

2017

Addressing calcium carbonate cycling in blue carbon accounting

Peter I. Macreadie

Oscar Serrano
Edith Cowan University

Damien T. Maher

Carlos M. Duarte

John Beardall

Follow this and additional works at: <https://ro.ecu.edu.au/ecuworkspost2013>



Part of the [Oceanography Commons](#)

10.1002/lol2.10052

Macreadie, P. I., Serrano, O., Maher, D. T., Duarte, C. M., & Beardall, J. (2017). Addressing calcium carbonate cycling in blue carbon accounting. *Limnology and Oceanography Letters*, 2(6), 195-201.

<https://doi.org/10.1002/lol2.10052>

This Journal Article is posted at Research Online.

<https://ro.ecu.edu.au/ecuworkspost2013/5395>

ESSAY

Addressing calcium carbonate cycling in blue carbon accounting

Peter I. Macreadie ^{1,*} Oscar Serrano ² Damien T. Maher ³ Carlos M. Duarte ⁴ John Beardall⁵

¹School of Life and Environmental Sciences, Centre for Integrative Ecology, Deakin University, Burwood, Victoria, Australia; ²School of Science & Centre for Marine Ecosystems Research, Edith Cowan University, Joondalup, Western, Australia, Australia; ³Southern Cross Geoscience, Southern Cross University, Lismore, New South Wales, Australia; ⁴Red Sea Research Center, King Abdullah University of Science and Technology, Thuwal, Saudi Arabia; ⁵School of Biological Sciences, Monash University, Clayton, Victoria, Australia

Scientific Significance Statement

There is considerable interest in measuring the capacity of the world's ecosystems to trap and store excess atmospheric carbon dioxide to mitigate human-induced climate change. Blue carbon describes the carbon storage potential of vegetated coastal ecosystems including tidal marshes, mangroves, and seagrasses. Efforts are now underway to include blue carbon in global carbon offset schemes by managing these ecosystems to enhance carbon sequestration by focusing on their effect on organic carbon processing. However, it is unclear what role inorganic carbon processing in blue carbon ecosystems plays in their overall carbon sequestration. Here, we argue that there are key uncertainties that will need to be addressed before we can account for this important process to more accurately estimate carbon offsets in blue carbon ecosystems.

The white elephant in the blue carbon room

The capacity of the world's ecosystems to sequester carbon dioxide (CO₂) is a major focus of research guiding conservation and restoration of these natural sinks to help mitigate climate change. Seven years ago the term “blue carbon” was coined to describe the disproportionately large organic carbon storage potential of coastal vegetated ecosystems (Nellemann et al. 2009). Efforts are now underway to include blue carbon ecosystems (tidal marshes, mangrove forests, and seagrass meadows) into global carbon offset schemes, focused on their optimal management to enhance CO₂ sequestration as well as minimize CO₂ emissions that result from disturbance (Macreadie et al. 2017).

However, the focus on organic carbon (IPCC 2007; Nellemann et al. 2009) in blue carbon ecosystems has left the globally significant process of calcium carbonate (CaCO₃)

production and dissolution unaccounted for, despite calcium carbonate cycling having been key drivers of changes in climate over Earth's history (Falkowski et al. 2000). Calcium carbonate production runs counter (i.e., an atmospheric CO₂ source) to the effects of organic carbon production (CO₂ sink through photosynthesis), because in the oceans calcification increases *p*CO₂ (by depleting CO₃²⁻ and therefore reducing total alkalinity, “TA”), which facilitates the return of CO₂ to the atmosphere (Frankignoulle et al. 1994; Zeebe and Wolf-Gladrow 2001). Specifically, for every mole of CaCO₃ precipitated, two moles of TA and one mole of DIC are consumed, resulting in increased *p*CO₂ and potential flux to the atmosphere (Fig. 1).

Hence, calcium carbonate production could represent a process that—depending on the timescale (Archer et al. 1998)—exacerbates climate change and/or fuels ocean acidification, whereas calcium carbonate dissolution would act as a CO₂ sink. Timescales are important to bear in mind; overall climate impacts resulting from such changes are predicted to be minor over the new few centuries, especially when compared to the influence of anthropogenic CO₂ emissions; however, the effects are expected to be significant in the long-term (Tyrrell 2008). Of immediate relevance, however, is how calcium carbonate cycling (i.e., precipitation and dissolution) is treated in national and global blue carbon

*Correspondence: p.macreadie@deakin.edu.au

Author Contribution Statement: All authors contributed extensively to the work presented in this paper.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Table 1. “Back-of-the-envelope” estimates of C fluxes in seagrass ecosystems based on the balance between their organic carbon accumulation (CO₂ sink) and inorganic carbon accumulation (CO₂ source) rates.

