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Control of net community production by microbial community respiration at Station ALOHA

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Abstract

Net community production (NCP) constrains the amount of carbon that is available for storage within or export from, the photic zone of marine ecosystems. With

the aim of studying the control exerted by microbial community respiration (MCR) and gross primary production (GPP) over NCP, short-term variability in rates of MCR, GPP and NCP were measured over a 13 day sampling period (August 23 – September 4, 2012) at Station ALOHA. During this period, picoplankton abundances and concentrations of photosynthetic pigments demonstrated weak to moderate decreases coincident with the passage of a low salinity water mass through the sampling area. During the same period, rates of MCR, measured using the iv-INT method, varied by 2.7-fold. Rates of primary production (PP) were estimated based on four different methodologies: Fast Repetition Rate Fluorometry (FRRF), ^{14}C-bicarbonate assimilation, diel changes in mixed layer O_2 concentrations based on Seaglider measurements, and isotopic composition ($^{17}\Delta O_2$) of dissolved O_2. Remarkably, these different methods for measuring microbial metabolism were consistent, suggesting that collectively these different approaches provide an accurate constraint on ecosystem metabolism, despite the different time and space scales over which these measurements integrate. FRRF-derived estimates of PP, which were similar in magnitude to ^{14}C-based NPP, were significantly correlated with variability in mixed layer MCR. None of the other independent measurements of PP demonstrated significant relationships to MCR. Day-to-day variability in MCR and bacterial growth efficiency (BGE), derived based on measurements of bacterial production (as estimated by ^{3}H-leucine incorporation) and MCR, were related to changes in NCP estimated from O_2/Ar ratios (O_2/Ar-NCP), suggesting short-term variability in the efficiency with which microorganisms consume dissolved organic matter exerts direct control on rates of NCP in this ecosystem. Our results highlight internal consistency among the derived rates of ecosystem metabolism using a suite of different methodologies to estimate productivity and respiration.

Moreover, we find that rates of MCR can be as variable as PP and that variability in MCR may regulate NCP in this ecosystem.

Keywords: microbial community respiration, primary production, net community production, euphotic zone, Station ALOHA

1. Introduction

Net community production (NCP) in the ocean is the local balance between gross primary production (GPP) and microbial community respiration (MCR) and constrains the amount of carbon that is available for storage within, or export from, the photic zone (Ducklow, 1983; del Giorgio and Duarte, 2002; Ducklow and Doney, 2013). Over short-time scales (<1 month), oceanic NCP can vary considerably due to changes in GPP, MCR, or both (Arístegui and Montero, 1995; Robinson et al., 1999; Williams et al., 2004; Teira et al., 2010; Aranguren-Gassis et al., 2011; Martínez-García and Karl, 2015). A long-lasting debate regarding net ecosystem metabolism (i.e., the balance between GPP and MCR) of oligotrophic systems (Ducklow and Doney, 2013, Serret et al., 2015) highlights the difficulty of sampling GPP and MCR at appropriate temporal and spatial scales (Arístegui and Harrison, 2002; Karl et al., 2003; Williams et al., 2004), since these two metabolic processes may not always be coupled. Traditionally, volumetric rates of GPP have been found to be more variable than MCR (Robinson and Williams, 2005), and therefore GPP has been hypothesized to control variability in the metabolic balance of the surface ocean (Arístegui et al., 2002; Westberry et al., 2012; Duarte et al., 2013; Regaudie-de-Gioux and Duarte 2013; Williams et al., 2013). However, relationships between GPP and MCR appear time and space variable (Serret et al., 2002; Gist et al., 2009; Serret et al., 2015) and depth-integrated MCR has been observed to vary as much as GPP (Duarte and Agustí, 1998; Robinson and Williams, 2005, Serret et al., 2015) especially in response to stochastic habitat variability (González et al., 2001; Maixandeau et al., 2005; Arístegui and Montero, 2005; Mouriño-Carballido, 2009).

Station ALOHA (22º45'N 158º00'W) is an oligotrophic site located in the North Pacific Subtropical Gyre, north of the Hawaiian island of Oahu. This site has been the

focus of near-monthly sampling since 1988 by the Hawaii Ocean Time-series (HOT) program (http://hahana.soest.hawaii.edu/hot/). During the summer of 2012, high-resolution fixed-point observations of hydrographic and biogeochemical parameters were measured to further extend the temporal resolution of these near-monthly time series observations (Wilson et al., 2015). This Eulerian sampling facilitated the detection of a distinct sea-surface salinity minimum feature, which was prominent in the upper water column (0 – 50 m) for a period of approximately 30 days. This feature was spatially heterogeneous and propagated through the ALOHA sampling region from late August to late September 2012. This feature appeared to advect into the ALOHA sampling region from southeast of the Hawaiian Islands (Wilson et al. 2015). During a 13-day period that coincided with the passage of this low-salinity feature, several simultaneous independent measurements of primary production (PP) were measured at Station ALOHA, including PP rates estimated from fast repetition rate fluorometry (FRRF); rates of net primary production (NPP) inferred from ^{14}C in vitro incubations; and GPP based on *in situ* measurements of O_2 isotopic composition as well as from diel O_2 cycles observed using Seagliders (Wilson et al., 2015, Nicholson et al., 2015). Simultaneously, independent measurements of NCP, based on time-varying changes in O_2/Ar ratios, were obtained. Such independent measurements of productivity are infrequently obtained together, particularly over a multi-day period at a fixed point in the oligotrophic ocean where these measurements present methodological challenges (Regaudie-de-Gioux and Duarte, 2013; Serret et al., 2015). Hence, this suite of productivity measurements offers a unique opportunity to assess consistency in derived rates of metabolism, and assess short-term (daily scale) variability in GPP, NPP, NCP, and MCR in the upper water column of the NPSG.

