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Key Points:

- Oceanic particulate organic matter uptake elevates net ecosystem calcification, even under low aragonite saturation states
- The rates of net ecosystem calcification and oceanic particulate organic matter uptake are sensitive to changes in water flow speeds

Supporting Information:

- Supporting Information S1
- Data Set S1

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Heterotrophy of Oceanic Particulate Organic Matter Elevates Net Ecosystem Calcification

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Abstract Coral reef calcification is expected to decline due to climate change stressors such as ocean acidification and warming. Projections of future coral reef health are based on our understanding of the environmental drivers that affect calcification and dissolution. One such driver that may impact coral reef health is heterotrophy of oceanic-sourced particulate organic matter, but its link to calcification has not been directly investigated in the field. In this study, we estimated net ecosystem calcification and oceanic particulate organic carbon (POC_{oc}) uptake across the Kāne'ohe Bay barrier reef in Hawai'i. We show that higher rates of POC_{oc} uptake correspond to greater net ecosystem calcification rates, even under low aragonite saturation states (Ω_{ar}). Hence, reductions in offshore productivity may negatively impact coral reefs by decreasing the food supply required to sustain calcification. Alternatively, coral reefs that receive ample inputs of POC_{oc} may maintain higher calcification rates, despite a global decline in Ω_{ar} .

Plain Language Summary Coral reefs are threatened by climate change stressors including ocean acidification and ocean warming. One way to measure and monitor coral reef health is to estimate coral reef calcification, which is influenced by several environmental factors including light, temperature, pH, and nutrient availability. By understanding the effects of these factors on calcification, we can better predict how corals will respond to climate change. One potentially important factor for calcification that has not been investigated in the field is coral reef ecosystem feeding on particulate organic matter supplied from offshore (i.e., oceanic particulate organic matter). In this study, we estimated net ecosystem calcification and oceanic particulate organic carbon (POC) uptake across the Kāne'ohe Bay barrier reef in Hawai'i. For the first time, we show a direct correlation between net ecosystem calcification and oceanic POC uptake, which suggests that the reef is using oceanic POC as an energy source to elevate calcification. However, since climate change reduces oceanic POC production through warming and stratification, our results imply coral reef calcification may decline. Alternatively, coral reefs located in regions of high oceanic productivity and that sustain greater rates of oceanic POC uptake may be able to maintain calcification longer into the future.

1. Introduction

Coral reefs support hundreds of millions of people worldwide by providing food, coastal protection, cultural sustenance, and economic revenue (Moberg & Folke, 1999). In order to maintain their structure and persist over time, coral reefs must produce more calcium carbonate (CaCO₃) than is removed by destructive processes including dissolution, physical erosion, and bioerosion (Chave et al., 1972; Eakin, 1996). Climate-related perturbations (e.g., ocean acidification and warming) threaten the delicate balance between calcification and dissolution, and considerable attention has been given to understanding the suite of environmental factors important for maintaining net calcification (Kleypas et al., 1999). Relationships between net ecosystem calcification (NEC; the difference between calcification and dissolution) and net ecosystem production (NEP; the difference between organic production and respiration), aragonite saturation state (Ω_{ar}), light, temperature, dissolved nutrient concentrations, coral cover and water flow have been documented, but the strength and slope of these correlations vary between ecosystems (Albright et al., 2013; Comeau

et al., 2014; Courtney et al., 2017; DeCarlo et al., 2017; Langdon & Atkinson, 2005; McMahon et al., 2013; Page et al., 2017; Shamberger et al., 2011; Silverman et al., 2007, 2009). Even when coral reefs experience conditions unfavorable for calcification, NEC can be positive (DeCarlo et al., 2017; Shamberger et al., 2018), which suggests that the range of factors that influence calcification have not been fully constrained.

Corals receive energy to meet their metabolic demands in two ways. First, through their symbiotic relationship with dinoflagellates (family Symbiodiniaceae), corals can receive up to 100% of their daily metabolic needs via photosynthesis (LaJeunesse et al., 2018; Muscatine et al., 1981). The photosynthetically fixed carbon provides energy for calcification (i.e., light-enhanced calcification; Chalker & Taylor, 1975). Heterotrophy is the second source of energy and can contribute up to 66% of the fixed carbon incorporated into coral skeletons (Houlbrèque & Ferrier-Pagès, 2009). The influences of light, carbon dioxide (CO₂) levels, and temperature on the relationship between heterotrophy and coral calcification have been explored primarily in laboratory settings. With the addition of particulate nutrients (e.g., brine shrimp and mixed zooplankton), calcification rates increase and growth rates are maintained under low light (Drenkard et al., 2013; Ferrier-Pagès et al., 2003). The effects of acidification on heterotrophy and calcification are mixed; some studies have found reduced heterotrophy under acidified conditions (Houlbrèque et al., 2015; Smith et al., 2016), while others show fed corals sustain calcification rates when exposed to elevated seawater CO₂ (Drenkard et al., 2013; Edmunds, 2011; Towle et al., 2015). While heterotrophy can account for up to 35% of daily metabolic requirements in healthy corals, bleached corals can receive up to 100% of daily metabolic requirements from heterotrophy (Grottoli et al., 2006), though metabolic needs of bleached corals may also be met by catabolism of energy-rich biomass (Wall et al., 2019). Combined, these studies suggest some corals can allocate more energy to calcification through increased heterotrophic feeding and that heterotrophy may allow corals to maintain calcification rates under some stressors.