	Mean	SD	Max	Min	References
PIC accumulation (g C m ⁻² yr ⁻¹)	126.3	31.5	157.8	94.8	Mazarrasa et al. (2015)
POC accumulation (g C m ⁻² yr ⁻¹)	138.0	38.0	176.0	100	McLeod et al. (2011)
Net CO ₂ sequestration (g C m ⁻² yr ⁻¹)	58.4		116.3	0.59	This study*
Global seagrass area (m ²)	3.9E+11		6.0E+11	1.8E+11	McLeod et al. (2011)
Global net CO ₂ sequestration (Tg C yr ⁻¹)	22.6		69.8	0.1	This study†

* Calculated by multiplying the PIC accumulation rate by 0.63 to meet the assumption that 0.63 moles of CO₂ is released per mole of CaCO₃ precipitated, then deducting this adjusted PIC value from the POC accumulation rates to get net CO₂ sequestration.

† Calculated by multiplying net CO₂ sequestration by global seagrass area.

Table 2. Uncertainties in the dynamics of calcium carbonate and organic carbon cycling within blue carbon ecosystems and research questions that will need to be addressed in order to account for those uncertainties.

	Uncertainties	Research questions	References
1	Stoichiometry and fate of CO ₂ fluxes during calcium carbonate cycling are unknown for blue carbon ecosystems	Is CO ₂ release during calcification buffered by metabolic processes (i.e., photosynthesis) and physical processes (e.g., tides, waves)?	Frankignoulle et al. (1994), Russell et al. (2013), Cox et al. (2016)
2	Varying temporal scales for preservation of organic carbon and calcium carbonate	What are the decay rates of calcium carbonate and organic carbon pools, and at what depth/age should organic carbon accumulation be considered a long-term sink?	Mazarrasa, et al. (2015), Burdige (2007), Maher et al. (2017)
3	The presence of geogenic calcium carbonates could lead to an overestimation of calcification rates	What proportions of the calcium carbonate pool are made up of geogenic calcium carbonate (fossil) and biogenic calcium carbonate (recent)?	Zamanian et al. (2016)
4	Calcium carbonate production may enhance sediment accumulation, organic carbon deposition, and preservation	Are there positive feedbacks between the accumulation of calcium carbonates and organic carbon?	McLeod et al. (2011), Le Quere, et al. (2016), Gattuso et al. (1998)
5	The net impacts of climate change on calcium carbonate precipitation/dissolution are not known	How will future climate change scenarios (ocean acidification, rising temperatures, and sea level rise) affect organic carbon and calcium carbonate cycling?	Gattuso et al. (1998)

accounting, and in quantifying the importance blue carbon ecosystems in climate change mitigation.

Current blue carbon offset schemes focus solely on organic carbon, ignoring calcium carbonate cycling. Further, there has been a rapid expansion of scientific literature on blue carbon, with minimal attention paid to the importance of calcium carbonate precipitation and burial. Yet some blue carbon ecosystems, particularly tropical seagrass meadows, are hotspots for calcium carbonate production owing to their provision of 3D habitat for calcifying organisms (Mazarrasa et al. 2015) (Fig. 2). Indeed, coastal sediments can hold

enormous quantities of calcium carbonate accumulated over geological time scales (e.g., the White Cliffs of Dover). The burning question is how accounting for the balance between calcium carbonate production and dissolution, i.e., net calcium carbonate production, in blue carbon ecosystems affects estimates of their CO₂ sink capacity based on organic carbon sequestration? And, importantly, how will the balance of calcium carbonate production and dissolution and its effects on blue carbon budgets change in the future as oceans warm and absorb anthropogenic CO₂ emissions? It has been demonstrated already that shallow-water oceans are