In the current study, we provide independent measurements of size-fractionated MCR in surface waters at Station ALOHA collected during this 13-day sampling period, and place the derived rates of MCR into context of the suite of measurements on productivity. We hypothesized that MCR could be as important in determining NCP as changes associated with GPP. In order to test this hypothesis we compared the short-term changes of different and independent measurements of MCR, PP and NCP in the mixed layer at Station ALOHA in summer 2012.

2. Methods

2.1. Study site, sampling and ancillary measurements- Samples were collected at Station ALOHA (22º45'N 158º00'W) on the HOE-DYLAN IX (Hawaii Ocean Experiment: DYnamics of Light And Nutrients) cruise from 23 August to 4 September 2012. This sampling was embedded in a set of oceanographic expeditions at Station ALOHA during summer 2012 (8 July – 11 September). To characterize the upper water column, vertical profiles (0 – 400 m) of hydrographic parameters were conducted every 4 h and in addition to shipboard CTD measurements, vertical profiles of salinity, temperature and O_2 were collected from Seagliders and Argo floats. Biogeochemical properties of the water column (nutrient, particulate, and pigment concentrations) were sampled at discrete depths (between 5 and 175 m) by conducting vertical profiles at least every 3 days. These vertical profiles were supplemented by higher temporal-resolution (daily-scale) sampling at 25 m. Water samples were collected in 12-L polyvinylchloride (PVC) bottles attached to a CTD rosette sampling system. Sampling and analytical procedures were similar to those currently used by the HOT program (http://hahana.soest.hawaii.edu/ hotcold.html). Mixed layer depths were determined based on a 0.125 unit change in potential density relative to the near-surface waters.

Extended information regarding study site, sampling, and methodological approach have been described in Wilson et al., (2015), Nicholson et al., (2015), and Viviani and Church (2017).

2.2. *In vivo INT Microbial Community Respiration (MCR)*- Seawater samples (two killed controls and three live) were collected from 25 m at 0400 local time on a daily basis. Seawater was subsampled from CTD rosette casts, and rates of MCR were estimated from the reduction of the tetrazolium salt 2-(p-iodophenyl)-3-(p-nitrophenyl)-5-phenyltetrazolium chloride (INT) to INT-formazan (INT-F) by Electron Transport System (ETS) dehydrogenase enzymes (Martínez-García et al., 2009). Formaldehyde-killed controls (2% v/v final concentration) were included to account for potential interferences of the water sample properties (fluorescence, turbidity, etc.) on spectrophotometric absorbance, and to account for any abiotic reduction of INT (Martínez-García et al., 2009). Initial time-course experiments (incubation times up to 24 h) were performed to determine the optimal incubation time; the resulting rates of MCR were based on 1.5 h incubations. After incubation in the presence of INT, samples were fixed by adding formaldehyde (2% v/v final concentration) and sequentially filtered through 0.8 μm and 0.2 μm pore size, 25 mm diameter polycarbonate filters. Rates of respiration estimated from the >0.8 μm size-fraction are referred to as >0.8 μm MCR, while rates estimated from the 0.2 – 0.8 μm size fraction are referred to as 0.2 – 0.8 μm MCR. Total-MCR is reported as the sum of respiration in both size fractions (i.e., >0.8 μm MCR + 0.2 – 0.8 μm MCR). In order to transform INT reduction rates into O_2 consumption, a MCR/ETS ratio of 12.8 mol O_2 / mol INT-F was used (Martínez-García et al., 2009). This empirical relationship was established for nonaxenic cultures of *Isochrysis galbana* with different bacterial to algal biomass ratios

using the same incubation time for measuring O_2 consumption and INT-F formation (Martínez-García et al., 2009). A large set (n=72) of field experiments using a wide range of marine microbial planktonic communities (sampled in oligotrophic North Atlantic Subtropical Gyre and in mesotrophic/eutrophic coastal area of NW Iberian Peninsula) was also performed to evaluate if the O_2 consumption to INT reduction ratio (R/ETS) obtained with nonaxenic algal cultures was applicable for natural samples. The mean R/ETS ratio obtained for natural oligotrophic waters (12.5 [±2.0]) was not significantly different from that derived from algal cultures (Martínez-García et al., 2009).

Using our measured rates of respiration and coincident rates of bacterial production (BP) (Viviani and Church, 2017), we also calculated bacterial growth efficiency (BGE) as BP divided by the sum of BP and 0.2 – 0.8 μm MCR. This assumes that the 0.2 – 0.8 μm MCR measurements reflect the respiratory activity of bacterioplankton. Bacterial production was estimated from rates of ^{3}H-Leu incorporation into protein following procedures described in Viviani and Church (2017). A conversion factor of 1.5 kg C per mole leucine incorporated (Simon and Azam, 1989) and a respiratory quotient (RQ) of 0.9 (Williams and del Giorgio, 2005) were used for the BGE calculations.

2.3. Statistical analysis- Least square linear regression analyses were used to assess changes with time and significance level (p) and coefficient of determination (R^2) are provided. Pearson correlation analyses (Sokal and Rohlf, 1995) were used in order to assess relationships between variables and significance level (p) and Pearson´s correlation coefficient (R) are provided. Student t-test was used to assess differences between mean values. A significance level of $p<0.05$ was used in all analyses.

3. Results and discussion

3.1. Biogeochemical context

During the observation period (23 August - 4 September 2012) an anomalous low salinity feature (mean ±SE 25 m salinity 35.26 ± 0.02), restricted to the upper 50 m, was prominent at Station ALOHA. Salinity measured at 25 m significantly decreased during the study period (least square linear regression, $R^2 = 0.42$, $p<0.01$, $n = 13$) (Fig. 1). Associated changes in temperature were also observed throughout the study (Fig. 1). An extended and detailed description of this low-salinity feature and a broader hydrographic and biogeochemical context is provided in Wilson et al. (2015).