Coral reefs live in oligotrophic environments yet maintain some of the highest production rates of any ocean ecosystem (Odum & Odum, 1955; Sargent & Austin, 1949). Early studies suggested that particulate organic matter (POM) transported to the reef from offshore was an insignificant source of nutrients, and high productivity was therefore attributed to efficient, internal nutrient recycling (Johannes et al., 1972). Although autochthonous POM is an important nutrient source for the reef, more recently, it has become apparent that oceanic-sourced POM in small size fractions (<5 μm) is a significant external source of nutrients to coral reefs, that reefs actively consume oceanic POM, and that advection of offshore POM to the reef is required to balance reef uptake (Patten et al., 2011; Wyatt et al., 2010, 2013; Yahel et al., 1998). Taken together, laboratory and field studies suggest that coral reef consumption of oceanic POM may elevate NEC.

In this study, we utilized metabolically induced changes in carbonate chemistry and particulate organic carbon (POC) to test for a correlation between NEC and oceanic POC uptake (POC_{oc-up}) on the Kāne'ohe Bay barrier reef off O'ahu, Hawai'i. We show that higher rates of NEC correspond to greater POC_{oc-up}, even at low Ω_{ar}. These results provide evidence for a relationship between oceanic POC uptake and reef scale calcification and suggest that offshore productivity could be a critical component to the resistance or susceptibility of coral reefs to climate change stressors.

2. Materials and Methods

We conducted two 4-day studies from 14–17 and 23–26 January 2017 on the southeast portion of the Kāne'ohe Bay barrier reef (Figure 1). Discrete near-surface (~1 m) seawater samples for total alkalinity, dissolved inorganic carbon, total POC concentration ([POC]), δ¹³C-POC, and dissolved inorganic nutrients were collected at morning (7:00–9:00), noon (12:30–13:30), and evening (16:00–17:00) along an assumed water flow path, from offshore of the reef crest (three offshore sites), across the reef flat (Sites 2 and 3) and into the lagoon (one lagoon site; Figure 1 and Table S1 in the supporting information). Due to time constraints, the middle offshore station was prioritized and sampled each period, and those samples were used in this analysis. Water for [POC] and δ¹³C-POC analyses were also collected on 20 January and 29 January from 'Āhuimanu Stream, which empties into central Kāne'ohe Bay (Figure 1a). Nortek Aquadopp Acoustic Doppler current Profilers were placed at Stations 2–5 and measured current velocity profiles at 4-min intervals (Figure 1). We used a quasi-Lagrangian framework (similar to that used in DeCarlo et al., 2017) to reconstruct water flow paths and residence time of water on the reef flat. For detailed methods, see Supporting Information S1.