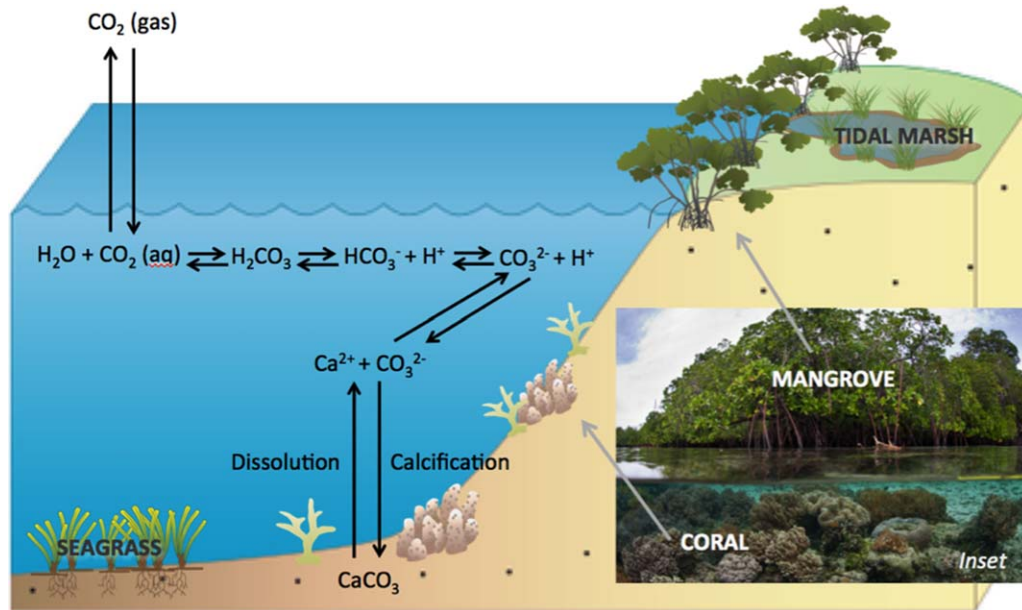


Fig. 1. Conceptual diagram showing the chemical reactions involved in CO_2 exchange between the air and coastal ocean, including the production (calcification) and dissolution of calcium carbonate (CaCO_3). Blue carbon ecosystems (seagrasses, mangroves, and tidal marshes) often occur in close proximity to sites with high rates of calcium carbonate cycling (e.g., coral reefs – see inset), resulting in interactions between the organic (blue) and inorganic (carbonate) cycles. Inset photo credit: Ethan Daniels/Shutterstock. Conceptual diagram produced using the Integration and Application Network (IAN), University of Maryland, Center for Environmental Science, Cambridge, Maryland.

particularly dynamic and can switch between acting as an atmospheric CO_2 source or sink depending on human activities (Andersson and Mackenzie 2004). Biogenic production of calcium carbonate is expected to decrease by 42% by 2100 due to declining carbonate saturation states of surface ocean waters (Andersson et al. 2003, 2005). The overall influence of the latter on climate will be relatively minor compared to anthropogenic emissions, but nevertheless should be taken into account in carbon budgets now, and into the future.

Taking sinks of seagrass soil organic carbon burial into account (ranging between 100 and 176 g C organic $\text{m}^{-2} \text{yr}^{-1}$; McLeod et al. 2011) and sources of non-organic carbon (net calcium carbonate deposition; ranging between 95 and 158 Tg C inorganic yr^{-1} ; Mazarrasa et al. 2015), seagrass meadows seem to constitute a net sink of CO_2 (ranging from 0.59 g C $\text{m}^{-2} \text{yr}^{-1}$ to 116 g C $\text{m}^{-2} \text{yr}^{-1}$) (Table 1). After accounting for release of CO_2 after calcification, our estimates suggest that seagrass meadows worldwide accumulate CO_2 at a mean rate of 22.6 Tg C yr^{-1} , which is about half of the accumulation potential accounting for organic carbon alone. It is important to note that the net drawdown of CO_2 by seagrasses and other blue carbon ecosystems will only offset a small fraction of anthropogenic CO_2 emissions ($\sim 0.23\%$ based on ~ 10 Pg C emitted per year; Le Quere et al. 2016), regardless of whether calcium carbonate cycling is taken into account. This is not to say that blue carbon should be ignored in climate change mitigation efforts, but that it should be considered as one of many strategies

necessary to limit temperature increase, which must involve an important reduction of emissions. This includes avoided emissions from destruction of blue carbon ecosystems, which is estimated to release about 0.04–0.28 Pg C per year (0.42–2.83% of global emissions) (Pendleton et al. 2012).