Sampling of the upper ocean during this period revealed that passage of this low salinity feature was accompanied by decreases in plankton biomass. For example, the abundances of *Prochlorococcus*, *Synechococcus*, and non-pigmented bacteria (NPB) all declined, with average abundances of all three picoplankton groups decreasing 1.5-fold (calculated as the ratio between initial and final values) throughout the observation period (least square linear regression, $R^2 = 0.50$, 0.49, and 0.69, respectively, $p<0.05$, $n = 13$; Fig. 2). The resulting decrease in picoplankton biomass may reflect conditions present in the ecosystem where this feature originated, and/or reflect time-variable changes in the balance of cell growth and removal during the propagation of this feature through the sampling region (Wilson et al., 2015). This is in accordance with previous studies at Station ALOHA and elsewhere that suggest biogeochemical changes in the euphotic zone can be related to the presence of isolated water masses associated with discrete hydrographic features (Letelier et al., 2000; Sakamoto et al., 2004; Fong et al., 2008).

3.2. Microbial community respiration (MCR) variability

Over the course of this study, samples were taken daily from 25 m to estimate size-fractionated MCR using the in vivo INT method. Total-MCR at 25 m ranged 0.43 to 1.37 mmol O_2 m^{-3} d^{-1} and averaged (±SE) 0.86 ± 0.07 mmol O_2 m^{-3} d^{-1} (Table 1 and Fig. 3A). Both the >0.8 μm and the 0.2 – 0.8 μm size fractions were important contributors to derived rates of MCR, with the 0.2 – 0.8 μm size fraction contributing, on average, 45±9% to total-MCR (Fig. 3B,C). A significant (least square linear regression, $R^2 = 0.51$, $p<0.02$, n=13) decrease in mixed layer total-MCR was observed over the period of study, with rates initially ~ 2.7-fold greater (calculated as the ratio between initial and final values) than total-MCR at the end of the cruise (Table 1). MCR estimated for the 0.2 – 0.8 μm size fraction decreased more than MCR in the >0.8 μm size fraction, with rates decreasing by 3.0- and 2.6-fold (calculated as the ratio between initial and final values), respectively.

Short-term changes in MCR were correlated with changes in abundance of NPB (Pearson correlation, R=0.73, $p<0.01$, n=13) and *Prochlorococcus* (Pearson correlation, R = 0.54, $p<0.06$, n=13) (Table 2), and as previously reported, such changes in picoplankton biomass further coincided with decreases in PP (Wilson et al. 2015, Nicholson et al. 2015). Rates of NPP estimated based on ^{14}C assimilation (^{14}C-PP), did not show a significant ($p>0.05$, n=13) trend with time throughout the period (Fig. 4A); however, a consistent and significant ($p<0.05$, n=13) downward trend in FRRF-derived PP (FRRF-PP) was observed during this period (Fig. 4B). Interestingly, day-to-day changes in FRRF-PP followed a similar pattern to those in picoplankton cell abundance and total-MCR (Figs. 2-4). In fact, short-term variability in FRRF-PP rates was significantly (Pearson correlation, R=0.67, 0.71, 0.76 and 0.58, respectively, $p<0.05$, n= 13) correlated to *Prochlorococcus, Synechococcus*, NPB cell abundance, and total-MCR rates throughout the studied period (Table 2).

In contrast, GPP, estimated based on diel changes in mixed layer O_2 concentrations obtained by Seaglider surveys (Seaglider-GPP) did not show a significant (least square linear regression, $p>0.05$, $n= 11$) trend throughout the studied period (Nicholson et al. 2015), with Seaglider-GPP 1.4-fold higher at the end of the observation period than at the beginning (Table 1 and Fig. 4C). Finally, there was no time-dependent trend (least square linear regression, $p>0.05$, $n= 10$) in derived rates of GPP estimated from in situ measurements of triple isotopic composition of dissolved O_2 ($^{17}\Delta O_2$-GPP) (Table 1 and Fig. 4D). It is important to note the differences in the temporal and spatial scales over which these measurements of metabolic rates integrate: discrete depth / depth-integrated, instantaneous / cumulative, and incubation / non-incubation (Table 1). For example, MCR, ^{14}C-PP, and FRRF-PP rates were measured at discrete depths and on daily time scales, while $^{17}\Delta O_2$-GPP, Seaglider-GPP, and O_2/Ar-NCP measurements integrate processes occurring in the upper mixed layer over weekly to monthly time scales. Moreover, measurements of MCR and ^{14}C-PP rates required incubation based methodologies (and hence short-term containment of microbial communities) while FRRF-PP, $^{17}\Delta O_2$-GPP, and Seaglider-GPP derived from non-incubation methodologies.

Several interesting observations follow these findings. First, the observed decrease in picoplankton abundances, presumably partially due to cell death, were not accompanied by an increase in nutrient concentrations (as might be associated with remineralization). Wilson et al. (2015) attribute this lack of increased nutrient concentrations to export of this material downward; hence, this material would not be available for remineralization *in situ*, which is consistent with the higher relative decrease of respiration (compared to that of picoplankton abundance) during this period.

Second, the proportionally larger decrease in MCR relative to changes in picoplankton abundance suggests decreases in per cell rates of respiration throughout the sampling period. This result is consistent with an annual study performed at Station ALOHA in which monthly changes in euphotic MCR were not related to changes in picoplankton abundance (Martínez-García and Karl, 2015) and suggests that respiration per cell fluctuates in response to temporal and spatial variability on both monthly and daily scales. In the present study, derived BGE appeared to increase over the period of observation (Fig. 3D), reinforcing the hypothesis of decreased respiration per cell.