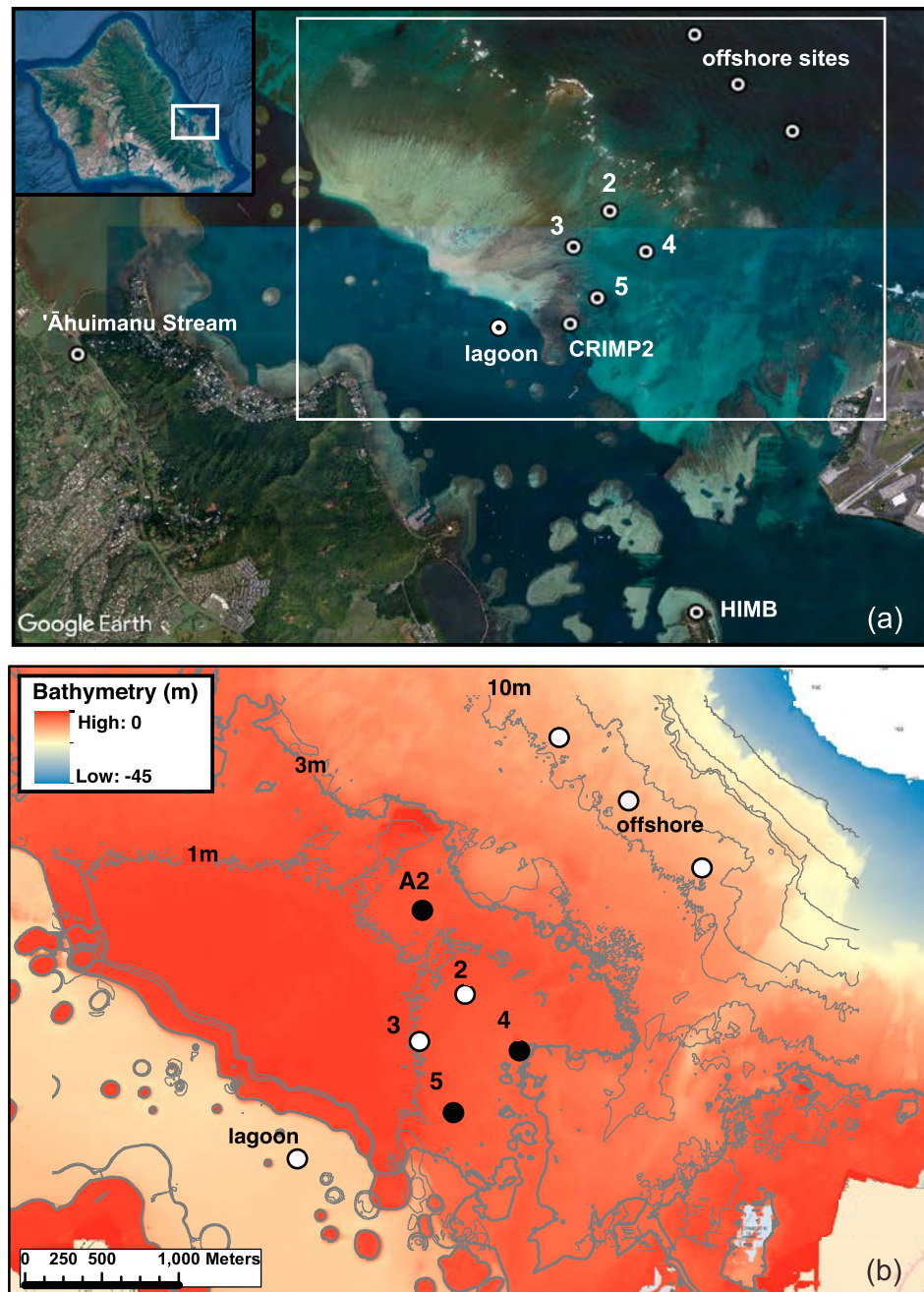


Figure 1. (a) Satellite image of O'ahu and location of Kāne'ohe Bay with study site boxed in white (inset) and image of bay with locations of sampling sites, Hawai'i Institute of Marine Biology (HIMB), CRIMP2 buoy, and 'Āhuimanu Stream; white box in (a) shows bathymetric image in (b) of study location and sampling sites. Discrete sampling sites in (b) are show in white. Instruments were deployed at Stations 2–5, but Stations 4 and 5 were not sampled for water chemistry. The primary offshore site for sampling was the middle station. A2 was used as a reference point in the residence time calculations (see Supporting Information S1; Lowe et al., 2009b).

3. Results

During the first deployment, average current speeds were 3.3 ± 1.8 cm/s at Site 3 and 7.4 ± 3.8 cm/s at Site 2. Stormy conditions during the second deployment increased average current speed to 7.4 ± 3.3 cm/s at Site 3 and 20.3 ± 6.9 cm/s at Site 2. This led to different water flow paths between the two deployments (Figure S1). Flow conditions during the first deployment were driven primarily by tides interacting with the shallow-