The wide range of values reported above and in Table 1 highlight the large uncertainty associated with current estimates of organic carbon burial, calcium carbonate burial, and even seagrass area. Therefore, caution should be exercised when interpreting these results. For example, the values reported by Mazarrasa et al. (2015) assumed that all calcium carbonate present in seagrass soils was biogenic, thereby ignoring the presence of calcium carbonate within the mineral matrix. Indeed, whereas organic carbon density drops substantially in sediments outside seagrass meadows, calcium carbonate density remains elevated, suggesting that calcium carbonate loads in sediments are not the sole result of calcification processes in seagrass meadows (Mazarrasa et al. 2015). Currently, these estimates can be useful to highlight the potential importance of calcium carbonate cycling within blue carbon ecosystems for carbon accounting and crediting, but are susceptible to large changes as the uncertainties pointed out are yet to be clarified. Determining calcification rates for a given blue carbon ecosystems using DIC and TA measurements, as well as actual rates of net community calcification, will help to determine the relative importance of the organic to inorganic carbon cycle, while also avoiding erroneous calcification estimates based on geogenic

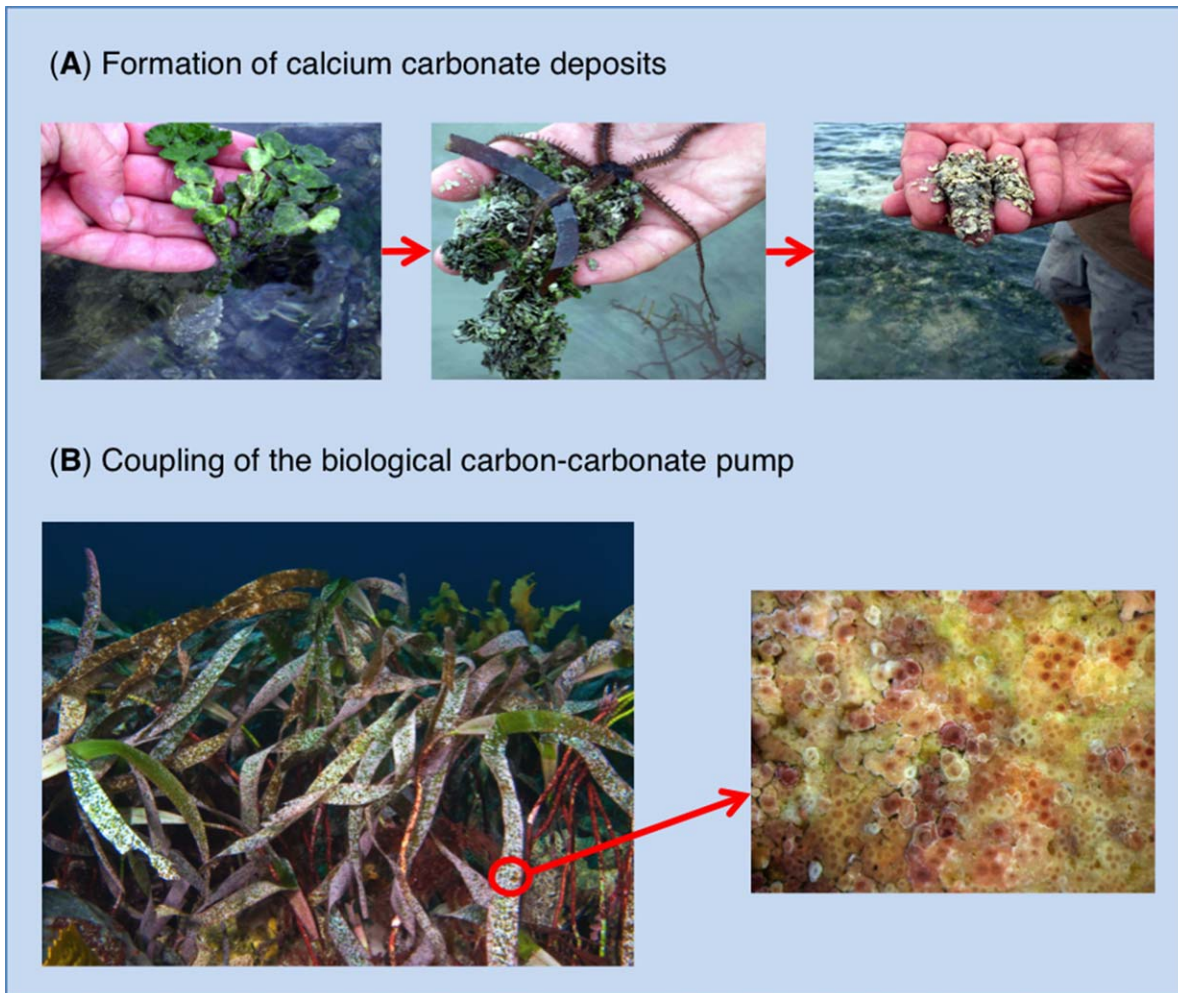


Fig. 2. (A) The calcifying green alga *Halimeda* showing various stages of thallus deterioration, from a healthy algae (left), through dead and partially disintegrated thalli (center) to the calcium carbonated tissues giving rise to gravel and sand in some tropical ecosystems (right); and (B) coupling of the biological carbon-carbonate pump. Here, carbonate-forming algae growing on seagrass *Thalassodendron pachyrhizum*, increase pCO₂ through calcification which may then enhance seagrass photosynthesis resulting in a positive feedback that could potentially avoid an atmospheric fate of the CO₂ released during calcification. Photos by Sven Beer (top row) and John Huisman (bottom row).

carbonates. On the other hand, however, translating short-term calcification rates into long-term calcium carbonate burial would be prone to error due to the potential for dissolution and temporal variability in calcification.

How should we deal with calcium carbonates in blue carbon science?

