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# Future seagrass beds: Can increased productivity lead to increased carbon storage?

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ABSTRACT

While carbon capture and storage (CCS) is increasingly recognised as technologically possible, recent evidence from deep-sea CCS activities suggests that leakage from reservoirs may result in highly $CO_2$ impacted biological communities. In contrast, shallow marine waters have higher primary productivity which may partially mitigate this leakage. We used natural $CO_2$ seeps in shallow marine waters to assess if increased benthic primary productivity could capture and store $CO_2$ leakage in areas targeted for CCS. We found that the productivity of seagrass communities (*in situ*, using natural $CO_2$ seeps) and two individual species (*ex situ*, *Cymodocea serrulata* and *Halophila ovalis*) increased with $CO_2$ concentration, but only species with dense belowground biomass increased in abundance (e.g. *C. serrulata*). Importantly, the ratio of below:above ground biomass of seagrass communities increased fivefold, making seagrass good candidates to partially mitigate $CO_2$ leakage from sub-seabed reservoirs, since they form carbon sinks that can be buried for millennia.



## 1. Introduction

Global emissions of $CO_2$ are predicted to accelerate over the coming decades (Meehl et al., 2007). As ~30% of these emissions are absorbed into the world's marine waters (Feely et al., 2004; Doney, 2010), there is increasing recognition that $CO_2$ is a marine pollutant, defined by the United Nations Convention on the Law of the Seas (UNCLOSs) as "the introduction by man, directly or indirectly, of substances or energy into the marine environment, including estuaries, which results or is likely to result in such deleterious effects as harm to living resources and marine life etc." (UNCLOS, 1982). Indeed, there is clear evidence that marine ecosystems face three combined pressures due to $CO_2$ emissions, those of warming, oxygen loss and ocean acidification (Connell and Russell, 2010; Rodolfo-Metalpa et al., 2011). This recognition has focussed urgent attention on mitigation strategies to reduce the impact of increasing concentrations of carbon dioxide. One such strategy is carbon capture and storage (CCS).

Once carbon dioxide has been captured from either the atmosphere or, more likely, as it is being emitted by industrial point sources (such as coal-fired power stations), one of the strategies already in use and with planned expansion is injection of the captured carbon into geological formations. Indeed, storage for millennia is one of the criteria for categorising a carbon storage technique as being deemed "successful". One of the potential problems with this geological injection is that a percentage of the injected $CO_2$ could seep from storage reservoirs back into the environment, yet estimates of potential leakage are difficult because of the number of factors involved (e.g. location of fractures in the rock bed). Seabed leakage of $CO_2$ could lead to two potential problems; (1) overestimation of the mitigation effectiveness because this carbon is released back into the environment, and (2) adverse impacts on benthic ecosystems (as demonstrated in coral reef and temperate coastal systems; Hall-Spencer et al., 2008; Fabricius et al., 2011). In some locations and cases, however, photosynthetic organisms may be able to capture some of this leakage, not only reducing the overestimation of $CO_2$ mitigation but also limiting the extent of further biological impacts of escaping sequestered $CO_2$ (e.g. the Blue Carbon Strategy; Herr et al., 2012).

Subtidal vegetation is receiving increasing attention as possible natural CCS ecosystems in shallow waters. Seagrass habitats are able to store carbon as some species have root mats which are buried for centuries to millennia (Romero et al., 1994; Mateo et al., 1997). While their slow growth under current environmental conditions means that seagrasses will have a relatively small effect on mitigating global $CO_2$ emissions (e.g. they may only capture ~0.1% of emissions globally; Irving et al., 2011), they may complement geological CCS activities by capturing a proportion of seabed leaks as well as absorbing carbon that enters surface waters from the atmosphere. This role would, however, be contingent on both their ability to survive highly carbonised conditions and become

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increasingly productive in the presence of elevated $CO_2$ at leakage sites (e.g. Vizzini et al., 2010).