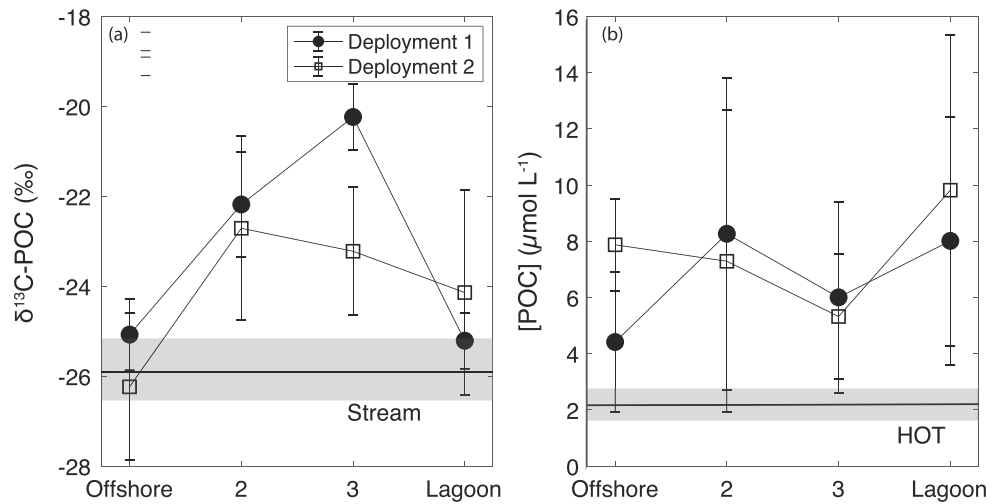


Figure 2. $\delta^{13}\text{C}$ -particulate organic carbon (POC; ‰) and total POC concentration ([POC], $\mu\text{mol/L}$) measured during first (closed circle) and second (open square) deployments; (a) $\delta^{13}\text{C}$ -POC (‰; mean \pm 1 std dev) at each site, including the 'Āhuimanu Stream mean (black horizontal line) \pm 1 standard deviation (shading), and (b) total POC concentration ([POC], $\mu\text{mol/L}$) at each site, including the Hawaii Ocean Time series (HOT) 1989–2016 mean (black horizontal line) and \pm 1 standard deviation (shading).

water bathymetry, causing water parcels to meander back and forth across the reef flat. Due to these conditions, eight water parcels traveled from the lagoon to our reef sites before they were sampled (Figure S2). An additional four reef samples had salinity-total alkalinity signatures of lagoon water based on this and previous studies (Figure S3; Courtney et al., 2018; Fagan & Mackenzie, 2007; Shamberger et al., 2011). All reef data determined to be influenced by lagoon water were not included in this analysis. During Deployment 2, breaking waves on the reef crest drove unidirectional flow across the reef (e.g., Lowe et al., 2009a). Consequently, average residence time during the first deployment was 13.4 ± 2.7 hr compared to 3.5 ± 1.5 hr during the second deployment (Table S2). After excluding samples affected by offshore flow from the lagoon, as well as several POM samples lost to laboratory analysis errors (e.g., carbonate contamination and dropped samples), a total of 29 of 47 paired NEC-POC_{oc-up} samples was deemed reliable for this analysis.

A two end-member isotope mixing model was used to calculate POC_{oc-up} (see Supporting Information S1). The mixing model relies on the assumptions that each of the sources have a distinct isotopic composition, there are no additional sources of POC other than the open ocean and the reef, and the $\delta^{13}\text{C}$ -POC increases as water traverses across the reef (e.g., from POC composed of autotrophic phytoplankton to POC derived from a mix of heterotrophic and autotrophic reef organisms). First and second deployment average offshore $\delta^{13}\text{C}$ -POC was -25.1 ± 0.86 ‰ and -26.2 ± 1.64 ‰, respectively (Figure 2a). At Site 2, mean $\delta^{13}\text{C}$ -POC was -22.8 ± 0.70 ‰ and -23.1 ± 1.20 ‰ for Deployments 1 and 2, respectively. Mean $\delta^{13}\text{C}$ -POC at Site 3 was -20.1 ± 0.73 ‰ and -23.2 ± 1.43 ‰ for Deployments 1 and 2, respectively. Within each site, there was no significant difference in average $\delta^{13}\text{C}$ between deployments, except at Site 3 which had a heavier (more positive) $\delta^{13}\text{C}$ during the first deployment. This is probably because water residence time was longer during Deployment 1, which allows reef POM to accumulate and contribute a greater proportion to the total POM pool. Offshore $\delta^{13}\text{C}$ -POC was significantly different from Sites 2 and 3 but not from the stream (-25.8 ± 0.80 ‰) or lagoon (first deployment = -25.2 ± 0.63 ‰, second deployment = -24.1 ± 2.27 ‰; Figure 2a). Although lagoon $\delta^{13}\text{C}$ -POC might be influenced by stream POC, samples at Sites 2 and 3 that originated in the lagoon (based on flow path reconstructions) were removed from this analysis. Hence, there should be no influence of lagoon or stream water at Sites 2 or 3 for samples with which we calculated POC_{oc-up}. There was no significant difference in mean total [POC] (6.41 ± 4.00 $\mu\text{mol/L}$) between sites or deployments (Figure 2b). Mean total [POC] for all sites in Kāne'ohe Bay was greater than the mean surface [POC] at Hawaii Ocean Time series (2.13 ± 0.50 $\mu\text{mol/L}$) and lower than or comparable to [POC] measured at other reefs worldwide (~ 10 $\mu\text{mol/L}$; Atkinson & Falter, 2003).