We maintain that calcium carbonate production should be accounted when estimating carbon sequestration potential of blue carbon ecosystems. But how? If calcium carbonate production is a net source of CO₂, then the release of CO₂ from calcium carbonate production should be subtracted from organic matter sequestration. For example, simply accounting for the ratio of OC : IC burial, the stoichiometry associated with the buffering of the CO₂ released during calcification (i.e., the assumption that 0.63 moles of CO₂ are released per

mole of CaCO₃ precipitated) and the decay of buried OC over time is a good starting point (Fig. 3). While seemingly simple, this accounting approach relies on complex assumptions that need be resolved.

In Table 2, we summarize five key uncertainties and questions that need be resolved in order to properly account for calcium carbonate cycling in blue carbon ecosystems. These range from equilibrium assumptions about CO₂ exchange between the land and sea (Smith 2013), to the extent to which blue carbon ecosystems utilize the higher CO₂ concentrations as a result of calcium carbonate production offsetting atmospheric CO₂ release (McConnaughey and Whelan 1997; Invers et al. 2001; Schneider and Erez 2006; Semesi et al. 2009).

The stoichiometry of the calcification reaction (Fig. 1) in coastal environments is complicated due to the buffering

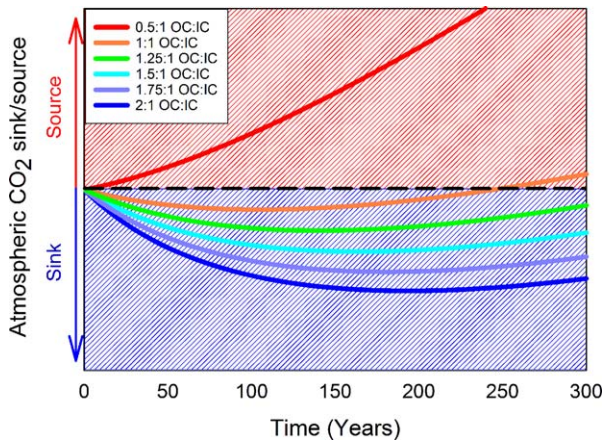


Fig. 3. Model of net atmospheric CO_2 sink associated with different ratios of organic carbon : inorganic carbon (OC : IC) burial. The model assumes a decay rate for OC of 0.0056 yr^{-1} (Serrano et al., 2016), no dissolution of calcium carbonates, and assumption of 0.63 moles of CO_2 released per mole of calcium carbonate precipitated.

effect in seawater (Frankignoulle et al. 1995), leading to less than 1 mole of CO_2 being released to seawater due to the reaction of CO_2 with bases in the water. This ratio has been estimated as ~ 0.63 under current atmospheric CO_2 concentrations (i.e., net emission of 0.63 mole CO_2 for every mole of CaCO_3 precipitated), and oceanic DIC and TA concentrations and is predicted to increase with increasing atmospheric CO_2 concentrations. Indeed, the natural variability in calcium carbonate dynamics (i.e., CO_2 emissions related to calcification) in blue carbon systems is largely driven by tidal, seasonal, and diurnal metabolic processes. Moreover, there is uncertainty in the fate of CO_2 released after calcification, which could determine whether calcification in blue carbon ecosystems constitutes a CO_2 source (e.g., in the form of atmospheric CO_2 release) or sink (e.g., through enhancement of organic matter production and burial rates).

