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How will ocean acidification affect marine photosynthetic organisms? A review

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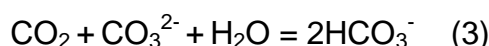
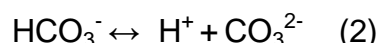
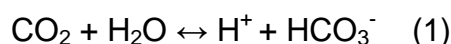
Abstract

Atmospheric carbon dioxide is increasing year on year, mainly as a result of burning fossil fuels. Although carbon dioxide dissolves in the oceans, mitigating atmospheric effects, it does result in a reduction of the alkalinity of sea water; an effect termed Ocean Acidification (OA). The subsequent changes in carbon chemistry will most likely affect marine photosynthetic organisms in a number of ways; including the ability of organisms to build calcium carbonate shells or skeletons (calcification) and primary production. Previous work indicates that both processes respond to OA, but not always in the same way. Consequently the aim of this review is to evaluate how our understanding of the effects of OA on calcification and primary production has progressed in recent years. It is concluded after examining the literature that our understanding has not developed, with recent work either agreeing with or contradicting past studies. However, there has been an increase in the number of multi-factorial studies, and so from this point of view our understanding has increased. To gain a better understanding, it is imperative that more comparable data becomes available, which although this sounds self-evident does mean that a consensus must be reached on the best methodology to use.

Introduction

It is now well documented that anthropogenic carbon dioxide (CO₂) emissions are causing a decrease in ocean pH (termed Ocean Acidification or OA) as well as warming the Earth (Caldeira and Wickett 2003, 2005; Feely et al. 2004; Orr et al. 2005; Solomon et al. 2007). This is why OA is often referred to as ‘the other CO₂ problem’ (Doney et al. 2009). The present day value of 384 parts per million volume (ppmv) (Meehl et al. 2007) is the highest over the past 800,000 years (Luthi et al. 2008), as a result of an increase in global atmospheric CO₂ partial pressure (pCO₂) from 0.03 to 0.04 kPa (Houghton et al. 2001).

Approximately a quarter of anthropogenic CO₂ released has been absorbed by oceans over the past 200 years (Sabine et al. 2004), therefore increasing pCO₂ levels in surface waters (referred to as hypercapnia) overloading the oceans natural ability to buffer changes in pH. Hypercapnia causes a shift in inorganic carbon chemistry, the net effect of which is to increase the concentrations of carbonic acid (H₂CO₃), bicarbonate (HCO₃⁻) and hydrogen (H⁺) ions, and decrease the concentration of carbonate ions (CO₃²⁻) and lower pH, (equations 1, 2 & 3 and figure 1). It is now understood that the present average surface ocean pH (8.1) is 0.1 units lower than pre-industrial times, correlating to a 30% increase in H⁺ ions (Fabry et al. 2008), and that future uptake will change ocean chemistry further.



	Glacial	Pre-industrial	Present	2XCO ₂	3XCO ₂	Change from pre-industrial to 3XCO ₂
pCO ₂	180	280	380	560	840	200%
$\text{CO}_2(\text{g}) \rightleftharpoons \text{CO}_2(\text{aq}) + \text{H}_2\text{O} \rightleftharpoons \text{H}_2\text{CO}_3$ Gas exchange Carbonic acid	7	9	13	18	25	178%
$\text{H}_2\text{CO}_3 \rightleftharpoons \text{H}^+ + \text{HCO}_3^-$ Bicarbonate	1666	1739	1827	1925	2004	15%
$\text{HCO}_3^- \rightleftharpoons \text{H}^+ + \text{CO}_3^{2-}$ Carbonate	279	222	186	146	115	- 48%
DIC	1952	1970	2026	2090	2144	8.8%
pH _(sws)	8.32	8.16	8.05	7.91	7.76	- 0.4

Figure 1: Seawater carbonate chemistry equations, concentrations of carbon species (in units of mmol kg⁻¹) and pH values of average surface seawater for pCO₂ concentrations (ppmv) during glacial, preindustrial, present day, two times pre-industrial CO₂, and three times pre-industrial CO₂. The last column shows the changes from the pre-industrial levels to three times atmospheric CO₂ (modified from Fabry et al. 2008).