Third, the suite of measurements of productivity and respiration utilized in this study allowed us to examine how these independent estimates of ecosystem metabolism compared over this 13-day sampling period in the oligotrophic open ocean. While the Seaglider-based diel changes in O_2 concentrations and $^{17}\Delta O_2$ measurements have been found to provide rates closer to GPP (Luz and Barkan 2009), measurements of ^{14}C-PP may approximate a rate closer to NPP (Marra 2002). The resulting $^{17}\Delta O_2$-GPP (mmol O_2 m^{-3} d^{-1}) / ^{14}C-PP (mmol C m^{-3} d^{-1}) ratios during the present study were on average 3.2 slightly higher than the previously reported average value of 2.8 in the summer at Station ALOHA (Quay et al., 2010) and than the ratio of 2.7 between gross O_2 production (GOP, mmol O_2 m^{-3} d^{-1}) (calculated as the difference between net oxygen production estimated from O_2/Ar ratios and MCR estimated from the *in vivo* INT method) and ^{14}C-PP rates (mmol C m^{-3} d^{-1}) previously reported at Station ALOHA (Ferrón et al., 2015). Similarly, the FRRF-PP (mmol O_2 m^{-3} d^{-1}) / ^{14}C-PP (mmol C m^{-3} d^{-1}) ratio averaged 1.6, similar to previously reported values (averaging ~ 1.6) from 25 m depth at Station ALOHA (Corno et al., 2006). Assuming a photosynthetic quotient (PQ) of 1.1 (Laws 1991) for the recycling intensive upper ocean waters at ALOHA, rates of GPP derived from measurements of Seaglider O_2 concentrations and $^{17}\Delta O_2$

averaged 1.54±0.12, and 1.83±0.23 mmol C m^{-3} d^{-1}, respectively (Table 1). Hence, GPP derived from the Seaglider and $^{17}\Delta O_2$ measurements were similar in magnitude, and the resulting rates were ~2.5-2.9-fold greater than the ^{14}C-based measurements of NPP. Rates of productivity estimated based on FRRF measurements (0.87±0.03 mmol C m^{-3} d^{-1}, PQ=1.1) were close in magnitude to the ^{14}C-based NPP measurements (0.62±0.02 mmol C m^{-3} d^{-1}, Table 1). Several studies have concluded that FRRF-based estimates approximate GPP (Corno et al., 2006), while in other studies FRRF-based estimates of productivity are similar in magnitude to ^{14}C-based estimates (Smyth et al., 2004).

In addition to convergence in estimates of GPP, the mean rate of MCR during this study (0.76±0.06 mmol C m^{-3} d^{-1}), measured by in vivo INT reduction and assuming a respiratory quotient of 0.9 (Williams and del Giorgio, 2005), was similar to ^{14}C- and FRRF-based estimates of PP (0.62±0.02 and 0.87 ±0.03 mmol C m^{-3} d^{-1}, respectively (Table 1). Notably, on average, rates of NCP determined by the O_2/Ar method were not significantly (Student t-test, $p>0.05$) different from zero (0.34±0.64 mmol C m^{-3} d^{-1}), consistent with the difference between PP (based on ^{14}C-PP or FRRF-PP) and MCR (Table 1). To our knowledge, such internal consistency between these different measures of ecosystem metabolism has been rarely shown, and suggests that collectively these different approaches provide accurate constraint on ecosystem metabolism. Moreover, such consistency in the mean rates of productivity during this 13 day sampling period is all the more remarkable given the known differences in time and space scales over which these measurements integrate.

Finally, despite internal consistency in the measured rates, the greater overall variability observed in rates of MCR relative to the various measures of PP highlight differential sensitivity of these measures of metabolism to spatio-temporal variability at Station ALOHA. Wilson et al. (2015) highlight this finding, reporting spatio-temporal

variability in NCP (based on O_2/Ar ratios) at Station ALOHA during the same sampling period. Interestingly, day-to-day variability in O_2/Ar-based NCP was significantly (Pearson correlation, R=-0.65, -0.58 and 0.54, respectively, $p<0.05$, n=13) related to variability in total-MCR, > 0.8 μm MCR, and BGE, while none of the four available PP estimations (^{14}C-PP, FRRF-PP, $^{17}\Delta O_2$-GPP and Seaglider-GPP) were related to O_2/Ar-NCP rates (Table 2). The greater variability in MCR relative to PP reported in the present study is consistent with recent work at Station ALOHA. Ferrón et al. (2015) reported greater daily variability in MCR (based on in vivo INT reduction) and NCP (based on O_2/Ar ratios) than in GPP. Similarly, Martínez-García and Karl (2015) observed that on monthly time scales variability in MCR (based on in vivo INT reduction) was greater than variability in estimates of NPP (based on the ^{14}C method).

Our results indicate that short-term variability in MCR may be at least as important as PP in controlling changes in NCP. Previous research has reported decreases in MCR associated with stochastic habitat variability (González et al., 2001; Maixandeau et al., 2005; Arístegui and Montero, 2005; Mouriño-Carballido, 2009), but the mechanisms responsible for such dynamics remain unclear. Previous investigations at Station ALOHA have shown that mesoscale variability can influence phytoplankton biomass (Letelier et al., 2000; Fong et al., 2008), and variations in dissolved O_2 concentrations that correspond to changes in NCP (Emerson et al., 2002, Nicholson et al., 2008; Johnson et al., 2010; Nicholson et al., 2015). Karl et al. (2003) and Williams et al. (2004) hypothesized a decoupling between a more constant heterotrophic metabolism and aperiodic bursts of GPP at Station ALOHA, related to short-term changes in grazing and/or viral lysis or resource control, determined time-variability in NCP in the open sea. Here we have shown that short-term variability in MCR can be as important as GPP in regulating NCP at Station ALOHA.