Over long time-scales it is assumed that CO_2 in the form of dissolved inorganic carbon (DIC) will remain in the oceans until CO_2 concentrations in the water body exceed those in the atmosphere. However, this equilibrium assumption, which applies for the global ocean (Smith 2013; Smith and Mackenzie 2016), may not apply in blue carbon ecosystems and over short time scales where fluxes can be influenced by weather (e.g., wind speeds, temperature) and metabolic processes (e.g., calcification, primary productivity, and respiration). For example, in the case of seagrasses, CO_2 produced through calcium carbonate formation can be rapidly utilized (through photosynthesis) by epiphytes and nearby plants, potentially offsetting rises in CO_2 (McConnaughey and Whelan 1997; Invers et al. 2001; Schneider and Erez 2006; Semesi et al. 2009), leading to greater productivity and higher rates of blue carbon sequestration (Russell et al. 2013). Conversely, photosynthetic activity within blue

carbon ecosystems could increase pH and enhance calcification of nearby calcareous organisms (De Beer and Larkum 2001).

Another key uncertainty relies on the fact that the organic carbon pool (i.e., organic matter) is more labile compared to the inorganic carbon pool (i.e., calcium carbonates), and it is therefore important to consider the temporal scale when accounting for the CO_2 sequestration capacity of blue carbon ecosystems. Indeed, the presence of geogenic calcium carbonates in blue carbon ecosystems could lead to an over-estimation of calcification rates. Therefore, there is a need to differentiate between geogenic and biogenic calcium carbonates within blue carbon soils in order to properly assess the role of carbon cycling in blue carbon accounting. Moreover, simple calculations also assume that calcium carbonate and organic carbon cycling in blue carbon ecosystems are independent processes. However, available evidence suggests that calcium carbonate and organic carbon cycling in blue carbon ecosystems are unlikely to be independent processes. For example, primary production is conducive to conditions that facilitate calcification, whereas respiration favors carbonate dissolution. In addition, calcium carbonate production can increase the burial efficiency of organic carbon, by interfering with microbial access to organic carbon in close physical association with calcium carbonate minerals (Mayer 1994; Ingalls et al. 2004). Calcium carbonates also support much of the sediment accretion rate in many seagrass meadows (Mazarrasa et al. 2015), a major component of the capacity of vegetated coastal ecosystems to preserve organic carbon and help adapt to sea level rise (Duarte et al. 2013). Further, respiration of organic matter produced in blue carbon ecosystems can fuel calcium carbonate dissolution, thereby resulting in no net effect of calcification on atmospheric CO_2 (Burdige et al. 2008). Addressing the key uncertainties arising from complexities of calcium carbonate cycling in blue carbon ecosystems, and resolving the key questions that currently preclude proper accounting for net calcium carbonate production in blue carbon ecosystems requires a concerted research effort.

In summary, calcium carbonate cycling makes an important contribution to global carbon budgets over geological timescales, yet the magnitude and direction of its influence on CO_2 sinks within blue carbon is unclear and currently unaccounted for. Considering the rapid rise of interest in blue carbon as a climate change mitigation and adaptation strategies, we argue that calcium carbonate cycling needs to be included when assessing the importance of these globally significant carbon stores as CO_2 sinks. Addressing calcium carbonate cycling in blue carbon accounting is timely given that anthropogenic activities and climate change may alter calcium carbonate cycling within coastal ecosystems with unknown feedbacks for climate change. For example, with increasing atmospheric CO_2 and ocean acidification, the ratio of released CO_2 to precipitated calcium carbonate is

expected to rise (Frankignoulle et al. 1995). Yet increased calcium carbonate dissolution (Fig. 1), and decreased calcification rates are also coupled to higher atmospheric CO₂, with both processes lowering the rate of CO₂ fluxed to the atmosphere. Moreover, partial dissolution of the large calcium carbonate stock deposited in blue carbon ecosystems may provide a buffer to ocean acidification while acting as a CO₂ sink. Clearly accounting for calcium carbonates in blue carbon systems is a tricky business.

