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Laura Stoltenberg
Southern Cross University

Kai G. Schulz
Southern Cross University

Coulson A. Lantz
Southern Cross University

Tyler Cyronak
Nova Southeastern University, tcyronak@nova.edu

Bradley D. Eyre
Southern Cross University

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Late afternoon seasonal transition to dissolution in a coral reef: An early warning of a net dissolving ecosystem?

Laura Stoltenberg^{1*}, Kai G. Schulz¹, Coulson, A. Lantz¹, Tyler Cyronak², Bradley D. Eyre¹

¹Centre for Coastal Biogeochemistry Research, Southern Cross University, Lismore, NSW 2480, Australia

²Halmos College of Natural Science and Oceanography, Nova Southeastern University, Dania Beach, Florida, USA

*laurastolten@gmail.com

Key points:

1. Ecosystem calcification and sediment calcification on Heron Island reef exceed dissolution such that NEC remains largely positive.
2. Shallow, calcium carbonate (CaCO₃) sediments contribute 8-12% of reef NEC during the day and at least 45-78% of reef NEC at night.
3. The seasonal shifts to negative net ecosystem calcification before dusk may be a precursor of periodic net ecosystem dissolution.

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ABSTRACT

There are concerns that reefs will transition from net calcifying to net dissolving in the near future due to decreasing calcification and increasing dissolution rates. Here we present in situ rates of net ecosystem calcification (NEC) and net ecosystem production (NEP) on a coral reef flat using a slack-water approach. Up until dusk, the reef was net calcifying in most months but shifted to net dissolution in austral summer, coinciding with high respiration rates and a lower aragonite saturation state (Ω_{arag}). The estimated sediment contribution to NEC ranged from 8 – 21 % during the day and 45 – 78 % at night, indicating that high rates of sediment dissolution may cause the transition to reef dissolution. This late afternoon seasonal transition to negative NEC may be an early warning sign of the reef shifting to a net dissolving state and may be occurring on other reefs.

Plain language summary

Positive rates of net ecosystem calcification and net ecosystem production are regarded as fundamental to the healthy functioning of coral reef ecosystems. In particular, positive ecosystem calcification is required to maintain the structural complexity that sustains many of the ecosystem functions of coral reefs. While most reefs are currently net calcifying, there is growing concern that increased pressures from rising sea surface temperatures and reductions in ocean surface pH (ocean acidification (OA)) will both depress coral calcification and increase dissolution. This could result in a shift of the whole ecosystem closer to a state of net dissolution before the end of the century. Here, we measured hourly afternoon rates of net ecosystem calcification and production on a coral reef flat over ten months of the year. We found that the reef flat was already showing signs of net dissolution during certain times of the year (austral summer), which may become more extreme under global climate change. These temporary shifts in coral reef metabolism may provide insight

into how the ecosystem will respond to future, more persistent periods of net dissolution driven by OA.

Keywords: coral reef metabolism, dissolution, community calcification, Great Barrier Reef, calcium carbonate, ocean acidification

1.) Introduction

Rising sea surface temperatures and declining surface ocean pH (ocean acidification – OA) are impacting coral reefs on local, regional, and global scales, leading to a reduction in coral cover [Gardner *et al.*, 2003; Hughes *et al.*, 2018; Perry *et al.*, 2018] and declining calcification rates [Cooper *et al.*, 2008; Pisapia *et al.*, 2019]. Net ecosystem calcification (NEC), or the balance between calcium carbonate production and dissolution, is regarded as one of the four cornerstones of coral reef functioning [Brandl, 2019]. Positive NEC is directly related to habitat provision and structural complexity, which is crucial for maintaining desirable reef attributes such as resilience and ecosystem services [Brandl, 2019; Graham and Nash, 2013]. Net ecosystem calcification has been shown to decrease significantly with decreasing seawater pH and aragonite saturation state (Ω_{arag}) [Albright *et al.*, 2018; Doo *et al.*, 2019], and the observed effect in situ is often much larger than those predicted based on laboratory or mesocosm studies [Carpenter *et al.*, 2018; Reynaud *et al.*, 2003]. A large proportion of the decline in NEC associated with experimental ocean acidification might be due to increases in calcium carbonate dissolution [Andersson *et al.*, 2009; Comeau *et al.*, 2015], which is most likely occurring in reef sediments and framework [Eyre *et al.*, 2014]. Teasing apart the relative impacts of constructive processes (e.g., biogenic calcification) versus the destructive process of dissolution on changes in NEC under ocean acidification remains a critical problem for assessing the tipping points of coral reefs into a state of net calcium carbonate loss [Alvarez-Filip *et al.*, 2009].