Due to today's human activities, atmospheric CO₂ concentrations are projected to rise at a rate of about 3.3% year⁻¹ (Solomon et al. 2007). Based on some climate change models, atmospheric levels of CO₂ are projected to rise to around 790ppmv ($p\text{CO}_2 = 0.08 \text{ kPa}$) by the year 2100 (IS92a 'business-as-usual' scenario, Meehl et al. 2007), and to around 2000ppmv ($p\text{CO}_2 = 0.2 \text{ kPa}$) by the year 2300 (logistics pathway, Caldeira and Wickett, 2003, 2005). At the current rate of CO₂ uptake, these predicted atmospheric CO₂ values are expected to lower surface ocean water pH values by a further 0.3-0.4 (Meehl et al. 2007) and 0.7 units (Caldeira and Wickett, 2005) respectively to values of 7.8-7.7 and 7.4.

Marine photosynthetic organisms play a major ecological role not only in the marine environment but on a global scale also (Field et al. 1998). They act as the primary producers for the majority of marine ecosystems. By converting inorganic carbon to organic carbon they provide more than 99% of the organic matter used in marine food webs (Field et al. 1998). The majority occur as microscopic free-living phytoplankton (coccolithophores, diatoms, foraminiferans, dinoflagellates and cyanobacteria) over the ocean's surface, and account for about 50% of total global primary production (Falkowski et al. 1998). The other major group of primary producers are the benthic photosynthetic organisms such as seagrasses, seaweeds and corals, all of which are restricted to shallow water areas. Despite the fact their net primary productivity is about fifty times less than phytoplankton, at only 1 Giga tonne of carbon per year (Field et al. 1998), they are important in coastal ecosystems, for example providing habitats for other species as well as recycling nutrients. Due to the important roles marine photosynthetic organisms play, it is crucial that the effects OA has on them is understood, as both positive and negative effects will potentially have huge ecological consequences.

Ocean acidification will most likely affect photosynthetic organism in two main ways. Firstly, a reduction in CO₃²⁻ is very likely going to affect the ability of calcifying photosynthetic organisms to build and maintain their carbonate based structures. Secondly, an increase in both CO₂ and HCO₃⁻ may in fact increase primary production, and therefore growth rates, in some species if they are limited by current levels of inorganic carbon. Due to the fact that recent OA review papers (Doney et al. 2009; Guinotte and Fabry, 2008; Wu et al. 2008) have included sections on these topics, the aim of this present review is twofold:

1. To summarize what these reviewers found and concluded, representing our understanding up to 2009 (Tables 1 and 2).
2. To compare what they found with a plethora of studies that have been published after 2009, concentrating on the most commonly studied groups, identifying any trends or highlighting any contradictions, in an attempt to see if our understanding has developed. Work done on coral calcification is not covered in this review. Extensive work is already carried out in this area, and good reviews on this topic exist (Langdon and Atkinson, 2005; Guinotte et al. 2006; Kleypas and Langdon, 2006).

Table 1: Summary of pre-2009 work of changes in calcification in response to increased $p\text{CO}_2$

Organism	Experimental Method	$p\text{CO}_2$ / pH	Results	References	Notes
Coccolithophores					
<i>Emiliania huxleyi</i>	Mesocosm (CO_2)	180-700ppmv	40% ↓	Delille et al. 2005	Delay in onset of calcification by 24-48h
<i>E. huxleyi</i>	Mesocosm (CO_2)	190-710ppmv	↓	Engel et al. 2005	Reduction in weight and coccosphere size
<i>E. huxleyi</i>	Batch Incubations (nutrient replete) (CO_2)	280-750ppmv	87% ↑ PIC	Iglesias-Rodriguez et al. 2008	↑ PIC = ↑ in calcite in coccospheres
<i>E. huxleyi</i>	Field work (box core)		44% ↑	Iglesias-Rodriguez et al. 2008	↑ CaCO_3 per coccolith from 1780-2008 Volume of coccospheres and coccoliths ↑
<i>E. huxleyi</i>	Monospecific cultures (acid/base)	280-750ppmv	15.7% ↓	Riebesell et al. 2000	↓ in CaCO_3 per cell
<i>E. huxleyi</i>	Chemostat cultures (nutrient limited) (CO_2)	400-700ppmv	25% ↓	Sciandra et al. 2003	
<i>Gephyrocapsa oceanica</i>	Monospecific cultures (acid/base)	280-750ppmv	44.7% ↓	Riebesell et al. 2000	↓ in CaCO_3 per cell
Foraminifera					
<i>Orbulina universa</i>	Laboratory culture (acid/base)	700ppmv	14% ↓	Spero et al. 1997; Bijma et al. 1999	↓ in shell weight
Coralline algae					
<i>Porolithon gardineri</i>		560ppmv	25% ↓	Agegian, 1985	