Seagrass are generally considered to be $CO_2$ limited and photosynthetically inefficient in seawater (Beer and Koch, 1996; Beardall et al., 1998; Palacios and Zimmerman, 2007) because they are inefficient in utilising bicarbonate ($HCO_3$), which forms the majority of dissolved inorganic carbon, for photosynthesis. As a result, many species will increase their use of $CO_2$ when it is available (Beer and Koch, 1996) and are predicted to increase growth rates and biomass under future $CO_2$ conditions (Palacios and Zimmerman, 2007; Hall-Spencer et al., 2008; Martin et al., 2008). Indeed, it seems that they could be one of the true "winners", as has been seen in locations of elevated $CO_2$ conditions (Hall-Spencer et al., 2008; Martin et al., 2008; Fabricius et al., 2011). In this study, we used three separate tropical volcanic $CO_2$ seeps in Papua New Guinea as natural "laboratories" to assess whether seagrass productivity and biomass increase in response to localised elevation of $CO_2$ concentrations as a proxy for what may occur near locations of CCS activities. These seeps have recently been used to test hypotheses about the structure of marine communities under future conditions, but they also provide a valuable opportunity to test how changes in productivity of these systems may enhance carbon capture at geographically localised extreme pH (e.g. <7). To understand whether biological capture of $CO_2$ may provide a solution to $CO_2$ emissions, we tested the hypothesis that seagrass productivity and biomass increase in response to localised elevation of $CO_2$ concentrations at volcanic seeps in Papua New Guinea. This provides the most accurate mimic for the conditions occurring at CCS leakage sites, and thus paints an ecologically realistic picture of the ecosystem response specifically to CCS leakage.

## 2. Materials and methods

### 2.1. Study sites

Seagrass was sampled along the shallow (0.1–2.0 m, below lowest astronomic tide) shore of three sites, separated by >7 km, in Milne Bay Province, Papua New Guinea (9°45′ S, 150°50′ E): Dobu on the northern coast of Dobu Island, Esa'Ala and Upa-Upasina along the north-eastern and north-western coast of Normanby Island, respectively (see maps in Fabricius et al., 2011), in April 2011. Tidal range in the region is <1 m. Volcanic $CO_2$ seeps acidify the seawater and increase its DIC availability, with seeping being most intense near the shore at <0.5 m depth. Two sampling stations of intermediate to low mean pH were selected at both Esa'Ala and Upa-Upasina and extremely low pH at Dobu and Esa'Ala. Reference stations with normal, relatively stable pH were chosen several hundred meters away from the seeps at comparable geophysical settings.

At all sites 20 quadrats (50 cm × 50 cm) were placed haphazardly within 15 × 3 m survey zones at each station along the $CO_2$ gradients. Within each quadrat the seagrass shoot density was recorded. Above-ground biomass of *Cymodocea serrulata* was cut from four quadrats per site. Samples were placed in individual bags, sun-dried for 48 h and then oven dried at 60 °C for a further 48 h immediately on returning to the laboratory.

In addition, on a previous trip (6–15 August 2010) to Esa'Ala, both above and below ground biomass of all seagrass species present in 15 quadrats was quantified in 15 plots consisting of both haphazardly placed 20 cm × 20 cm quadrats and 15.5 cm diameter cylindrical incubation chambers. Photosynthesis and respiration were measured on August 15 at ~1:00 pm using replicate underwater incubation chambers to assess oxygen evolution over four plots of mixed seagrass communities, both in and outside of a high $CO_2$ area. Winkler titrations on before and after water samples were used to measure photosynthesis by oxygen evolution. Chambers deployed were exposed to normal sunlight (mean 327 $\mu E\ m^{-2}\ s^{-1}$) for ~30 min between the hours of 1:00 and 2:00 pm at a depth of 1–1.5 m. Circulation was continuously provided by 75 ml bulbs pumped every 3 s to provide water movement within the chambers. Tests performed with dye showed that water was circulated within the chamber within 30 s. Plots were then harvested to quantify the amount of epibionts, the shoot density and the above and below-ground biomass of all species present. All quadrats and chamber contents were collected and returned to the boat to allow for detailed quantification. Shoots were counted prior to drying for 24 h in the boat engine room and then shipped back to the lab. Below-ground biomass from high $CO_2$ sites at Esa'Ala was extremely dense, forming large mats of interwoven live and dead rhizomes. For these samples, additional rinsing was performed in the field and in the lab on dried and separated samples which allowed for the dried below-ground biomass to stay on the surface of the rinse water and the sinking of any remaining sediment in the sample. Final drying was performed in a drying oven at 65 °C until a steady mass was obtained.