On any given reef, NEC represents the combined contributions of all calcifying organisms (including corals, calcifying algae, mollusks, benthic foraminifera, and sediment infauna and associated microbes), plus some level of inorganic calcium carbonate (CaCO_3) precipitation/dissolution occurring within the sediments and framework [Burdige *et al.*, 2010; Courtney *et al.*, 2016; Webb, 2001; Wurgaft *et al.*, 2016]. The largest contribution to NEC

most likely comes from organisms such as corals and calcifying algae, largely due to their disproportionately high rates of calcification. Even though sediments tend to have lower rates of net community calcification ($NCC_{\text{sediments}}$), they could also be an important component of NEC_{reef} due to their large benthic habitat coverage [Gattuso *et al.*, 1998]. For example, sediments could be responsible for up to 50% of NEC for the Heron Island reef flat [Cyronak and Eyre, 2016]. $NCC_{\text{sediments}}$ is expected to decline with ocean acidification at an order of magnitude greater rate than biogenic calcification [Cyronak *et al.*, 2013; Eyre *et al.*, 2018]. Based on previously published fluxes and the large areal extent of coverage, sediments could represent a significant contribution to coral reef NEC and play an important role in the response of reef ecosystems to ocean acidification.

Over a diel cycle, coral reefs and sediments are typically net calcifying (positive NEC) during the day and net dissolving (negative NEC) at night. Generally, daytime calcification exceeds nighttime dissolution, resulting in positive NEC over 24 hours [McMahon *et al.*, 2013; Stoltenberg *et al.*, 2019]. There are some exceptions to this; for example, in the Gulf of Eilat, Red Sea, the reef maintained positive NEC throughout the night [Silverman *et al.*, 2007] and a barrier reef flat in Hawaii was net dissolving at night in only about half of the measurements [Shamberger *et al.*, 2011]. In contrast, some reefs and reef sediments already show seasonal net dissolution [Eyre *et al.*, 2018; Meléndez *et al.*, 2018; Muehllehner *et al.*, 2016; Stoltenberg *et al.*, 2019]. Periods of net dissolution have been attributed to instances of very high cloud cover and turbidity [Takeshita *et al.*, 2016; Yates and Halley, 2006] regional acidification events [Yeakel *et al.*, 2015] or when the reef is net heterotrophic (e.g., negative net ecosystem production; NEP) [Bates *et al.*, 2009, 2010; McMahon *et al.*, 2013]. In contrast, high NEC is often related to periods of increased NEP that alter the carbonate chemistry in favor of calcification [Bates *et al.*, 2009]. Based on these

observations, the first instances of shifts to negative NEC are likely to occur at nighttime and then shift to early mornings and late afternoons as conditions change that favor dissolution.

There are a few in situ measurements of reef NEC that cover diel and/or seasonal cycles but none of them have specifically looked at the transition between daytime calcification and nighttime dissolution [Albright *et al.*, 2015; Davis *et al.*, 2019; DeCarlo *et al.*, 2017; McMahon *et al.*, 2013; McMahon *et al.*, 2018; McMahon *et al.*, 2019; Shamberger *et al.*, 2011; Shaw *et al.*, 2014; Silverman *et al.*, 2007; Silverman *et al.*, 2012]. We hypothesize that this boundary varies seasonally, in line with a range of environmental parameters such as irradiance, Ω_{arag} , and temperature. We measured NEC over a seasonal cycle at Heron Island (Great Barrier Reef), and specifically targeted the afternoon hours to detect the shift between net calcification and dissolution. In addition, we estimated the contribution of $\text{NCC}_{\text{sediments}}$ to whole reef NEC during both day and night to better understand the drivers of reef NEC, its temporal variation, and potential response to future ocean conditions.