References

- Andersson, A. J., F. T. Mackenzie, and L. M. Ver. 2003. Solution of shallow-water carbonates: An insignificant buffer against rising atmospheric CO₂. *Geology* **31**: 513–516. doi:10.1130/0091-7613(2003)031<0513:SOSCAI>2.0.CO;2
- Andersson, A. J., and F. T. Mackenzie. 2004. Shallow-water oceans: A source or sink of atmospheric CO₂? *Front. Ecol. Environ.* **2**: 348–353. doi:10.2307/3868359
- Andersson, A. J., F. T. Mackenzie, and A. Lerman. 2005. Coastal ocean and carbonate systems in the high CO₂ world of the anthropocene. *Am. J. Sci.* **305**: 875–918. doi:10.2475/ajs.305.9.875
- Archer, D., H. Kheshgi, and E. Maier-Reimer. 1998. Dynamics of fossil fuel CO₂ neutralization by marine CaCO₃. *Global Biogeochem. Cycles* **12**: 259–276. doi:10.1029/98GB00744
- Burdige, D. J. 2007. Preservation of organic matter in marine sediments: Controls, mechanisms, and an imbalance in sediment organic carbon budgets? *Chem. Rev.* **107**: 467–485. doi:10.1021/cr050347q
- Burdige, D. J., R. C. Zimmerman, and X. Hu. 2008. Rates of carbonate dissolution in permeable sediments estimated from pore-water profiles: The role of sea grasses. *Limnol. Oceanogr.* **53**: 549–565. doi:10.4319/lo.2008.53.2.0549
- Cox, T. E., F. Gazeau, S. Alliouane, I. E. Hendriks, P. Mahacek, A. Le Fur, and J.-P. Gattuso. 2016. Effects of in situ CO₂ enrichment on structural characteristics, photosynthesis, and growth of the Mediterranean seagrass *Posidonia oceanica*. *Biogeosciences* **13**: 2179–2194. doi:10.5194/bg-13-2179-2016
- De Beer, D., and A. W. D. Larkum. 2001. Photosynthesis and calcification in the calcifying algae *Halimeda discoidea* studied with microsensors. *Plant Cell Environ.* **24**: 1209–1217. doi:10.1046/j.1365-3040.2001.00772.x
- Duarte, C. M., I. J. Losada, I. E. Hendriks, I. Mazarrasa, and N. Marba. 2013. The role of coastal plant communities for climate change mitigation and adaptation. *Nat. Clim. Chang.* **3**: 961–968. doi:10.1038/nclimate1970
- Falkowski, P., and others. 2000. The global carbon cycle: A test of our knowledge of earth as a system. *Science* **290**: 291–296. doi:10.1126/science.290.5490.291
- Frankignoulle, M., C. Canon, and J. P. Gattuso. 1994. Marine calcification as a source of carbon dioxide: Positive feedback of increasing atmospheric CO₂. *Limnol. Oceanogr.* **39**: 458–462. doi:10.4319/lo.1994.39.2.0458
- Frankignoulle, M., M. Pichon, and J. P. Gattuso. 1995. Aquatic calcification as a source of carbon dioxide. In Beran M.A., (eds.), *Carbon Sequestration in the Biosphere*. NATO ASI Series. Springer, Berlin, Heidelberg.
- Gattuso, J. P., M. Frankignoulle, and R. Wollast. 1998. Carbon and carbonate metabolism in coastal aquatic ecosystems. *Annu. Rev. Ecol. Syst.* **29**: 405–434. doi:10.1146/annurev.ecolsys.29.1.405
- Ingalls, A. E., R. C. Aller, C. Lee, and S. G. Wakeham. 2004. Organic matter diagenesis in shallow water carbonate sediments. *Geochim. Cosmochim. Acta* **68**: 4363–4379. doi:10.1016/j.gca.2004.01.002
- Invers, O., R. C. Zimmerman, R. S. Alberte, M. Perez, and J. Romero. 2001. Inorganic carbon sources for seagrass photosynthesis: An experimental evaluation of bicarbonate use in species inhabiting temperate waters. *J. Exp. Mar. Biol. Ecol.* **265**: 203–217. doi:10.1016/S0022-0981(01)00332-X
- IPCC. 2007. *Climate change 2007: The physical science basis*. In Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller [eds.], *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge Univ. Press.
- Le Quere, C., and others. 2016. *Global Carbon Budget 2016*. *Earth Syst. Sci. Data* **8**: 605–649. doi:10.5194/essd-8-605-2016
- Macreadie, P. I., and others. 2017. Can we manage coastal ecosystems to sequester more blue carbon? *Front. Ecol. Environ.* **15**: 206–213. doi:10.1002/fee.1484
- Maher, D. T., I. R. Santos, K. G. Schulz, M. Call, G. E. Jacobsen, and C. J. Sanders. 2017. Blue carbon oxidation revealed by radiogenic and stable isotopes in a mangrove system. *Geophys. Res. Lett.* **44**: 4889–4896. doi:10.1002/2017GL073753
- Mayer, L. M. 1994. Relationships between mineral surfaces and organic-carbon concentration in soils and sediments. *Chem. Geol.* **114**: 347–363. doi:10.1016/0009-2541(94)90063-9
- Mazarrasa, I., and others. 2015. Seagrass meadows as a globally significant carbonate reservoir. *Biogeosciences* **12**: 4993–5003. doi:10.5194/bg-12-4993-2015
- McConnaughey, T. A., and J. F. Whelan. 1997. Calcification generates protons for nutrient and bicarbonate uptake. *Earth Sci. Rev.* **42**: 95–117. doi:10.1016/S0012-8252(96)00036-0
- McLeod, E., and others. 2011. A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Front. Ecol. Environ.* **9**: 552–560. doi:10.1890/110004
- Nellemann, C., E. Corcoran, C. M. Duarte, L. Valdés, C. De Young, L. Fonseca, and G. Grimsditch [eds.]. 2009. *Blue carbon. A rapid response assessment*. United Nations Environment Programme, GRID-Arendal.