### 2.2. Carbonate chemistry measurements

A calibrated pH metre was used to measure pH (NBS scale) at each sampling station (Hach or Oakton, two-point calibration, with readings cross-checked against a Tris buffer seawater standard, A.G. Dickson, Scripps Institute of Oceanography, Dixon, Batch 5). Temperature and salinity were also measured alongside each pH reading. Mean pH (calculated via back-transformed hydrogen ion concentrations) were calculated for each station (25th and 29th April 2011, $n = 6–9$). Total alkalinity data for Papua New Guinea used in calculations of the carbon system parameters were taken from Fabricius et al., (2011). Carbon chemistry parameters were derived using the CO2SYS package (Lewis and Wallace, 1998).

### 2.3. Seagrass productivity and respiration incubations

Productivity and respiration incubations were carried out onboard the research vessel for both *C. serrulata* and *Halophila ovalis* at Upa-Upasina in April 2011. Incubations were done using 2 cm sections of leaf for *C. serrulata* and entire leaves for *H. ovalis*. Leaves were cut from their stems and placed in mesh bags at their collection station overnight to ensure that respiration was not over-estimated due to stress responses. Leaves were then collected and placed in sealed 20 ml glass vials which contained water from either reference or high $pCO_2$ water from the collection stations ($n = 6$ leaves per species per station for both productivity and respiration). An additional six vials for each treatment were filled with seawater only as blank controls for both respiration and productivity incubations. Prior to sealing vials, concentration of dissolved oxygen was measured using a luminescent dissolved oxygen optode (HQ10-HQ20 Meters HACH, Hydrolab oxygenmeter, USA). This was repeated at the end of the incubations. Respiration was calculated by subtracting final from initial oxygen concentration. Oxygen production was calculated by subtracting both average oxygen concentration following the respiration incubation and changes in final blank values from each final oxygen reading. All respiration and productivity was standardised to g dry mass of the seagrass leaves. To maintain stable water temperatures (30 °C), vials were placed in 40 L tubs with constant seawater flow-through for the duration of incubations. The water flow in the tubs ensured continual movement and rotation of the experimental vials so that leaves moved inside the vials, stirring the water inside the vials. Respiration incubations were done in blackened tubs, productivity in open tubs, for approximately 2 h between 11:0 am and 3:00 pm. It is important to note that

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end-point measurements of oxygen concentration assume that metabolic processes (respiration and photosynthesis) are linear throughout the incubation period and may underestimate actual rates if metabolic limitations were experienced.

### 2.4. Statistical analyses

Seagrass biomass and shoot density were analysed using two-factor ANOVAs with sites (Dobu, Esa'Ala and Upa-Upasina) and $CO_2$ stations (Reference, Mid-$CO_2$ and High-$CO_2$) treated as random $CO_2$ station nested within site, $n = 4$ plots for biomass and $n = 12$ plots for shoot density. Differences in respiration and productivity were tested using single-factor ANOVAs for $CO_2$ concentration (Reference v. High $CO_2$; fixed), $n = 6$ replicate leaves per $CO_2$ concentration.

## 3. Results

### 3.1. Water chemistry at field locations

The mean $pH_{(NBS)}$ of the reference stations were 8.07, 8.17 and 8.26 (Dobu, Esa'Ala, and Upa-Upasina, respectively), at the mid-$CO_2$ stations 7.88 and 7.85 (Esa'Ala and Upa-Upasina, respectively), and the high-$CO_2$ stations 6.80, 6.98 and 6.90 (Dobu, Esa'Ala, and Upa-Upasina, respectively). While carbonate chemistry parameters differed among sites, in general $CO_2$ and $HCO_3^-$ concentration increased with decreasing pH, while $CO_3^{2-}$ concentration decreased (Table 1).

The mean pH in the productivity and respiration incubations for *C. serrulata* and *H. ovalis* increased during the experiment but retained the relative difference between reference-$CO_2$ (8.03–8.40, start and end of productivity trials, respectively) and high-$CO_2$ (6.31–6.45) stations.