Previous studies have reported a temporal and spatial decoupling in rates of PP and MCR in the oligotrophic ocean, including at Station ALOHA (Karl et al., 2003; Williams et al., 2004; Martínez-García and Karl, 2015, Serret et al., 2015). Such decoupling may be controlled by both biotic and abiotic factors, including episodic delivery of nutrients (Karl et al. 2003), temporal variability in the types and activities of heterotrophic bacteria, and changes in the quality of available organic matter. Explicit linkages between bacterial metabolism and phytoplankton production may be confounded by the complexity of microbial food webs. In particular, the large pool of DOM may dampen direct coupling between PP and subsequent MCR; while production of cellular (particulate) material may be readily available for passage through the food web on short time scales (via predation), channeling of PP into DOM may decouple its consumption from contemporaneous PP on short (daily) time scales. Measurements of DOC production (based on the passage of ^{14}C-bicarbonate into DOC) at Station ALOHA suggest that rates of net production of DOC demonstrate greater temporal variability than in production of particulate matter (Karl et al., 1998, Viviani et al., 2015). Variability in DOM production depends on complex and interacting factors like composition and physiological state of the phytoplanktonic community, nutrient and light availability, and the intensity of predation and/or viral lysis (Nagata 2000, Carlson 2002). Such controls likely influence the composition and quality of the recently produced DOM, thereby directly regulating rates of bacterial consumption (Williams and Yentsch, 1976, Judd et al., 2006). Moreover, decoupling between production and respiration may reflect bacterial utilization of DOM pools that were not produced via contemporaneous phytoplankton growth (Carlson and Ducklow, 1996). In the current study, changes in O_2/Ar-NCP coincided with changes in BGE, suggesting that the efficiency of DOM consumption by bacteria directly affected NCP.

3. Conclusions

In summary, we have presented a detailed dataset showing that: 1) a suite of indpendent measurements yielded consistent approximations of primary production, suggesting that collectively these different approaches provide an accurate constraint on ecosystem metabolism, despite differences in time and space scales over which these measurements integrate; 2) during the 13 day observation period, rates of NCP, estimated based on measurements of O_2/Ar ratios and the difference between primary production (estimated from ^{14}C-PP rates and FRRF-PP rates) and in vivo INT-based estimates of MCR, were similar and not significantly different from zero; 3) day-to-day microbially-mediated rates of O_2 consumption can be as variable as photosynthetic production in response to upper ocean spatio-temporal variability. In conclusion, our findings highlight the need for future studies aimed at elucidating those processes controlling variability in respiration relative to that in production, with special attention on identifying how time-varying changes in the reactivity and production of dissolved organic matter influence ecosystem metabolism in the open ocean.

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Table 1. Summary of productivity and respiration measurements conducted as part of this study. For comparison, rates of metabolism are reported in carbon-based units; photosynthetic and respiratory quotients used to convert oxygen-based measurements were 1.1 and 0.9, respectively (Laws 1991, Williams and del Giorgio, 2005). Tendency with time depicts the results of least-squares linear regression analyses of the measured rates over the time-period of observation.

Abbreviation (units)	**Assumed process measured**	**Principle of technique**	**Incubation/ Non-incubation**	**Timescale of measurement**	**Mean value [±SE]** (mmol C m^{-3} d^{-1})	**Tendency with time**
MCR	Microbial Community Respiration	INT reduction	Incubation	Daily	0.76 [±0.06]	Significant decrease
BP	Bacterial Production	^{3}H-leucine incorporation	Incubation	Daily	0.03 [±0.00]	Not significant
BGE	Bacterial Growth Efficiency	BP / (BP + <0.2µm MCR)	Incubation	Daily	0.09[±0.01]	Significant increase

^{14}C-PP	Particulate Net Primary Production	^{14}C incorporation	Incubation	Daily	0.62 [±0.02]	Not significant
FRRF-PP	Gross Primary Production	Fluorescence parameters	Non-incubation	Daily	0.87 [±0.03]	Significant decrease
Seaglider-GPP	Gross Primary Production	Diurnal periodicity in dissolved oxygen	Non-incubation	Weekly/ Monthly	1.54[±0.12]	Not significant
$^{17}\Delta O_2$-GPP	Gross Primary Production	Triple oxygen isotope composition	Non-incubation	Weekly/ Monthly	1.83[±0.23]	Not significant
O_2/Ar-NCP	Net Community Production	O_2/Ar saturation	Non-incubation	Weekly/ Monthly	0.34[±0.64]	Not significant

Table 2. Pearson correlation coefficients between *Prochlorococcus* (Proch.), *Synechococcus* (Synech.), picoeukaryotes (Picoeuk.), and non-pigmented bacteria (NPB) cell abundance, primary production estimated as ^{14}C assimilation (^{14}C-PP), FRRF-based measurements (FRRF-PP), diel changes in mixed layer O_2 concentrations obtained by a Seaglider (Seaglider-GPP), and in situ measurements of triple isotopic composition

of dissolved O_2 ($^{17}\Delta O_2$-GPP), total microbial community respiration (Total MCR), respiration in the 0.2–0.8 μm size-fraction (0.2–0.8 μm MCR), respiration in the size-fraction >0.8 μm (> 0.8 μm MCR), bacterial production (BP), bacterial growth efficiency (BGE) and net community production estimated from O_2/Ar ratios (O_2/Ar-NCP) in the mixed layer. P values (between brackets) and number of samples are also provided. NS = not significant A significance level of $p<0.05$ was used in all analysis.

	Prchl.	Synech.	Picoeuk.	NPB	^{14}C-PP	FRRF-PP	SeaGlider-GPP	$^{17}\Delta$O-GPP	Total-MCR	0.2-0.8µm-MCR	>0.8 µm-MCR	BP	BGE
Synech.	0.881 (0.000)												
Picoeuk.	0.619 (0.024)	NS											
NPB	0.825 (0.001)	0.742 (0.004)	NS										
^{14}C-PP	NS	NS	NS	NS									
FRRF-PP	0.671 (0.012)	0.705 (0.007)	NS	0.761 (0.002)	NS								
SeaGlider-GPP	NS	NS	NS	NS	NS	NS							
$^{17}\Delta$O-GPP	NS	NS	NS	NS	NS	NS	NS						
Total-MCR	0.538 (0.058)	NS	NS	0.732 (0.007)	NS	0.578 (0.038)	NS	NS					
0.2-0.8µm-	NS	NS	NS	0.701	NS	NS	NS	NS	0.802				

MCR				(0.008)					(0.001)				
>0.8µm-MCR	NS	NS	NS	0.589	NS	NS	NS	NS	0.832	NS			
				(0.044)					(0.000)				
BP	0.669	0.591	NS	0.666	NS	NS	NS	NS	NS	NS	NS		
	(0.012)	(0.033)		(0.013)									
BGE	NS	NS	NS	NS	-0.579	NS	NS	NS	NS	-0.930	NS	NS	
					(0.038)					(0.000)			
O_2/Ar-NCP	NS	NS	NS	NS	NS	NS	NS	NS	-0.654	NS	-0.581	NS	0.542
									(0.015)		(0.037)		(0.050)

Figure captions

Fig. 1. Daily averaged (109 total samples): A) salinity at 25 m, B) temperature at 25 m and C) mixed layer depth calculated using 0.125 potential density surface offset at Station ALOHA during the study period. Error bars represent the standard error; where error bars are not visible, they are smaller than the symbol size.