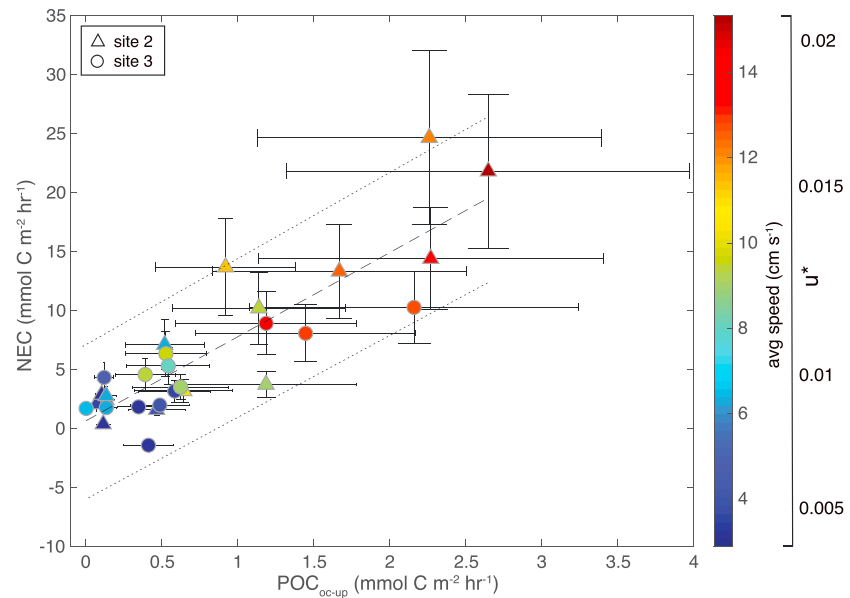


Figure 3. Oceanic particulate organic carbon uptake (POC_{oc-up}) and net ecosystem calcification (NEC) for Sites 2 (triangles) and 3 (circles), with linear regression (dashed line) and 95% confidence interval (dotted lines). The color bar represents average flow speed and calculated turbulent velocity (u^*) across the transect, for each water parcel sampled. The black bars represent uncertainties determined by a Monte Carlo simulation (see Supporting Information S1).

NEC and POC_{oc-up} were calculated across two flow paths: from the reef crest to Site 2 and from the reef crest to Site 3 (Figures 1 and S1; see Supporting Information S1 for all calculations). During Deployment 1, there was no significant difference in NEC between sites, but POC_{oc-up} was higher at Site 3 (Table S3). During Deployment 2, NEC was higher at Site 2, but there was no significant difference in POC_{oc-up} between sites. Average NEC for Deployments 1 and 2 were 1.62 ± 1.40 and 8.45 ± 6.40 $mmol\ C\ m^{-2}\cdot hr^{-1}$, respectively. Average POC_{oc-up} for Deployments 1 and 2 were 0.30 ± 0.20 and 1.03 ± 0.81 $mmol\ C\ m^{-2}\cdot hr^{-1}$, respectively (Table S3). Both NEC and POC_{oc-up} were significantly higher during the second deployment. A linear, positive correlation exists between NEC and POC_{oc-up} (slope \pm SE = 9.39 ± 1.22 , $n = 29$, $R^2 = 0.76$, $p < 0.001$), with higher NEC and POC_{oc-up} corresponding to faster average flow speeds and presumably greater turbulent velocities ($u^* = \sqrt{C_d \cdot U^2}$, where C_d is the bottom drag coefficient, $C_d = 0.02$ for Kāne'ohe Bay, Lowe et al., 2009b; and U is the magnitude of the velocity along the flow path; Figure 3 and Table S4). Average flow speed was linearly correlated to NEC ($R^2 \geq 0.62$), and both linearly and exponentially correlated to POC_{oc-up} ($R^2 \geq 0.69$ and $R^2 \geq 0.76$, respectively; Figure S4 and Table S4). No strong correlations existed between either NEC or POC_{oc-up} and NEP, Ω_{ar} , light, dissolved inorganic nutrients, and temperature (Table S4).