### 3.2. Seagrass density and biomass

Seagrass species showed different responses to increasing $CO_2$ concentrations. Both the shoot density and above-ground biomass of *C. serrulata* increased with elevated $CO_2$ (Fig. 1a and b, and Table 2). The above-ground biomass of *C. serrulata* was greater at high than reference $CO_2$ stations at all three sites, and between the medium and high $CO_2$ stations at Upa-Upasina, but not between the medium and reference $CO_2$ stations at any of the sites (Fig. 1a and Table 2, SNK tests). Shoot density was greater at high $CO_2$ than reference and medium-$CO_2$ stations at all sites, but did not differ between reference and medium-$CO_2$ stations at any of the sites (Figs. 1b and 2 and Table 3). The smallest increase in shoot density was found at Dobu (194% increase) and the greatest at Upa-Upasina (350%) (Fig. 1a). Esa'Ala had the smallest increase in above-ground biomass (32% and 67% for mid- and high-$CO_2$, respectively) with Upa-Upasina increasing by 987% (Fig. 1b). *H. ovalis* abundance was only quantified at Esa'Ala but was an order of magnitude less abundant than *C. serrulata* and showed the opposite relationship to $CO_2$, with shoot density decreasing from reference (mean ± SE; 189 $m^{-2}$ ± 48.9) to high-$CO_2$ (93 $m^{-2}$ ± 45.6) stations at Esa'Ala.

While we do not have below-ground biomass data at all sites, at Esa'Ala the ratio of below- to above-ground biomass of all seagrass

**Table 1**
Seawater carbonate chemistry measurements for Dobu (D), Esa'Ala (E) and Upa-Upasina (U), R = reference station, M = medium $CO_2$ station, H = high $CO_2$ station. Temperature (range 27.6–28.4 °C), pH and salinity (34.5 ppt) were measured in April 2011. The pH and total alkalinity (median $A_T$ values taken from Fabricius et al. (2011)) were used to calculate the remaining parameters using the CO2SYS programme (using the constants of Mehrbach et al. (1973) refit by Dickson and Millero (1987)).

| Site & station | pH range (NBS scale) | $A_T$ (μmol $kg^{-1}$) | $TCO_2$ (μmol $kg^{-1}$) | $CO_3^{2-}$ (μmol $kg^{-1}$) | $HCO_3^-$ (μmol $kg^{-1}$) |
|---|---|---|---|---|---|
| D–R | | | | | |
| Max | 8.2 | 2296 | 1963 | 235 | 1718 |
| Mean | 8.07 | | 2039 | 186 | 1838 |
| Min | 8.03 | | 2061 | 173 | 1871 |
| D–H | | | | | |
| Max | 7.08 | 2267 | 2403 | 23 | 2210 |
| Mean | 6.8 | | 2576 | 12 | 2237 |
| Min | 6.66 | | 2707 | 8 | 2245 |
| E–R | | | | | |
| Max | 8.24 | 2288 | 1935 | 248 | 1677 |
| Mean | 8.17 | | 1978 | 220 | 1747 |
| Min | 8.03 | | 2056 | 170 | 1869 |
| E–M | | | | | |
| Max | 8 | 2298 | 2081 | 161 | 1902 |
| Mean | 7.88 | | 2137 | 128 | 1985 |
| Min | 7.74 | | 2194 | 96 | 2062 |
| E–H | | | | | |
| Max | 7.29 | 2298 | 2351 | 36 | 2208 |
| Mean | 6.98 | | 2491 | 18 | 2253 |
| Min | 6.43 | | 3082 | 5 | 2285 |
| U–R | | | | | |
| Max | 8.32 | 2296 | 1890 | 283 | 1600 |
| Mean | 8.26 | | 1931 | 256 | 1665 |
| Min | 8.21 | | 1963 | 236 | 1717 |
| U–M | | | | | |
| Max | 7.95 | 2316 | 2124 | 147 | 1956 |
| Mean | 7.85 | | 2168 | 120 | 2021 |
| Min | 7.83 | | 2177 | 116 | 2032 |
| U–H | | | | | |
| Max | 6.96 | 2319 | 2527 | 17 | 2276 |
| Mean | 6.9 | | 2565 | 15 | 2281 |
| Min | 6.87 | | 2586 | 14 | 2284 |