Nearly all organisms tested to date show reduced calcification in response to elevated $p\text{CO}_2$ and decreased carbonate ion concentration and carbonate saturation state. (Modified from Kleypas et al. 2006).

↑ = increase, ↓ = decrease, PIC = particulate inorganic carbon, CaCO_3 = calcium carbonate

Table 2: Summary of pre-2009 work of changes in primary production in response to increased $p\text{CO}_2$

Organism	Experimental Method	$p\text{CO}_2$ / pH	Results	References	Notes
Coccolithophores					
<i>Emiliania huxleyi</i>	Mesocosm (CO_2)	180-700ppmv	No change in net community productivity	Delille et al. 2005	No difference in community respiration
<i>E. huxleyi</i>	Batch Incubations (nutrient replete) (CO_2)	280-750ppmv	114% \uparrow POC	Iglesias-Rodriguez et al. 2008	\uparrow POC = \uparrow POC production
<i>E. huxleyi</i>	Monospecific cultures (acid/base)	280-750ppmv	8.5% \uparrow carbon fixation	Riebesell et al. 2000	\downarrow calcite/POC ratio by 21%
<i>Gephyrocapsa oceanica</i>	Monospecific cultures (acid/base)	280-750ppmv	18.6% \uparrow carbon fixation	Riebesell et al. 2000	\downarrow calcite/POC ratio by 52.5%
Cyanobacteria					
<i>Synechococcus</i>	Semicontinuous cultures (CO_2)	380-750ppmv	No difference in maximum photosynthetic rate	Fu et al. 2007	\uparrow in efficiency of photosystem 2 and chlorophyll a
<i>Prochlorococcus</i>	Semicontinuous cultures (CO_2)	380-750ppmv	Maximum photosynthetic rate unaffected	Fu et al. 2007	No change in any photosynthetic parameters
<i>Trichodesmium</i>	Steady state growth (CO_2)	150-750ppmv	12-128% \uparrow carbon fixation	Hutchins et al. 2007	35-100% \uparrow nitrogen fixation rates
Diatoms					
<i>Thalassiosira weissflogii</i>	Batch cultures (CO_2)	180-1800ppmv	CO_2 uptake and O_2 production rates unaffected	Burkhardt et al. 2001	CO_2 main carbon source at higher $p\text{CO}_2$; \downarrow in carbonic anhydrase activity

<i>Phaeodactylum tricornutum</i>	Batch cultures (CO ₂)	180-1800ppmv	CO ₂ uptake and O ₂ production rates unaffected	Burkhardt et al. 2001	CO ₂ main carbon source at higher pCO ₂ ; ↓ in carbonic anhydrase activity
Seagrasses					
<i>Zostera marina</i>	Grown in 4 litre plastic pots (CO ₂)	8.1- 6.2	3-fold ↑ in photosynthesis	Zimmerman et al. 1997	Amount of light required to maintain plant reduced from 7 to 2.7 hours
<i>Z. marina</i>	Grown in 4 litre plastic pots (CO ₂)	8.1- 6.2	↑ in reproductive output, below ground biomass and vegetative proliferation	Palacios and Zimmerman, 2007	No change in biomass specific growth rates
Macroalgae					
<i>Gracilaria</i> sp	Grown in vessels enriched with nitrogen and phosphorus (CO ₂)	350-1250ppmv	190% ↑ in growth rates	Gao et al. 1993	
<i>Lomentaria articulata</i>	Hydroponic cultures (CO ₂)	350-700ppmv	52% ↑ in daily net carbon gain	Kubler et al. 1999	314% ↑ in wet biomass production rates
<i>Hizikia fusiforme</i>	Grown in aquaria with filtered seawater (CO ₂)	360-700ppmv	50% ↑ in growth rates	Zou, 2005	200% ↑ in nitrate uptake
<i>Porphyra linearis</i>	Cultured in 0.5l (inside) cylinders of 40l tanks (outside) (CO ₂)	8.7- 6.0	↓ in growth rates	Israel et al. 1999	Photosynthetic rates remained uniform between pH treatments

Organisms tested to date show a varied response of primary production to elevated pCO₂, with strong differences between and within groups.