2.) Methods

Study site

This study was conducted on Heron Island (23° 27' S, 151° 55' E) between October 2015 and November 2016. Heron Island is a lagoonal platform reef situated at the southern end of the Great Barrier Reef, Australia, and covers an area of ~0.16 km², with a lagoon and reef flat extending over 26.4 km² (Figure S1). The study site was located within the inner reef flat on a sandy patch, approximately 100 m off the beach, interspaced with patches of coral. Most of the lagoon and reef flat is covered in CaCO₃ sediments with 68.2 % sand found on the inner reef flat [Allen Coral Atlas, 2019]. Average water depth of the reef flat is 1.1 m, with a semi-diurnal tidal cycle and range of 0.3-2.6 m [Kline *et al.*, 2019].

Discrete sampling and processing

Approximately every six weeks, discrete water samples were taken to measure total alkalinity (TA), dissolved inorganic carbon (DIC), and dissolved inorganic nutrients (nitrate and nitrite [NO_x], phosphate [PO₄³⁻] and ammonium [NH₄⁺]). All samples were taken using a plastic syringe which was flushed with sea water three times. Samples for DIC and TA were gently filtered (0.45 µm cellulose acetate syringe filters) into borosilicate glass bottles filled from the bottom using a silicone tube and allowed to overflow. Sample collection bracketed the low tide while the reef flat was isolated from the surrounding ocean, with one sample collected every hour for a total of four samples per low tide (14:30 - 18:30; or 4 h from sunset to 1 h after sunset). A total of 40 samples were collected for 10 low tides from October 2015 to November 2016. In order to capture a composite diurnal cycle, we also sampled at different times of the day during low tide between 11 – 21 November 2016 (n = 9 low tides) using the same methods described above. The remaining carbonate chemistry parameters (pH_T, fCO₂, Ω_{arag}) were calculated using CO2SYS in MATLAB [van Heuven *et al.*, 2011], with in situ temperature and salinity, and equilibrium constants from Mehrbach *et al.* [1973] refit by Dickson and Millero [1987].

Reef metabolism calculations

Due to its geomorphology, the Heron Island reef flat becomes isolated from offshore waters at low tide, allowing for a slack-water approach to calculate NEC and NEP from TA and DIC measurements using equations (1) and (2) [Kinsey, 1978; Langdon *et al.*, 2010]. This approach assumes that changes in water chemistry are directly caused by the biological activity of the benthic communities, with minimal influence from water column processes.

$$NEC = - \frac{0.5 \Delta TA \, d \, \rho}{\Delta t} \quad (1)$$

$$NEP = - \frac{(\Delta DIC - 0.5 \Delta TA) \, d \, \rho}{\Delta t} - F_{CO2} \quad (2)$$

where ΔTA and ΔDIC are the change in TA and DIC between sampling pairs, d is the average water depth (m) between sampling points, ρ is the sea water density (kg m⁻³)

calculated using in situ temperature and salinity, Δt is the sampling interval between two samples (h), and F_{CO_2} ($\text{mmol m}^{-2} \text{h}^{-1}$) is the air-sea flux of CO_2 . Further details on the approach, calculations, and statistical analysis can be found in the supplementary material.

3.) Results

Temporal variability in environmental data

A nested ANOVA showed that $\mathcal{Q}_{arag}$ was significantly different in certain months of the year, with low $\mathcal{Q}_{arag}$ in December 2015 and November 2016 ($F = 5.513$, $df = 9$, $p = 0.013$, Figure S4). Mean monthly temperature ranged between 20.6°C in austral winter to 26.5°C in austral summer (Table S1), while mean pH and salinity exhibited little seasonal variation. Light showed a clear seasonal trend with highest daily irradiance in spring and summer (47.6 to $44.8 \text{ mol photons m}^{-2} \text{d}^{-1}$) and about half in winter ($27.9 \text{ mol photons m}^{-2} \text{d}^{-1}$). A principal component analysis (PCA) showed that along the first principal component (PC1) 28.7 % of the variability can be explained by the combination of instantaneous irradiance, hours until sunset, NEC, and NEP (Figure S3). On the second principal component (PC2) 19.7 % of variability is explained pH, NO_x , which were positively correlated to each other and negatively correlated to temperature and mean irradiance and daily integrated irradiance.