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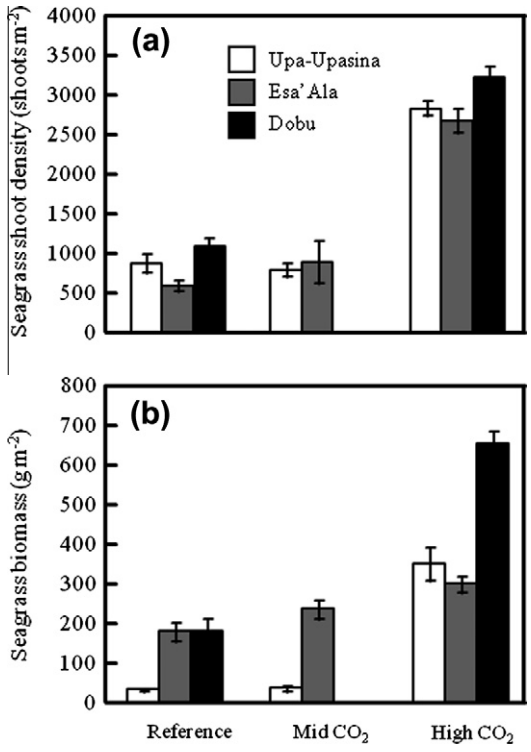


**Fig. 1.** (a) Shoot density (shoots $m^{-2}$) and (b) above-ground biomass (g $m^{-2}$) of *Cymodocea serrulata* at Reference-, Mid- and High-$CO_2$ stations at Dobu, Esa'Ala and Upa-Upasina. Note that densities were not recorded for mid-$CO_2$ at Dobu. Error bars indicate standard error of the mean.

**Table 2**
The above-ground dry mass (g $m^{-2}$) of *Cymodocea serrulata* at different sites (Dobu, Esa'Ala and Upa-Upasina) and $CO_2$ stations (Reference, Mid-$CO_2$ and High-$CO_2$) as detected by two factor ANOVA. Sites and $CO_2$ station were treated as random with $CO_2$ station nested within site. Note that there was no mid-$CO_2$ station at Dobu. Significant *p*-values in bold.

| Source | *df* | *MS* | *F* | *p* |
|---|---|---|---|---|
| Site | 2 | $1.8 \times 10^5$ | 1.24 | 0.365 |
| $CO_2$ station (site) | 5 | $1.5 \times 10^5$ | 55.28 | **0.001** |
| Residual | 24 | 2695.7 | | |

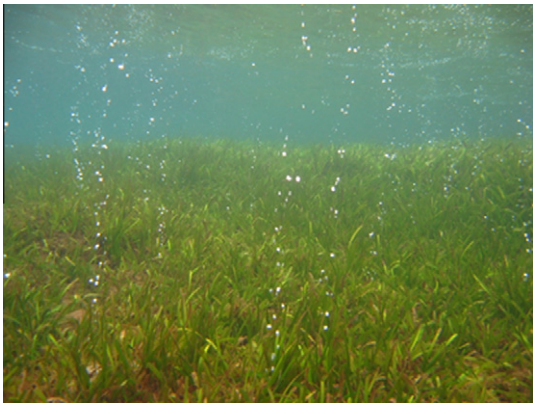

**Fig. 2.** The seagrass bed at the mid-$CO_2$ station at Upa-Upasina. Note the bubbles of $CO_2$ seeping through the seabed, much like could be expected with CCS leakage.

species increased from 3.1 ± 0.47 (mean ± SE) at the reference station to 16.4 ± 2.57 at the high $CO_2$ station. This increase in ratio reflects the increase in mean below-ground biomass increasing from 342 ± 43 g $m^{-2}$ to 1630 ± 110 g $m^{-2}$ from the reference to high $CO_2$ sites, respectively, and indicates that the increased productivity associated with high [$CO_2$] disproportionately increases accumulation of below-ground biomass.

**Table 3**
The shoot density (shoots $m^{-2}$) of *Cymodocea serrulata* at different sites (Dobu, Esa'Ala and Upa-Upasina) and $CO_2$ stations (Reference, Mid-$CO_2$ and High-$CO_2$) as detected by two factor ANOVA. Sites and $CO_2$ station were treated as random with $CO_2$ station nested within site. Note that there was no mid-$CO_2$ station at Dobu. Significant *p*-values in bold.

| Source | *df* | *MS* | *F* | *p* |
|---|---|---|---|---|
| Site | 2 | $4.64 \times 10^6$ | 0.26 | 0.780 |
| $CO_2$ station (site) | 5 | $1.77 \times 10^7$ | 101.77 | **0.001** |
| Residual | 84 | $1.73 \times 10^5$ | | |