↑ = increase, ↓ = decrease, POC = particulate organic carbon, CaCO₃ = calcium carbonate

The Calcification Response

Biogenic calcification is thought to have evolved sometime during the Cambrian period, due to a sudden rise of Ca^{2+} (Kleypas et al. 2006) in the oceans. It is now a widespread process occurring across a range of animal phyla, used for structural support and protection against predation. The production and sinking of calcareous body parts is important in carbon cycling, generating a continuous rain of calcium carbonate (CaCO_3) to the deep ocean and the sediments. Without a doubt, the most important and abundant producers of CaCO_3 in the oceans are members of the phytoplankton (mainly coccolithophores and foraminifera's), an exception being crustose coralline algae, which are most important in coral reef environments.

Coccolithophores

Recent work indicates that the calcification responses of coccolithophores might be more complex than previously thought. Both Iglesias-Rodriguez et al. (2008) and Shi et al. (2009) showed a trend of increased calcification at elevated $p\text{CO}_2$ in *E. huxleyi*, which contradicts the majority of past studies (Table 1). *E. huxleyi* is regarded as a 'species complex' that is a diverse assemblage of genotypes each with distinct calcification characteristics (Ridgwell et al. 2009). This could be one reason for why a wide range of responses to changes in carbonate chemistry has been reported so far, along with the fact that different methods of culture and culture conditions have been used between studies. There have been contradictory results reported in the literature so far about how OA will affect calcification rates in coccolithophores, which has been put down to strain-specific responses, therefore this hypothesis was examined (Langer et al. 2009). Four strains of *E. huxleyi* (RCC1212, RCC1216, RCC1238 and RCC1256) were exposed to $p\text{CO}_2$ levels from 200-1200ppmv, where differing responses were reported. These results suggest a varying level of sensitivity between strains, which the authors suggested was most likely down to genetic adaptation. Contrary to this study and previous work, Findlay et al. (2011) reported no strain-specific responses in *E. huxleyi*, this was still true irrespective of method of acidification, which as previously mentioned has been suggested as a reason for differences between studies so far. They also proposed that *E. huxleyi* exhibits a plastic response to carbonate conditions and not a pre-determined genetic adaptation as suggested by Langer et al. (2009).

Since 2009, there has been a greater focus on the responses of coccolithophores to OA in combination with other environmental factors, such as increased temperature and ultraviolet radiation (UVR), as these are also predicted to increase in future years. OA exacerbates the effects of UVR; causing an even greater significant decrease in calcification in *E. huxleyi* (Gao et al. 2009). This is most likely related to an increase in UVR penetration negatively affecting the algal cell due to the reduced coccolith thickness under elevated $p\text{CO}_2$, as it has been shown that increased coccolith thickness reduces the negative impacts of UVR (Guan and Gao, 2010). Fiorini et al. (2011) examined the effects of both OA and elevated temperature on *Syracosphaera pulchra*. Prior to this study, the combined effects of these two factors had only been looked at in two strains of *E. huxleyi*, with both studies reporting a decrease in calcification at elevated $p\text{CO}_2$, while a significant temperature effect was observed in only 1 of the 2 strains (Feng et al. 2008; De Bodt et al. 2010). They found that both elevated $p\text{CO}_2$ and temperature, separately or combined, had no significant effect on the content of PIC or POC production, contrasting with work by

Feng et al. (2008), De Bodt et al. (2010) and the majority of pre-2009 work on *E. huxleyi* (Table 1). In contrast to this, a decrease in calcification due to an increase in $p\text{CO}_2$ and temperature, was reported when using a natural North Atlantic spring bloom community, although an increase in $p\text{CO}_2$ alone had no effect (Feng et al. 2009).