Fig. 2. *Prochlorococcus*, *Synechococcus*, picoeukaryotes and non-pigmented bacteria (NPB) cell abundances at 25 m during the study period.

Fig. 3. (A) Daily rates of total microbial community respiration (Total MCR), (B) respiration in the 0.2 – 0.8 μm size-fraction (0.2 – 0.8 μm MCR), (C) respiration in the size-fraction >0.8 μm (> 0.8 lm MCR), (D) bacterial production (BP) and (E) bacterial growth efficiency (BGE) at 25 m. Error bars represent the standard error; where error bars are not visible, they are smaller than the symbol size.

Fig. 4. Various estimates of primary productivity during the study period. A) ^{14}C assimilation (^{14}C-PP), B) FRRF-based measurements of productivity (FRRF-PP), C) diel changes in mixed layer O_2 concentrations obtained by a Seaglider (Seaglider-GPP), and D) *in situ* measurements of triple isotopic composition of dissolved O_2 ($^{17}\Delta O_2$-GPP). Samples for A, B, and D were taken at 25 m. No Seaglider based O_2 data were available on August 31 and September 2; similarly, $^{17}\Delta O_2$-based estimates of GPP on not available for August 25, 27, and September 2. Error bars in 3A represent the standard error; where error bars are not visible, they are smaller than the symbol size.

Fig. 5. Net community production in the mixed layer at Station ALOHA during the study period estimated from O_2/Ar ratios (O_2/Ar-NCP) from samples collected from 25 m.