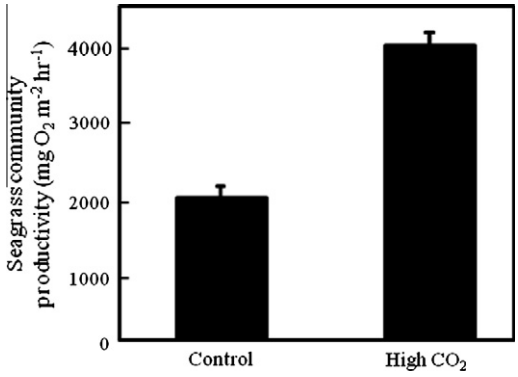


**Fig. 3.** The net primary productivity (mg $O_2$ $m^{-2}$ $h^{-1}$) of all species of seagrass measured using *in situ* field respirometry chambers under Reference v. High $CO_2$ concentrations at Esa'Ala. Incubations were done at mid-day for ~30 min with mean light levels of 327 μE $m^{-2}$ $s^{-1}$. Error bars indicate standard error of the mean.

### 3.3. Photosynthesis

The seagrass community at Esa'Ala showed elevated photosynthetic rates during *in situ* experiments, with rates of net production almost twice as high as those under normal $CO_2$ conditions. Mean net primary productivity (NPP) within *in situ* incubation chambers deployed at Esa'Ala was greater under high $CO_2$ (mean ± SE; 4094 ± 136 mg $O_2$ $m^{-2}$ $h^{-1}$) than reference (2059 ± 153 mg $O_2$ - $m^{-2}$ $h^{-1}$) site (Fig. 3, $F_{1,9} = 94.56$ and $p < 0.005$). In the *ex situ* productivity measurements, both *C. serrulata* and *H. ovalis* showed a positive relationship between NPP and $CO_2$ concentration (Fig. 4a and b). In *C. serrulata*, there was a 26% increase in NPP ($F_{1,10} = 3.81$, $p < 0.05$) under high $CO_2$ conditions, as well as a 20% reduction in respiration (Fig. 3a; $F_{1,10} = 10.95$, and $p < 0.05$). *H. ovalis* demonstrated a greater response to increased $CO_2$ concentration, with NPP increasing 189% ($F_{1,10} = 66.43$, $p < 0.01$), but no change in respiration (Fig. 3b; $F_{1,10} = 1.04$, $p > 0.05$). The increase in NPP in *H. ovalis* was therefore due to an increase in productivity *per se*, with GPP almost doubling ($F_{1,10} = 118.57$, $p < 0.005$).

## 4. Discussion

There is global interest in techniques that allow the capture and store carbon dioxide. These methods range from injection of liquefied $CO_2$ into the deep ocean or geological reservoirs (Bachu, 2008; Chalmers and Gibbins, 2010) to biological capture through planting of terrestrial forests or, more recently, marine vegetation (Laffoley et al., 2009; Pidgeon, 2009). Here, we demonstrate that one type of marine vegetation, seagrasses, can increase productivity and biomass under elevated $CO_2$ concentrations. While current estimates suggest that seagrasses could only capture 0.1% of

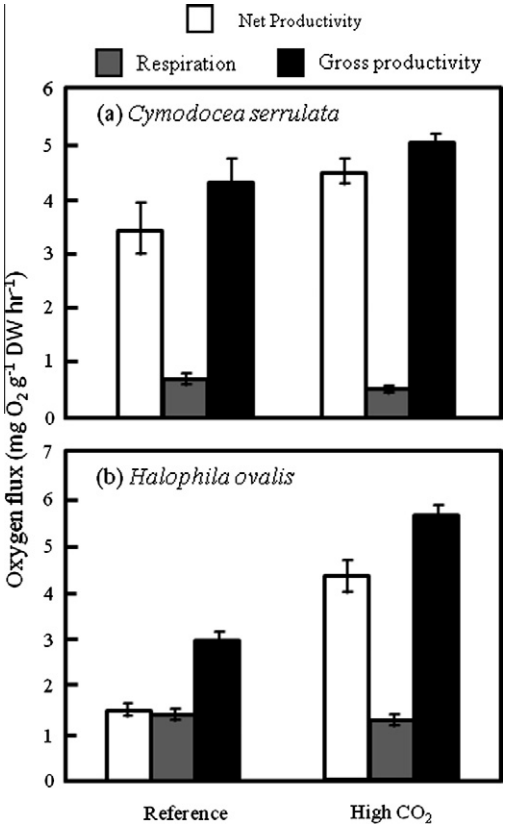


**Fig. 4.** The gross and net primary productivity and respiration (mg $O_2$ flux $g^{-1}$ DW $h^{-1}$) of (a) *Cymodocea serrulata* and (b) *Halophila ovalis* in *ex situ* productivity incubations under different reference and high-$CO_2$ concentrations at Upa-Upasina. Error bars indicate standard error of the mean.