Symbiont-bearing foraminiferans

To my knowledge only one study has investigated the calcification responses of symbiont-bearing foraminiferans (SBF's) prior to 2009 (Spero et al. 1997). In recent years, there has been an increase in the work carried out on SBF's because their response to changes in pH was unclear (Fabry et al. 2008). Kuroyanagi et al. (2009) were the first to look at the effects of OA on calcification of large SBF's in the dinoflagellate-bearing species *Marginopora kudakajimensi*. After 10 weeks of culture, they reported a significant decrease in growth rates between a pH range of 8.3-7.7. Although, like Spero et al. (1997), acid was used to lower pH, instead of bubbling CO_2 which better reproduces the present anthropogenic changes and the ocean's response, as it has less impact on total alkalinity, which will not change significantly in the next few decades, and so the results have to be treated with some caution. The authors recognised and built on this by exposing a range of species to elevated $p\text{CO}_2$ levels achieved by bubbling CO_2 (Fujita et al. 2011). They showed that net calcification of large SBF's, *Baculogypsina sphaerulata* and *Calcarina gaudichaudii* (diatom-bearing), which secrete a hyaline shell, increased under intermediate levels of $p\text{CO}_2$ (580-770ppmv), and decreased at a higher $p\text{CO}_2$ level (970 ppmv). However, net calcification of the SBF *Amphisorus hemprichii* (dinoflagellate-bearing), which secretes a porcelaneous shell, tended to decrease at elevated $p\text{CO}_2$. The differences between species are believed to be related to differences in calcification methods and links between calcification and photosynthesis of the symbiont. McIntyre-Wressnig et al. (2011), reported that the test growth of *Amphistegina gibbosa* (diatom-bearing), which has a low magnesium-calcite test, was unaffected by $p\text{CO}_2$ levels up to 2000ppmv. At the same level, *Archaias angulatus* showed greatly reduced test growth. The studies above again show that responses to OA are highly species-specific, and in the case of the SBF's seem to be closely linked to test composition and symbiont type, with evidence so far suggesting that diatom-bearing species may be the most resistant. Further work is needed to test this observation. Even though there was only one study pre-2009, the increase in work in recent years, although providing more information, has not really developed our understanding due to mixed results reported.

Crustose coralline algae

Due to the fact that all previous work (Agegian, 1985; Buddemeier, 2007; Kuffner et al. 2008) has shown a uniform response of decreased calcification with elevated $p\text{CO}_2$ levels, there has been a switch in focus to examining responses to OA in combination with other environmental parameters. Martin and Gattuso (2009) maintained *Lithophyllum cabiochae* in culture for one year at either 400 or 700ppmv at ambient or elevated temperature (+3°C). Temperature was altered throughout the year to match seasonal change in their natural environment. Only during the first month was net calcification significantly reduced under elevated $p\text{CO}_2$ which suggests acclimation. A net decrease of 50% was observed at the end of the summer period when both $p\text{CO}_2$ and temperature were elevated, while no effect was found separately. One important finding was that elevated $p\text{CO}_2$ had a strong effect

on the net dissolution of skeletal tissue increasing it by 200-400%. This, along with necrosis and mortality, which were also observed, meant there was a mean annual net calcification decrease by 90% in *I. Cabiochae*. Gao and Zheng (2010) cultured *Corallina sessilis* at 380ppmv and 1000ppmv with, or without UVR. In the non UVR treatment high $p\text{CO}_2$ caused a decrease in net calcification rates by 25.6%. At the same $p\text{CO}_2$ there was a further inhibition of 8% under UVR. Both these studies agree with previous work, showing a decrease in calcification rates under elevated $p\text{CO}_2$ levels. More importantly, they additionally show that other environmental factors, like elevated temperature and UVR, interact with OA to worsen the situation. This poses a serious threat for the future of coralline algae species as mentioned by Anthony et al. (2008).