Diurnal and seasonal variability in reef NEC and NEP

For monthly rates between 14:30 and 18:30, corresponding to 4 hours before sunset to one hour after sunset, NEC and NEP generally declined over time (Figure 1). NEC remained positive up to sunset, with the notable exceptions of December 2015 and November 2016 where NEC shifted to negative (i.e., net reef dissolution) and no longer calcifying in February 2016 (Figure 1). NEP and NEC were highly correlated ($R = 0.896$ $p < 0.0001$, $n = 31$, Figure S6). The transition to net respiration between 30 min and 1 h from sunset was consistent throughout the year, with the exception of May 2016, which had very high rates of NEP (Figure 1). NEC and NEP were fit to PAR with a polynomial function which represented the

best fit (Figure S7). NEC was also significantly correlated to Ω_{arag} ($R = 0.548$, $p = 0.002$, $n = 28$, Figure S8). No correlation of NEP or NEC with temperature was found (Figure S9).

In the November 2016 diel cycle, NEC ranged between -4.3 and $21.5 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$ with average daytime NEC of $8.3 \pm 4.3 \text{ mmol m}^{-2} \text{ h}^{-1}$ and nighttime NEC of $-1.7 \pm 2.7 \text{ mmol m}^{-2} \text{ h}^{-1}$. NEP had a larger amplitude than NEC and ranged between -35.1 and $48.6 \text{ mmol m}^{-2} \text{ h}^{-1}$ (Figure S5). Average daytime NEP was $25.3 \pm 10.2 \text{ mmol C}^{-2} \text{ h}^{-1}$ and average nighttime NEP was $-13.4 \pm 11.1 \text{ mmol m}^{-2} \text{ h}^{-1}$. Integrated NEC and NEP remained positive during the day and negative at night, with positive NEC and NEP maintained over 24h (Table S2).

4.) Discussion

NEC seasonality and transition to net CaCO₃ dissolution

Integrated rates of day and night NEC from the November 2016 diel cycle show that the reef maintains net calcification during the day and over 24 h. Based on what we know from a typical diel cycle, it is likely that Heron Island reef flat maintains a state of net CaCO₃ accretion over an annual cycle. This is further supported by a positive carbonate budget recently estimated for Heron Island [Brown *et al.*, 2020]. Our integrated NEC and NEP rates were similar to previous in situ studies of reef metabolism at this site (Table S2). Recent reviews on coral reef NEC suggest that the majority of reefs show positive net NEC [Courtney and Andersson, 2019; DeCarlo *et al.*, 2017]. There are, however, reef systems that are presently no longer net calcifying, or already net dissolving. For example, Enrique fore-reef and off-reef areas are net dissolving year-round with active CaCO₃ accretion only occurring between January to mid-April, with net heterotrophy being the primary driver of CaCO₃ dissolution [Melendez *et al.*, 2018]. Similarly, across the Caribbean, many reefs are no longer contributing to the net production of CaCO₃ due to declining coral cover [Perry *et al.*, 2018]. While informative, these CaCO₃ budgets can miss finer details, including the

transition to net dissolution over diel or seasonal time scales. Many CaCO_3 budget studies don't include the contribution of sediment dissolution to net ecosystem dissolution, with some notable exceptions [*Courtney et al.* 2016; *Brown et al.* 2020, also see reviews by *Eyre et al.*, 2014 and *Lange et al.*, 2019].

Over both diel and seasonal time scales, NEP and NEC were highly correlated and largely positive. The correlation of NEP and NEC is most likely driven by light, through light-enhanced calcification (LEC) [*Gattuso et al.*, 1999, and references therein]. There are various mechanisms that have been proposed to explain LEC; the most accepted involves the uptake of CO_2 during photosynthesis, which elevates pH and Ω_{arag} , creating a favorable environment for calcification [*Goreau and Goreau*, 1959]. However, a recent study demonstrated that light enhanced calcification could be decoupled from photosynthesis at different wavelengths of light, indicating that the processes may be controlled by separate light influenced mechanisms [*Cohen et al.*, 2016].