annual global $CO_2$ emissions (Irving et al., 2011), the up to 200% increase in productivity shown by seagrass in our experiments could be used to supplement and improve the efficacy of other CCS strategies, such as near-shore geological injection, by mitigating some of the losses from leakage back into the atmosphere. We are not suggesting that these seagrass beds would capture all of the carbon leakage, but rather that they could help to slightly improve the efficiency of geological storage of carbon dioxide. Further, the capacity for seagrasses to capture carbon is quantifiable, so actual losses of $CO_2$ from geological storage facilities could be calculated. Importantly, this increase in productivity and growth response is greatest at the extreme pH close to $CO_2$ seeps (tropical waters, this study; temperate waters, Hall-Spencer et al., 2008; Martin et al., 2008), similar to conditions that could be expected from leakage of CCS.

Increased productivity and growth of marine primary producers under elevated concentrations of $CO_2$ is being recognised for an increasing number of taxa (e.g. brown algae, Hurd et al., 2009; Connell and Russell. 2010; Johnson et al., 2012; symbiotic foraminifera, Uthicke and Fabricius, 2012). For these taxa, however, this increased productivity and biomass is quickly recycled back into the environment through consumption, respiration and detrital pathways, meaning that they have little overall effect on the carbon cycle. This is also true of above-ground biomass in benthic vegetation such as seagrasses. In contrast, the below-ground biomass of primary producers with root systems can be buried for centuries to millennia (Romero et al., 1994; Mateo et al., 1997). Importantly, this biological storage is on a similar time-scale to that proposed for the injection of captured carbon into rock formations. Therefore, while capture of atmospheric carbon by seagrasses is beneficial in its own right, the increased rate of capture and below-ground storage under extremely low pH conditions (e.g. <7 seen in this study) could mitigate some localised carbon leakage from other CCS activities in the photic zone of the ocean (often <50 m).

Both seagrass community NPP and biomass increased with proximity to the $CO_2$ seeps, yet this effect was not even across all species. Productivity of both *H. ovalis* and *C. serrulata* increased with $CO_2$ concentration, yet of the two, only *C. serrulata* increased in abundance closer to the seeps. This differential response may not be physiological, however, but rather a reflection of the competitive abilities of the two species. *H. ovalis* is an early-successional species which forms sparse root rhizome structures compared to *C. serrulata* which is later-successional and under elevated $CO_2$ conditions formed extremely dense and deep root mats. The species which seem to demonstrate the greatest increase in biomass are those which form dense beds and have large mats of below-ground biomass. Indeed, the mass of below-ground biomass may have been underestimated by some of the collection methods used in this study. While the dense below-ground biomass tends to trap more sediment, thus potentially elevating measures of below-ground biomass, the rhizomes extended vertically into the sediment to depths that exceeded the ability to collect them with the coring methods used, thus potentially underestimating the degree of below-ground biomass amassing at depth. Importantly, the depth of the root mass adds to accretion and the length of time that this biological material is buried, effectively storing the captured carbon.

In other research, medium-term mesocosm experiments have also demonstrated increases in seagrass below ground biomass in response to $CO_2$ enrichment. For example, *Zostera marina* showed greater reproductive outputs, increases in below-ground biomass and shoot density to increased $CO_2$ over a 1 year experiment (Palacios and Zimmerman, 2007). Positive photosynthetic responses to $CO_2$ enrichment have also been observed in *Posidonia oceanica*, *Cymodocea nodosa* and *Phyllospadix torreyi* (Invers et al., 2001). Not unlike *C. serrulata* in this study, at temperate $CO_2$ seeps *P. oceanica* increased in not only biomass but also in relative abundance (Hall-Spencer et al., 2008). While such dominance by one species may reduce seagrass community richness, from a carbon storage perspective this shift is beneficial as these species form thick root mats which in the absence of human disturbance can remain buried for millennia (Romero et al., 1994; Mateo et al., 1997).