Primary production response

At current surface ocean pH, less than 1% of the added CO_2 remains as dissolved CO_2 , while the rest is converted into HCO_3^- (ca. 90%) and CO_3^{2-} (ca.9%). This means that at current pH some photosynthetic organisms may be CO_2 -limited, despite the fact that many species have carbon-concentrating mechanisms that accumulate inorganic carbon, either as CO_2 , HCO_3^- or both (Giordano et al. 2005). Primary production can also take place as nitrogen fixation, which may be enhanced, and could lead to increased total primary productivity in warm, nutrient-poor tropical and subtropical regions. In these regions, continued ocean absorption of anthropogenic CO_2 along with increased thermal stratification of the upper ocean reduces the vertical mixing of nutrients to surface waters (Guinotte and Fabry, 2008).

Calcifiers

With calcifying marine photosynthetic organisms, it is important to note that photosynthesis is linked to calcification, although this relationship still remains unclear. In planktonic species (coccolithophores and foraminiferans), studies suggest they are not coupled (Herfort et al. 2002; Paasche, 1964; Zeebe and Sanyal, 2002), although it has been shown that photosynthesis in SBF's enhances calcification (Anderson and Faber, 1984; Lea et al. 1995). The relationship also remains unclear in benthic calcifiers, even though a number of theories have been put forward (Cohen and McConnaughey, 2003; Gattuso et al. 2000; Goreau, 1959; Muscatine, 1990). In terms of how the relationship responds to elevated $p\text{CO}_2$, so far the evidence shows they vary inversely (Langdon and Atkinson, 2005; Marubini and Davies, 1996; Marubini and Thake, 1999; Riebesell et al. 2000).

Coccolithophores have shown mixed responses. Although their calcification rates decreased, *E. huxleyi* has been shown to have its carbon fixation increased at a pH of 7.9, whereas no difference was found between 7.6 and 8.2 under photosynthetically active radiation alone. However, when UVR was added, a decrease in all pH treatments was measured (Gao et al. 2009). This study shows a similar pattern to Riebesell et al. (2000) and Barcelos e Ramos et al. (2010), and suggests some sort of trade-off between calcification and photosynthesis. However, work by Fiorini et al. (2011) disagrees with these studies, where elevated $p\text{CO}_2$ was shown to decrease organic carbon production. Along with these studies contradicting one another, one study showed differences between strains in organic carbon production (Langer et al. 2009). From recent and past studies it is clear that coccolithophores do not exhibit a uniform response, which again could be down to strain differences.

To my knowledge, the effect of elevated $p\text{CO}_2$ on the primary production of crustose coralline algae has only been investigated in recent years, although despite this our understanding has not really grown, as varied responses have been reported. The temperate species *Corallina sessilis*, was shown to have its net photosynthetic rate significantly decreased at 1000ppmv along with its calcification rates, and this effect was compounded when UVR was present (Gao and Zheng, 2010). Contrary to this, the tropical coralline algae *Hydrolithon* sp., was shown to have its photosynthetic rate enhanced at a pH of 7.8, whilst its calcification rates decreased. This, along with the fact that at high pH values calcification increased whilst photosynthesis decreased, provides evidence that the two processes are not linked (Semesi et al. 2009). Responses again appear to be species-specific and this is enforced by work that showed differences in response between two species within the same genus (*Halimeda*) (Price et al. 2011). Unlike the calcification response to elevated $p\text{CO}_2$, which from the evidence suggests is uniform; the opposite appears to be so for primary production.

Non-calcifiers

Diazotrophic cyanobacteria (dinitrogen-fixers) contribute largely to overall marine primary production, by providing reactive nitrogen to nitrogen-limited regions. The cyanobacterium *Trichodesmium*, was shown to respond positively to elevated $p\text{CO}_2$, with both increased photosynthesis and nitrogen fixation (Kranz et al. 2009), which agrees with previous work (Barcelos e Ramos et al. 2007 and Hutchins et al. 2007). Up until this point, it was uncertain how sensitivity to elevated $p\text{CO}_2$ was affected by other environmental factors. Kranz et al. (2010) examined the response of *Trichodesmium* grown at high and low levels of $p\text{CO}_2$ and light. They found that the $p\text{CO}_2$ -dependent stimulation of organic carbon and nitrogen production was highest at low light, and that high $p\text{CO}_2$ stimulated rates of nitrogen fixation and prolonged duration while light affected only maximal rates. It has been suggested that these positive results could stimulate productivity in nitrogen limited regions, thus providing a negative feedback on rising atmospheric CO_2 levels (Kranz et al. 2009). Not all cyanobacteria species tested, however, have responded positively. The bloom-forming *Nodularia spumigena* showed a decrease in nitrogen fixation rates (Czerny et al. 2009), which could be explained by the contrasting ecological strategies of non-heterocystous (*Trichodesmium*) and heterocystous (*Nodularia*) species.