The Heron Island reef flat maintained largely positive NEC until dusk in 7 out of 10 months. In the early (austral) summer months of December 2015 and November 2016 the system transitioned from net calcifying to net dissolving, and no longer calcifying in February 2016, between 30 – 60 min before sunset. Periods of net respiration preceded periods of net CaCO_3 dissolution and there was a seasonal trend of increased net respiration earlier in the afternoon in summer months. Based on a linear relationship between temperature and respiration one would expect March and May to have highest respiration rates (or to transition to negative NEP earlier), however this was not the case. This could be due to spring organic matter storage which provides the substrate for increased respiration with high light and temperatures increasing in spring and early summer (also see Figure S3). Hansen et al. [1992] show that organic matter content of the sediments and detrital input at

Davis reef (GBR) were highest in spring, subsequently fueling high community respiration rates in summer.

In addition, Ω_{arag} was significantly lower in December 2015 and November 2016, probably due to net respiration, which could have contributed to the early onset of dissolution (Figure S4). The late afternoon shift to net dissolution occurred despite relatively high Ω_{arag} (4.1 - 4.6) compared to other studies that have measured dissolution [Meléndez *et al.*, 2018; Muehllehner *et al.*, 2016]. However, Ω_{arag} was measured in the afternoon at low tide, as opposed to daytime averages, and hence expected to be high due to daytime photosynthesis drawing down DIC [Cyronak *et al.*, 2019; Jokiel *et al.*, 2014]. Even if bulk seawater Ω_{arag} is high, low Ω_{arag} and undersaturation of Ω_{ca} in porewaters can cause dissolution in the sediments [Drupp *et al.*, 2016; Eyre *et al.*, 2014; Hu and Burdige, 2007], which could be the reason for the observed shift to net dissolution. It remains unknown if this late afternoon onset of negative NEC has always occurred on the Heron Island reef flat, if it is a seasonal phenomenon, or if it is a response to lower Ω_{arag} in the water column due to ongoing ocean acidification, or a combination [Cyronak *et al.*, 2014]. A study on a nearby reef, One Tree Island, has found a 3-fold increase in nighttime dissolution since the 1970s; however, net CaCO_3 dissolution was not measured until ~30 min before sunset [Silverman *et al.*, 2012], compared to up to 60 minutes before sunset on Heron Island.

The role of CaCO_3 sediments in future transitions to net dissolution

When comparing NEC_{reef} to $\text{NCC}_{\text{sediment}}$, they show similar patterns in monthly and seasonal variation [Stoltenberg *et al.*, 2019]. Most importantly, some of the months in which reef NEC was negative before sunset coincide with the months where highest sediment dissolution rates were measured [Stoltenberg *et al.*, 2019]. In December, for example, our estimated contribution of $\text{NCC}_{\text{sediment}}$ to reef NEC is also among the highest (78%), indicating that the reef-wide dissolution measured in that month may be a direct result of increased rates

of sediment dissolution (Table 1). Our estimates of CaCO_3 sediments contribution to reef NEP and NEC show that the sediments are contributing proportionately more to NEC at night (44 - 78 %) as opposed to during the day (8.3 - 21 %). The higher contribution of the sediments to NEC at night is likely due to generally lower nighttime gross biogenic calcification compared to daytime rates [Gattuso *et al.*, 1999], which allows sediment dissolution to exert a stronger control on NEC at night. In contrast, there was not much difference between daytime and nighttime contributions of sediments to NEP, which averaged 13.5 ± 7 % and is similar to the range (3-30 %) reported for a reef in French Polynesia [Boucher *et al.*, 1998].