The general consensus appears to be that seagrass photosynthesis is DIC limited under contemporary $CO_2$ conditions because of inefficient use of $HCO_3$ (Durako, 1993; Beer and Koch, 1996; Invers et al., 2001), which is readily abundant compared to dissolved $CO_2$ (Table 1). In contrast, some experiments have suggested that some species of seagrass, such as *C. serrulata*, are carbon saturated at current $pCO_2$ and that elevated concentrations $CO_2$ may not enhance productivity (Schwarz et al., 2000). We show, however, that primary productivity in *C. serrulata* in PNG does increase under elevated $CO_2$ conditions. What we cannot determine from our study is whether this increased productivity is a result of release from carbon limitation experienced under current $pCO_2$ conditions or increased GPP by down-regulating the carbon concentrating mechanisms (CCMs) and increased use of $CO_2$ in photosynthesis (Beardall et al., 1998). As such, increased productivity could be driven by a decrease in metabolic cost of photosynthesis rather than an increase in photosynthesis *per se*. Regardless of the mechanism, however, this increase in productivity is likely to increase in the coming century as $CO_2$ concentration increases with elevated temperatures, subsequently altering metabolic rates (Collier et al., 2012).

Habitat-formers, or biogenic habitats, are well known to modify the immediate physical environment in which they occur, potentially resulting in increased physical habitat and improved chemical conditions (i.e. $CO_2$ draw-down from photosynthesis).

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Importantly, habitat-formers are renowned for reducing the harshness of environmental stress across physical gradients to allow colonisation by organisms that would otherwise be excluded (Crain and Bertness, 2006). It appears that seagrass meadows may be one of the few marine ecosystems that may benefit from increasing concentrations of $CO_2$ and the resulting ocean acidification (c.f. coral reefs, Fabricius et al., 2011). The increase in productivity, biomass and coverage of the benthos by seagrass has the potential to positively influence the diverse range of organisms which rely on these primary habitats. Indeed, there is increasing recognition of the importance of the cascade of positive effects that habitat forming species, such as seagrass, can create throughout ecosystems, facilitating greater biodiversity and energy flows (Stachowicz, 2001; Thomsen et al., 2010). Not only will this increase in productivity enhance energy flows within systems, but seagrass photosynthetic activity can increase surrounding seawater pH by >1 pH units by uptake of $CO_2$ (Semesi et al., 2009). This ability to of benthic communities to regulate the coastal $CO_2$ chemistry has been well demonstrated (Smith and Key, 1975; Kleypas et al., 2011; Uddin et al., 2012) and in light of the results presented here has the potential to substantially increase as $CO_2$ fertilisation from either atmospheric $CO_2$ or from CCS leakage increases. This localised influence on pH has also been recognised in other systems. For example, large stands of canopy-forming algae may have the capacity to buffer against some of the negative effects associated with increased concentrations of carbon dioxide and reduced pH (Middelboe and Hansen, 2007; Hurd et al., 2009), meaning that this effect may be more widespread across marine primary producers than initially anticipated. While this buffering effect is likely to be over small spatial scales, probably only meters to ten's meters, the effect may be disproportionately positive on species which inhabit these locations, particularly during pH susceptible life-stages (e.g. larvae and juveniles) of calcareous species.

## 5. Conclusions

There is increasing evidence, especially from recent ecosystem-based studies at both temperate (Hall-Spencer et al., 2008; Porzio et al., 2011; Arnold et al., 2012) and tropical $CO_2$ seeps (Fabricius et al., 2011), that some marine primary producers are not only likely to survive under forecasted high $CO_2$ conditions but benefit from them. Not only does this knowledge allow us to plan for the future in terms of which habitat formers will be available to provide refugia for other species (e.g. fish and shellfish) but also allows us to assess locations which will allow biological capture of some CCS leakage. With an increasing body of literature demonstrating the negative effects of increasing $CO_2$ concentrations on habitat forming species, such as reef building corals (Fabricius et al., 2011), issues of leakage from CCS activities are likely to be viewed very negatively. In contrast, we provide information that under the correct circumstances and in the correct locations, not only may some of these negative effects be partially mitigated, but some of this leakage may be captured biologically, increasing the efficacy of the CCS activities.

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