Macroalgal and seagrass communities perform a range of ecosystem services in shallow coastal systems such as providing food, forming substrata for settlement, offering protection from predators and shelter from disturbances. In the past, the majority of work focused on individual organisms, and the responses have been varied (Table 2). CO_2 enrichment considerably enhanced the relative maximum electron transport rate (photosynthesis) of the seagrass *Thalassia hemprichii* (Jiang et al. 2010), and could be the mechanism responsible for observed increase in photosynthesis of *Zostera marina* by Zimmerman et al. (1997). In recent years, the focus has switched to examine if elevated $p\text{CO}_2$ will increase the potential of phase shifts in assemblages, and what impacts these would have on community structure. The common coral reef seaweed *Lobophora papenfussii*, was shown to have increased growth rates between 400-560ppmv, and between 400-1140ppmv the mortality of the coral *Acropora intermedia* increased threefold due to contact from *L. Papenfussii*. This indicates that coral reefs may become increasingly susceptible to

seaweed proliferation under OA (Diaz-pulido et al. 2011). Connell and Russell (2010) investigated the effects of future $p\text{CO}_2$ levels on kelp forest communities. They found that elevated $p\text{CO}_2$ had no effect on the cover of turf algae at ambient temperatures, but it did increase dry mass. When temperature was increased, however, a synergistic effect was observed which had a positive effect on turf algae abundance, consequently reducing kelp abundance, primarily by negatively impacting kelp recruitment. It seems evident that OA will cause shifts in macroalgal assemblages, and this can be seen presently where natural pH gradients occur (Porzio et al. 2011).

To conclude, compared with calcifiers, there seems to be a larger fraction of species of non-calcifiers, studied both in the past and recently, showing increased rates of photosynthesis as CO_2 is increased above the present atmospheric level. Overall, the effects of OA on primary production are highly species-specific, and are most likely dependent on the physiological aspects such as capability to actively take up inorganic carbon, and the differences between the carbon concentrating mechanisms used.

Summary

In summary, past work has shown that across the range of calcareous and non-calcareous photosynthetic organisms tested, there were no clear patterns regarding the responses of primary production or calcification rates to OA alone. Recent work also shows no clear pattern, and has not increased our understanding of how OA alone will affect marine photosynthetic organisms at an individual level. A wider range of organisms, however, have now been tested, so from that point of view our knowledge has increased. Recent studies give results that both agree and contradict previous work; however this is of little surprise, due to the fact that between these studies there is very little truly comparable data, due to differences in experimental method and species/strains used. To truly understand how OA will affect marine photosynthetic organisms, it is imperative that more comparable data becomes available. This means an agreement must first be reached on the best experimental designs to use (reviewed in Hurd et al. 2009). Advancements in recent years include the increased amount of multi-factorial studies that have taken place combining OA with other factors of climate change. This is important because even though studying the effects of OA is informative, it means little for the future, as OA will not be the only consequence of climate change and so it is important these studies continue.

Another important fact to note, is that all OA studies to date, both short and long term, have really only measured the plastic response of the organism. It is very possible that natural selection over the time scale OA will occur, will lead to different responses to those seen in laboratory experiments. For example, it has been shown by Iglesias-Rodriguez et al. (2008) and Grelaud et al. (2009), with down-cores of sediment, coccolith mass of some species of coccolithophores has increased over the past decades as a response to OA so far. This unexpected result occurs because the fitness benefit of choosing a better-defended, slower growth strategy in more acidic conditions outweighs that of accelerating the cell cycle, as this occurs by producing less calcified exoskeleton (Irie et al. 2010). So in terms of better understanding the calcification response to OA, it may be better to concentrate on this type of work in the future. However, this is not possible when it comes to looking

at the effects on primary production, so for this area of study we are limited to plastic response experiments.

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