With pre-industrial Ω_{arag} at the study site estimated to be around one unit higher (Table 2), the seasonal transition we observed might be due in part to ongoing ocean acidification and may be an early warning of a pending negative reef NEC. Ocean acidification will likely result in a reduction in NEC during the day driven by the reduction in coral calcification, at least for some species and communities [Albright *et al.*, 2018; Doo *et al.*, 2019; Langdon and Atkinson, 2005; Schneider and Erez, 2006], and a much more substantial reduction in NEC at night driven by the increase in dissolution of the sediments [Cyronak *et al.*, 2013; Eyre *et al.*, 2018; Fink *et al.*, 2017]. Due to the natural diurnal cycle in coral reef NEC, we could expect the first transitions to net dissolution associated with ocean acidification to occur at night. As ocean acidification on coral reefs is expected to intensify [Cyronak *et al.*, 2014], these transitions could spill over on both sides of the diel curve with periods of net dissolution occurring earlier in the afternoon and later into the morning (see Figure 2; Table 2). In a recent field study using a free ocean CO_2 enrichment (FOCE) Doo *et al.* [2019] showed that OA decreased both daytime and nighttime NEC, but the effect on dissolution at night was almost twice as high. As a result of both daytime and nighttime decreases, net NEC declined by about 50% [Doo *et al.* 2019]. Interestingly, the effect of OA

on nighttime dissolution decreased over time [Doo *et al.* 2019], which could indicate a buffering effect of increased sediment dissolution against high pCO₂ treatments. However, it is unclear if the system was fully flushed between measurements or if a build-up of alkalinity was the cause of this attenuation [Doo *et al.* 2019].

The reef slope and outer reef flat of Heron Island have high coral cover and are considered a healthy reef system which is consistent with high rates of NEC [Albright *et al.*, 2016; McMahon *et al.* 2013; Salmond *et al.*, 2018] and net carbonate production [Brown *et al.*, 2020]. Coral cover and carbonate production in the inner reef flat and lagoon are significantly lower [Brown *et al.* 2020]. Despite this, we measured periods of net CaCO₃ dissolution before dusk on Heron Island, which have not been seen before [McMahon *et al.*, 2013, 2018; Albright *et al.*, 2015]. It is likely that these periods of negative NEC are also occurring on reefs elsewhere, but a lack of high-resolution measurements that include these transitional periods of late afternoon and early mornings means these trends are not being detected. There have been several in situ studies of coral reef NEC that have included diel and/or seasonal cycles [Silverman *et al.*, 2007, 2012; Shamberger *et al.*, 2011; McMahon *et al.*, 2013, 2018, 2019; Shaw *et al.*, 2014; Albright *et al.*, 2015; Davis *et al.*, 2019; DeCarlo, 2017]. In most of these studies negative NEC does not occur before dusk or remained positive even into the night [De Carlo *et al.*, 2017], except on a similar study on One Tree Island, Great Barrier Reef [Shaw *et al.*, 2014]. However, none of these studies have specifically focused on the transition from positive to negative NEC and it is not always evident exactly when NEC became negative. Additionally, some of the older literature [for example Kinsey, 1978; Gattuso *et al.*, 1996] might not be reflective of the ongoing changes we could already be seeing due to ocean acidification. We postulate that these periods of periodic net CaCO₃ dissolution could be more widespread than presently thought.

While the slack-water method is traditionally used for tidal pools or small areas of reef, we believe that it is valid to use this approach at Heron Island because the flow is highly unidirectional and consistent during the slack tide. The unique tidal isolation and drainage patterns on the reef flat lead to a predictable area of the reef flat that could influence changes in seawater chemistry (see Figure S1). Nonetheless, this approach comes with certain assumptions and limitations and the rates calculated here should be used with caution when comparing absolute rates (refer to the supplementary material for a more in-depth discussion on methods and limitations). Our metabolic rates compare well to previous measurements made in the same general area and a recent carbonate budget for Heron Island [Brown et al. 2020]. Platform-wide carbonate production was $4.06 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ and $1.53 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ within the reef flat which compares well with our net integrated NEC rates from November 2016 for the inner reef flat ($42 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ converted from Brown et al 2020 versus $65 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$; Table S2). Importantly, they showed that the reef flat was the largest contributor to platform wide sediment production (55%). This means that the transition to afternoon dissolution we measure here (driven by -NEP and sediment dissolution) could be relevant for platform-wide carbonate budgets.