4. Discussion

4.1. Environmental Drivers of NEC

The Kāne'ohe Bay barrier reef was net calcifying during most of this study, and NEC rates appear to overlap with previous Kāne'ohe Bay studies (Courtney et al., 2018; Shamberger et al., 2011). However, methodological differences between the studies make it difficult to directly compare NEC rates across the three studies. As noted by Courtney et al. (2018), differences between studies may be attributed to differences in the method used to estimate residence time and in the spatial scales over which sampling was performed. For example, Courtney et al. (2018) and Shamberger et al. (2011) used a model to estimate currents and residence time on the reef (Lowe et al., 2009a), whereas currents were directly measured in this study. In addition, this study and Shamberger et al. (2011) measured NEC across a reef transect, while Courtney et al.'s (2018) sites span the entire width of the barrier reef as well as offshore and lagoon waters. Measuring currents during this study revealed that NEC is positively correlated with flow speed. Faster flow speeds imply larger turbulent velocities and enhanced vertical exchange, creating thinner boundary layers and promoting mass flux

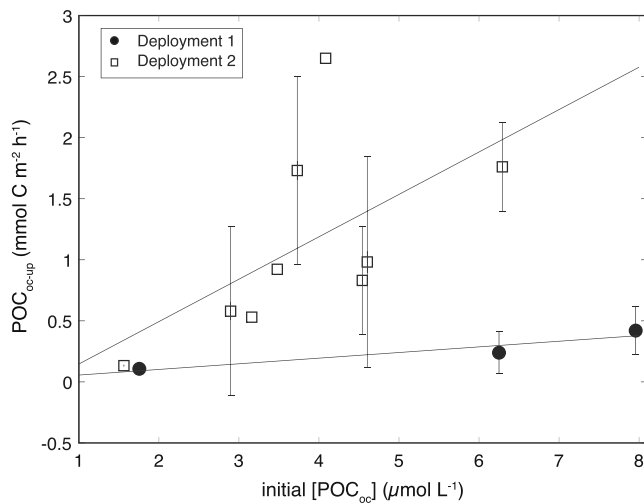


Figure 4. Relationship between initial oceanic particulate organic carbon (POC) concentration ($[POC_{oc}]$, $\mu\text{mol/L}$) and average POC_{oc-up} ($\text{mmol C}\cdot\text{m}^{-2}\cdot\text{hr}^{-1}$) at Sites 2 and 3, for Deployments 1 (circles) and 2 (squares). Since multiple parcels at Sites 2 and 3 were tracked back to the same initial oceanic POC measurement, we used the average POC_{oc-up} associated with each offshore POC measurement. The error bars represent ± 1 standard deviation.

(Davis & Monismith, 2011). This may have benefitted calcification by enhancing uptake of carbonate and bicarbonate ions and export of hydrogen ions between coral reef calcifiers and the surrounding water (Comeau et al., 2014; Jokiel, 2011).

NEC was also significantly correlated with POC_{oc-up} , which suggests that the ecosystem can utilize this external food source to elevate calcification (Figure 3 and Table S4). Heterotrophy has been hypothesized to elevate NEC on other reefs (DeCarlo et al., 2017; Shamberger et al., 2011; Yeakel et al., 2015). For example, Yeakel et al. (2015) observed a correlation between enhanced offshore productivity and NEC on a Bermuda coral reef and speculated that pulses of external nutrition were increasing heterotrophy and NEC on the reef. DeCarlo et al. (2017) measured the highest coral reef NEC rates, despite low Ω_{ar} , at Dongsha reef in the northern South China Sea, a region affected by strong internal waves (Alford et al., 2015). Internal waves can deliver nutrient-rich water to the surface layer via upwelling, enhance phytoplankton productivity, and increase the flux of organic matter to nearby coral reefs (Leichter et al., 1998). Although Palardy et al. (2005) documented reduced coral feeding during upwelling in the Gulf of Panama, Roder et al. (2010) found that corals exposed to large internal waves in the western Pacific show signs of enhanced heterotrophy and growth relative to corals sheltered from internal waves. While the effects of upwelling on coral reef heterotrophy are unclear, and likely influenced by multiple co-occurring factors

(e.g., temperature and pH), external inputs of POM and subsequent heterotrophic consumption of this organic matter may have provided additional nutrients to elevate NEC at Dongsha and other reefs (DeCarlo et al., 2017).

4.2. Environmental Drivers of Oceanic POC Uptake

The rate of POC_{oc-up} appears to be affected by flow regime, where faster speeds lead to greater POC_{oc-up} (Figure 3 and Table S4). The effects of flow speed on capture rates by suspension feeders have been explored in both laboratory and field studies, and in most cases, optimal speeds for particle trapping are approximately 10–30 cm/s (Fabricius et al., 1995; Ribes et al., 2003; Sebens et al., 1998; Sebens & Johnson, 1991). We measured the greatest POC_{oc-up} rates during Deployment 2, when average current speed was near or within the range of optimal flow for particle capture (Figures 3 and S4). Calculated turbulent velocity (u^*) was also greater during the second deployment, suggesting that stronger, vertical turbulent mixing aids POC consumption by breaking down the bottom boundary layer and replacing POC removed by reef organisms (Monismith et al., 2010). Alternatively, low flow conditions (e.g., during Deployment 1) reduce turbulent mixing, increase residence times, and may lead to a depleted POM boundary layer.