Figure 1

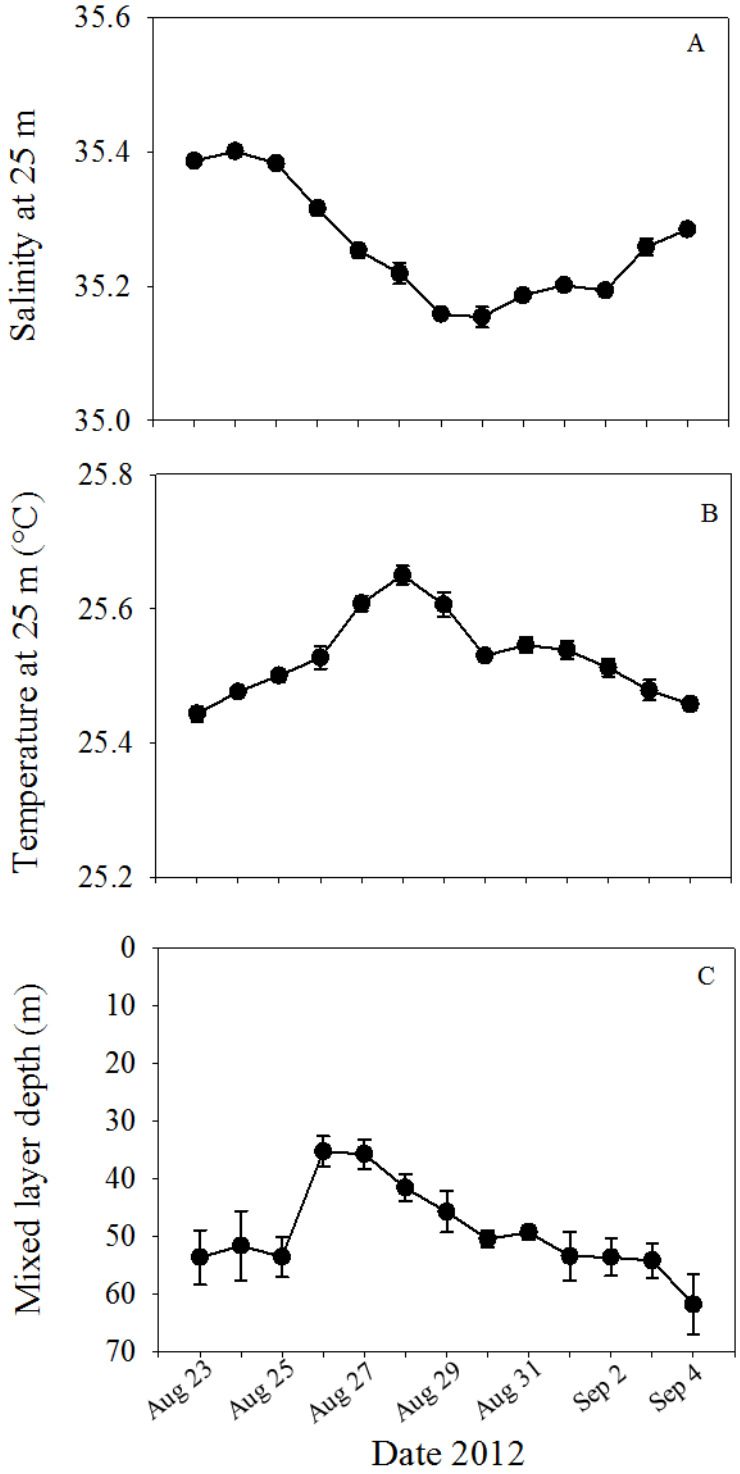


Figure 2

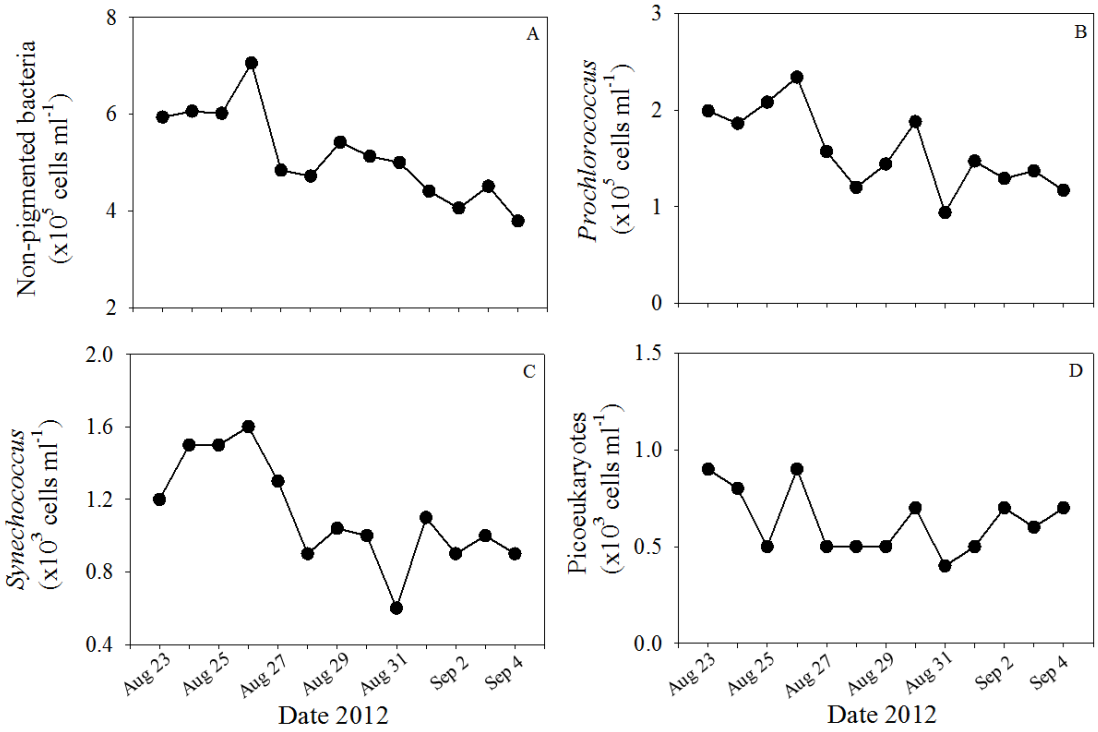


Figure 3.

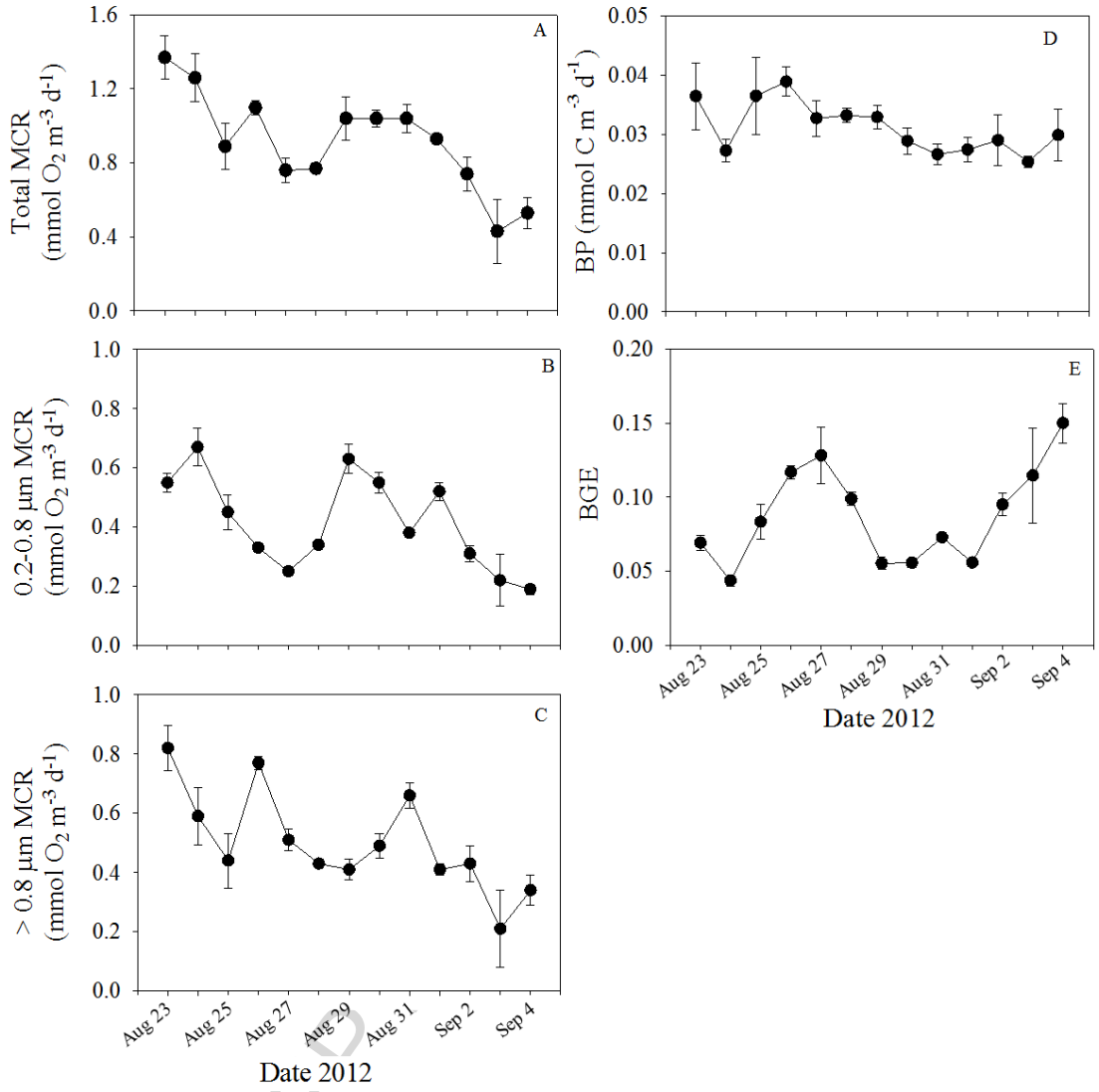


Figure 4.

