Zhu, Y. (2010). *Macroalgae as a Biomass Feedstock: A Preliminary Analysis.* US Department of Energy PNNL-19944.

Rossoll, D., Bermúdez, R., Hauss, H., Schulz, K.G., Riebesell, U., Sommer, U. & Winder, M. (2012). Ocean acidification-induced food quality deterioration constrains trophic transfer. *PLoS ONE*, 7: e34737. doi: 10.1371/journal.pone.0034737.

Sabine, C.L., Feely, R.A., Gruber, N., Key, R.M., Lee, K., Bullister, J.L., Wanninkhof, R., Wong, C.S., Wallace, D. W., Tilbrook, B., Millero, F.J., Peng, T.H., Kozyr, A.,

Ono, T. & Rios, A.F. (2004). The oceanic sink for anthropogenic CO_2. *Science*, **305**: 367–371.

Saintilan, N., Hossain, K. & Mazumder, D. (2007). Linkages between seagrass, mangrove and saltmarsh as fish habitat in the Botany Bay estuary, New South Wales. *Wetlands Ecology and Management*, 15: 277–286.

Salimen, J-P. & Karonen, M. (2011). Chemical ecology of tannins and other phenolics: we need a change in approach. *Functional Ecology*, 25: 325–338.

Sarker, M.Y., Bartsch, I., Olischläger, M., Gutow, L. & Wiencke, C. (2013). Combined effects of CO_2, temperature, irradiance and time on the physiological performance of *Chondrus crispus* (Rhodophyta). *Botanica Marina*, 56: 63–74.

Sarojini, Y., Sujatha, B. & Santha, P.R. (2016). The variation in distribution of total phenols and antioxidant activity in five species of marine macro algae. *Der Pharmacia Lettre*, 8: 30–37.

Smale, D.A., Burrows, M.T., Moore, P., O'Connor, N. & Hawkins, S.J. (2013). Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecology and Evolution*, 3: 4016–4038.

Small, C. & Nicholls, R.J. (2013). A global analysis of human settlement in coastal zones. *Journal of Coastal Research*, 19: 584–599.

Sohn, C.H. (1993). *Porphyra, Undaria* and *Hizikia* cultivation in Korea. *Korean Journal of Phycology*, 8: 207–216.

Somero, G.N. (2010). The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *Journal of Experimental Biology*, 213: 912–920.

Sondak, C.F.A., Ang, P.O., Beardall, J., Bellgrove, A., Boo, S.M., Gerung, G.S., Hepburn, C.D., Hong, D.D., Hu, Z., Kawai, K., Largo, D., Lee, J.A., Lim, P.E., Mayakun, J., Nelson, W.A., Oak, J.H., Phang, S.M., Sahoo, D., Peerapornpis, Y., Yang, Y. & Chung, I.K. (2016). Carbon dioxide mitigation potential of seaweed aquaculture beds (SABs). *Journal of Applied Phycology*, doi: 10.1007/s10811-016-1022-1.

Southward, A.J., Hawkins, S.J., & Burrows, M.T. (1995). Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the Western English Channel in relation to rising sea temperature. *Journal of Thermal Biology*, 20: 127-155.

Steinberg, P. (1988). Effects of quantitative variation in phenolic compounds on feeding in three species of marine invertebrate herbivores. *Journal of Experimental Marine Biology and Ecology*, 120: 221–237.

Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A. & Tegner, M.J. (2002). Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation*, 29: 436–459.

Stévant, P., Rebours, C. & Chapman, A. (2017). Seaweed aquaculture in Norway: recent industrial developments and future perspectives. *Aquaculture International*, 25: 1373–1390.

Suárez-Álvarez, S., Gómez-Pinchetti, J.L. & García-Reina, G. (2012). Effects of increased CO_2 levels on growth, photosynthesis, ammonium uptake and cell composition in the macroalga *Hypnea spinella* (Gigartinales, Rhodophyta). *Journal of Applied Phycology*, 24: 815–823.

Tang, Q., Zhang, J. & Fang, J. (2011). Shellfish and seaweed mariculture increase atmospheric CO_2 absorption by coastal ecosystem. *Marine Ecology Progress Series*, **424**: 97–104.

Terada, R., Vo, T.D., Nishihara, G.N., Shioya, K., Shimada, S. & Kawaguchi, S. (2016). The effect of irradiance and temperature on the photosynthesis and growth of a cultivated red alga *Kappaphycus alvarezii* (Solieriaceae) from Vietnam, based on in situ and in vitro measurements. *Journal of Applied Phycology*, 28: 457.

Trevathan-Tackett, S.M., Kelleway, J., Macreadie, P.I., Beardall, J., Ralph, P. & Bellgrove, A. (2015). The capacity of marine macrophytes to contribute to blue carbon sequestration. *Ecology*, 96: 3043–3057.

UNFCC (2016). *CDM Methodology Booklet Eighth Edition November 2016*. United Nations Framework on Climate Change. https://cdm.unfccc.int/methodologies/.

Van Alstyne, K.L. (1988). Herbivore grazing increases polyphenolic defenses in the intertidal brown alga *Fucus distichus*. *Ecology*, **69**: 655–663.

Vierros, M. (2013). Communities and blue carbon: the role of traditional management systems in providing benefits for carbon storage, biodiversity conservation and livelihoods. *Climate Change*, doi: 10.1007/s10584-013-920-3.

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck Jr., K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T. & Williams, S.L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, **106**: 12377–12381.

Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T., Bennett, S., & Rousseaux, C.S. (2013). An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, 3: 78–82.

Wylie, L., Sutton-Grier, A.E. & Moore, A. (2016). Keys to successful blue carbon projects: lessons learned from global case studies. *Marine Policy*, 65: 76–84.

Yamamoto, M., Watanabe, Y. & Kinshita, H. (1991). Effects of water temperature on the growth of red alga *Porphyra yesoensis* form *narawaensis* (Nori) cultivated in an outdoor raceway tank. *Nippon Suisan Gakkaishi Bulletin*, 57: 2211–2217.

Yesson, C., Bush, L.E., Davies, A.J., Maggs, C.A. & Brodie, J. (2015). Large brown seaweeds of the British Isles: evidence of changes in abundance over four decades. *Estuarine, Coastal and Shelf Science*, 155: 167–175.

Young, C.S. & Gobler, C.J. (2016). Ocean acidification accelerates the growth of two bloom-forming macroalgae. *PLoS ONE*, 11: e0155152. doi: 10.1371/journal.pone.0155152.

Zou, D. & Gao, K. (2009). Effects of elevated CO_2 on the red seaweed *Gracilaria lemaneiformis* (Gigartinales, Rhodophyta) grown at different irradiance levels. *Phycologia*, 48: 510–517.

Zou, D.H., Gao, K.S. & Ruan, Z.X. (2007). Daily timing of emersion and elevated atmospheric CO_2 concentration affect photosynthetic performance of the intertidal macroalga *Ulva lactuca* (Chlorophyta) in sunlight. *Botanica Marina*, 50: 275–279.