Ribes et al. (2003) found that particle removal by coral communities was proportional to particle concentration. At global scales, corals have been shown to consume more carbon via heterotrophy in areas with higher concentrations of chlorophyll *a*, a proxy for phytoplankton (Fox et al., 2018). We observed a significant correlation (slope \pm SE = 0.44 ± 0.54 , $R^2 = 0.58$, $p < 0.001$) between offshore $[POC]$ ($[POC_{oc}]$) and POC_{oc-up} during the second deployment, but POC_{oc-up} was less sensitive to changes in $[POC_{oc}]$ during the first deployment (slope \pm SE = 0.05 ± 0.01 , $R^2 = 0.94$, $p < 0.05$) when flow speeds were below optimal for particle capture (Figure 4). These relationships suggest that at optimal flow, the availability of offshore POC can either limit or enhance particle consumption. However, reduced flow may inhibit POC consumption by the reef as a result of limited advection and mixing, or other means, despite sufficient offshore availability.

4.3. Implications for Coral Reef Health Under Climate Change Stressors

Significant relationships between NEC and Ω_{ar} and between NEC and NEP have been observed in individual reef ecosystems, though these relationships are highly variable (Albright et al., 2013; Andersson et al., 2009; Shamberger et al., 2011; Shaw et al., 2015). However, when examining all the data in this study, there is no correlation between NEC and reef Ω_{ar} or NEP (Figure 5 and Table S4). Similarly, when

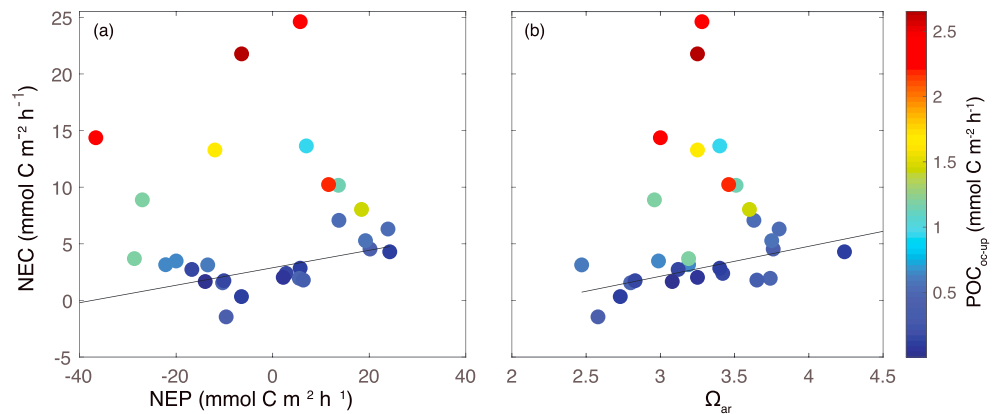


Figure 5. Relationships between (a) net ecosystem calcification (NEC)-net ecosystem production (NEP) and (b) NEC-reef Ω_{ar} . Colors represent oceanic particulate organic carbon uptake (POC_{oc-up}). Significant correlations ($p < 0.01$) for NEC-NEP ($R^2 = 0.58$) and NEC- Ω_{ar} ($R^2 = 0.63$) exist at $POC_{oc-up} < 0.9 \text{ mmol C}\cdot\text{m}^{-2}\cdot\text{hr}^{-1}$, which also corresponds to lower NEC (approximately $< 6 \text{ mmol C}\cdot\text{m}^{-2}\cdot\text{hr}^{-1}$).