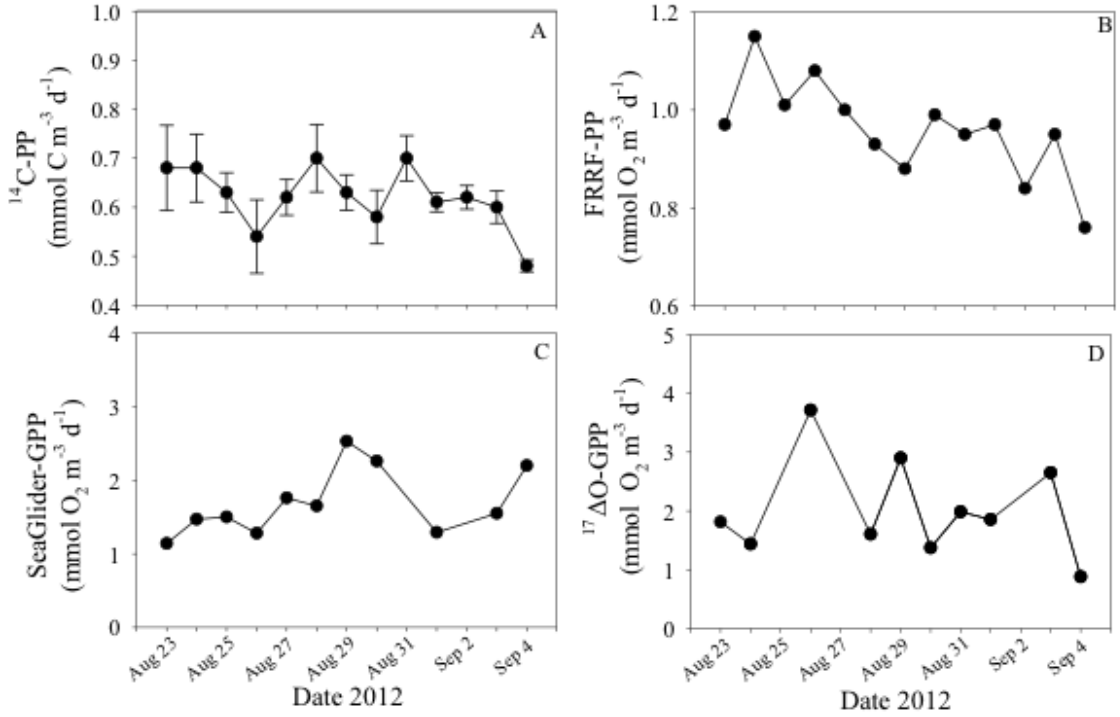
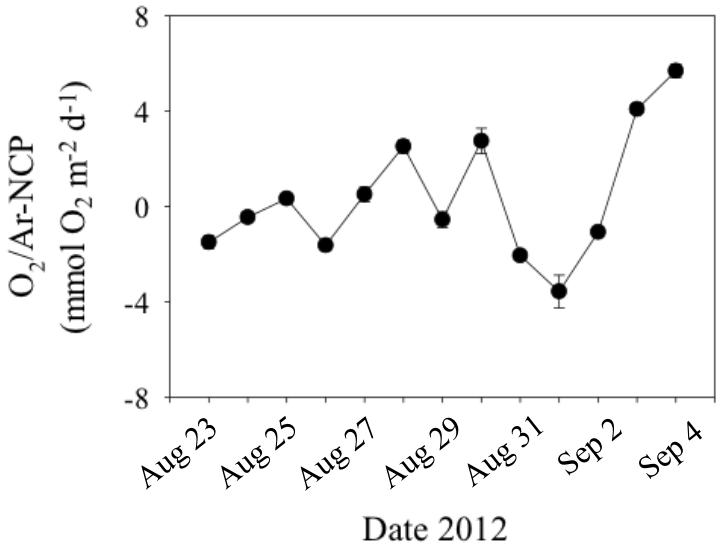


Figure 5



Control of net community production by microbial community respiration at Station ALOHA

Sandra Martínez-García, Robert R. Bidigare, Daniela A. del Valle, Laurie W. Juranek, David P. Nicholson, Donn A. Viviani, Samuel T. Wilson, and Matthew J. Church

Highlights:

- Over a 13-day period at Station ALOHA, we found internal consistency among the derived rates of ecosystem metabolism using a suite of different methodologies to estimate productivity and respiration (FRRF-, ^{14}C-, SeaGlider- and $^{17}\Delta O_2$-primary production (PP), ivINT-Microbial Community Respiration (MCR) and O_2/Ar-Net Community Production (NCP), suggesting that collectively these different approaches provide an accurate constraint on ecosystem metabolism.
- FRRF-derived estimates of PP, which were similar in magnitude to ^{14}C-based NPP, were significantly correlated with variability in mixed layer MCR. None of the other independent measurements of PP demonstrated significant relationships to MCR.
- Day-to-day variability in MCR and bacterial growth efficiency (BGE) were related to changes in NCP estimated from O_2/Ar ratios (O_2/Ar-NCP), suggesting short-term variability in the efficiency with which microorganisms consume dissolved organic matter exerts direct control on rates of NCP in this ecosystem.
- Rates of MCR can be as variable as PP and variability in MCR may regulate NCP at Station ALOHA.