- Pendleton, L., and others. 2012. Estimating global “blue carbon” emissions from conversion and degradation of vegetated coastal ecosystems. *PLoS One* **7**: e43542–e43542. doi:10.1371/journal.pone.0043542
- Russell, B. D., S. D. Connell, S. Uthicke, N. Muehllehner, K. E. Fabricius, and J. M. Hall-Spencer. 2013. Future seagrass beds: Can increased productivity lead to increased carbon storage? *Mar. Pollut. Bull.* **73**: 463–469. doi:10.1016/j.marpolbul.2013.01.031
- Schneider, K., and J. Erez. 2006. The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral *Acropora eurystroma*. *Limnol. Oceanogr.* **51**: 1284–1293. doi:10.4319/lo.2006.51.3.1284
- Semesi, I. S., S. Beer, and M. Bjork. 2009. Seagrass photosynthesis controls rates of calcification and photosynthesis of calcareous macroalgae in a tropical seagrass meadow. *Mar. Ecol. Prog. Ser.* **382**: 41–47. doi:10.3354/meps07973
- Serrano, O., and others. 2016. Key biogeochemical factors affecting soil carbon storage in *Posidonia* meadows. *Biogeosciences* **13**: 4581–4594. doi:10.5194/bg-13-4581-2016
- Smith, S. V. 2013. Parsing the oceanic calcium carbonate cycle: A net atmospheric carbon dioxide source, or a sink? L&O e-Books. Association for the Sciences of Limnology and Oceanography (ASLO).
- Smith, S. V., and F. T. Mackenzie. 2016. The role of CaCO₃ reactions in the contemporary oceanic CO₂ cycle. *Aquat. Geochem.* **22**: 153–175. doi:10.1007/s10498-015-9282-y
- Tyrrell, T. 2008. Calcium carbonate cycling in future oceans and its influence on future climates. *J. Plankton Res.* **30**: 141–156. doi:10.1093/plankt/fbm105
- Zamanian, K., K. Pustovoytov, and Y. Kuzyakov. 2016. Pedogenic carbonates: Forms and formation processes. *Earth Sci. Rev.* **157**: 1–17. doi:10.1016/j.earscirev.2016.03.003
- Zeebe, R. E., and D. Wolf-Gladrow. 2001. CO₂ in seawater: Equilibrium, kinetics, isotopes. Elsevier.

Acknowledgments

We thank Patricia A. Soranno, Stephen V. Smith, and an anonymous reviewer for their advice in revising this paper. PM was supported by an Australian Research Council DECRA Fellowship (DE130101084) and a Linkage Project (LP160100242). OS was supported by the CSIRO Flagship Marine and Coastal Carbon Biogeochemical Cluster and an ARC DECRA (DE170101524). DM was supported by an ARC DECRA Fellowship (DE150100581). CMD was supported by baseline funding from KAUST.

Submitted 22 February 2017

Revised 26 May 2017; 25 July 2017

Accepted 25 September 2017