combining data from coral reefs globally, no significant relationship is found between NEC and Ω_{ar} or NEP (DeCarlo et al., 2017). In contrast, our data do show relationships between NEC and reef Ω_{ar} and between NEC and NEP when POC_{oc-up} rates were low ($< 0.9 \text{ mmol C}\cdot\text{m}^{-2}\cdot\text{hr}^{-1}$; Figure 5 and Table S4). It is possible that a global relationship between NEC and Ω_{ar} or NEP is not apparent because data from reefs with both high and low POC_{oc-up} are being combined. Furthermore, the Kāne'ohe Bay barrier reef ecosystem maintained positive NEC at low POC_{oc-up} , indicating that there are other important factors driving NEC at low POC_{oc-up} . We do not have enough data to evaluate the sensitivity of NEC to Ω_{ar} or NEP under high POC_{oc-up} , but laboratory experiments on adult corals suggest heterotrophy may ameliorate ocean acidification effects (Edmunds, 2011). Experiments on coral spat suggest that heterotrophy increases the rate of calcification but does not change the sensitivity of calcification to decreasing Ω_{ar} (i.e., coral calcification decreases at similar rates under fed and unfed conditions; Drenkard et al., 2013). In other words, coral reefs with higher POC_{oc-up} may not respond any differently to ocean acidification, but they may persist longer because their initial food supply is greater and hence supports higher initial NEC rates. Considering heterotrophy of oceanic POM in NEC studies may help to resolve variability across individual reefs and in the global NEC- Ω_{ar} relationship and identify coral reefs that are likely to maintain net calcification further into the future under climate change stressors.

Rising sea surface temperatures have enhanced stratification in low-latitude regions, where coral reefs reside (Gruber, 2011). These areas experience reduced nutrient fluxes to the upper ocean and a decrease in surface ocean productivity. Furthermore, ocean acidification is expected to impair calcification and enhance dissolution in phytoplankton that form calcium carbonate tests (e.g., coccolithophores; Beaufort et al., 2011). Altering the structure of oceanic phytoplankton communities may affect coral feeding, although the ability of corals to selectively feed on phytoplankton based on prey species or size remains somewhat speculative (Leal et al., 2013). Changes in small- and large-scale circulation patterns may also affect phytoplankton diversity and dispersal (Barton et al., 2010). Combined, these processes could alter or reduce oceanic POM export to coral reefs, thereby decreasing the availability of external nutrients required to maintain high ecosystem calcification rates.

This is the first study to examine the relationship between offshore POC uptake and NEC, and more studies are needed to comprehensively understand this relationship in the context of ecosystem-wide processes, different environmental conditions and temporal scales, and multistressor interactions at Kāne'ohe Bay and other coral reefs worldwide. For example, greater POC_{oc} inputs may support calcification, but high amounts of organic matter and subsequent decomposition within sediments enhance $CaCO_3$ dissolution (Andersson & Gledhill, 2013). In addition, NEC is a measure of calcification by all coral reef calcifiers (e.g., corals and coralline algae), and both calcifying and noncalcifying taxa (e.g., detritivores and sponges) consume POC, which could impact the relationship between NEC and POC_{oc-up} . Furthermore, we acknowledge that the

observed correlation may be driven by the dependency of both NEC and $\text{POC}_{\text{oc-up}}$ on flow speeds. However, given the experimental evidence linking heterotrophy and coral calcification in laboratory studies (Drenkard et al., 2013; Edmunds, 2011; Towle et al., 2015), the field correlation between $\text{POC}_{\text{oc-up}}$ and NEC deserves further exploration.

5. Conclusions

The results of our study indicate that the reef ecosystem is consuming oceanic POC and may be utilizing this external resource to elevate calcification. $\text{POC}_{\text{oc-up}}$ appears to be sensitive to flow speeds, as well as the availability of offshore POC. Reductions in offshore productivity via changes in surface ocean temperatures, stratification, and nutrient supply have already been documented (Behrenfeld et al., 2006; Boyce et al., 2010; Polovina et al., 2008). Ocean acidification, warming, and circulation changes will also impact phytoplankton community composition and dispersion (Barton et al., 2010; Beaufort et al., 2011; Karl et al., 2001; Riebesell et al., 2000). These changes could decrease or alter the food supply to coral reefs, resulting in reef-scale calcification declines and negatively impacting the structure and health of reef ecosystems. Alternatively, coral reefs that receive an ample supply of oceanic POC (e.g., via internal waves and upwelling) and that have faster water flow may be more resistant to stressors that impede calcification.

Acknowledgments

Data needed for calculations are available in the supporting information. Additional data can be provided upon request directly from the corresponding author or accessed by links provided in the supporting information. The authors declare no competing financial interests. We thank Texas Sea Grant for providing partial funding for this project to A. Kealoha through the Grants-In-Aid of Graduate Research Program. We also thank the NOAA Nancy Foster Scholarship for PhD program funding to A. Kealoha and Texas A&M University for funds awarded to Shamberger that supported this work. This research was also supported by funding from National Science Foundation Grant OCE-1538628 to Rappé. The Hawaii Institute of Marine Biology (particularly the Rappé Lab and Jason Jones), NOAA's Coral Reef Ecosystem Program, Connie Previti, Serena Smith, and Chris Maupin were instrumental in sample collection and data analysis.

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