5.) Conclusion

We show that the transition to net reef dissolution on Heron Island reef flat can occur before dusk for certain times of the year, most likely driven by reductions in Ω_{arag} due to net heterotrophy and increased sediment dissolution. Projected future warming and ocean acidification will likely increase the contribution of sediments to reef NEC as the effect of ocean acidification will be higher on night dissolution than day calcification. The adverse effects of OA will be exacerbated on reefs with low coral cover and where rates of coral calcification and therefore daytime NEC are already low, as the relative contribution at night will play a more significant role if daytime rates are depressed. As such, these changes will

not be uniform, but instead we will most likely start to see effects on reefs that are already experiencing low rates of NEC today, and in parts of the reef with the most sediments.

The late afternoon seasonal transition to negative NEC, as seen on the Heron Island reef flat in certain times of the year, may be an early warning of a pending negative reef NEC. Other reefs with higher NEC will most likely start to show the first signs of periodic net dissolution in the late afternoon, which could lead to seasonal transitions to net dissolution over a diel cycle, eventually transitioning to net dissolution over an annual cycle. In the context of future ocean acidification, warming, and sea-level rise, the reductions of $NCC_{\text{sediments}}$ could further contribute to reductions in reef NEC and lead to loss of reef sediments and reef framework with potential declines in structural complexity, which could have far-reaching impacts and cascading effects for coral reef ecosystem functioning.

Data availability statement

In accordance with FAIR data principles, the data set to produce the figures and analyses in this manuscript was uploaded to Zenodo (available at <https://doi.org/10.5281/zenodo.4291744>).

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Author contributions

B.D.E., K.G.S. and L.S. conceived the project, L.S. carried out the field work and analyzed the samples and data. All authors assisted with the field work. L.S. wrote the manuscript with input from all co-authors. All authors approved the final manuscript.

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Table 1

Contribution (%) of $NCC_{sediments}$ and $NCP_{sediments}$ to NEC and NEP of the reef flat.

Month	NEC afternoon	NEP afternoon	NEC night	NEP night
Oct-15	12.17	14.40	--	11.26
Nov-15	9.06	12.86	--	--
Dec-15	8.29	24.18	78.23	14.31
Feb-16	20.76	25.00	--	12.73
Mar-16	21.12	14.13	--	19.13
May-16	10.81	11.41	--	--
Jul-16	8.17	6.06	--	13.82
Aug-16	10.43	6.58	--	18.44
Oct-16	9.42	6.53	--	31.88
Nov-16 ^a	11.36	17.08	44.44	11.54

^a Percent contribution calculated from integrated rates of daytime and nighttime NEC and NEP from a diel cycle.

Table 2

Comparison of pre-industrial, present day, and future Ω_{arag} estimated using DIC concentrations of past, present and future fCO_2 . See supplementary material for details on calculations. Highlighted area denotes months where negative NEC was measured before dusk.

Season	Month	Ω_{arag} pre-industrial	Ω_{arag}	Ω_{arag} RCP 8.5
Spring	Oct'15	5.27	4.37	3.06
	Nov'15	5.76	4.52	3.42
	Oct'16	5.67	4.57	3.43
Summer	Nov'16	4.91	4.09	2.69
	Dec'15	4.85	4.06	2.59
	Feb '16	5.00	4.29	2.76
Autumn	Mar'16	5.35	4.50	3.13
	May'16	--	--	--
Winter	Jul '16	5.29	4.18	3.19
	Aug '16	5.24	4.39	3.09

Figure 1 – Afternoon rates of NEC ($\text{mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$) (a) and NEP ($\text{mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$) (b) for different months of the year with black horizontal dashed lines indicating transition to net dissolution and net respiration, respectively. Shaded areas represent the minimum and maximum NEC and NEP calculated with a 30% uncertainty in depth measurements.

Figure 2 – Conceptual diagram of sediment contribution to net ecosystem calcification illustrating how ocean acidification could shape the relationship of NEC versus time of day to favor an early onset of dissolution accounting for the higher relative contribution of sediment dissolution at night. The black line represents NEC, the blue line represents the present-day contribution of sediment net community calcification to NEC, and the red line represents the estimated contribution of sediments with future ocean acidification. Red arrows highlight the differences in expected shifts in contributions during the day and night, as well as shifts in the onset of net calcification and net dissolution over a diel cycle.