Deep-Sea Research II 55 (2008) 1300–1309

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Primary production and implications for metabolic balance in Hawaiian lee eddies

Patricia M. McAndrew *, Robert R. Bidigare, David M. Karl

Department of Oceanography, University of Hawaii, 1000 Pope Road, Honolulu, HI 96822, USA

ARTICLE INFO

Article history:
Accepted 25 January 2008
Available online 6 June 2008

Keywords:
Primary production
Metabolic balance
Mesoscale eddies
Photosynthesis
North Pacific Ocean

ABSTRACT

Recent discrepancies between geochemical and biological approaches for determining whether ocean ecosystems are net heterotrophic or net autotrophic have led to uncertainty in the net metabolic state of open ocean ecosystems. Geochemical approaches indicate that the oceans are net positive autotrophic, but direct observations based on short-term incubation techniques suggest that the ocean is in a state of net heterotrophy. One hypothesis for the apparent discrepancy is that net autotrophic production occurs in aperiodic "bursts," which are superimposed on a more constant background state of net heterotrophy. Mixing events, which introduce new nutrients to the surface ocean, provide one mechanism for fueling such aperiodic bursts of net production. In conjunction with the Eddy Flux (E-Flux) program in the lee of the Hawaiian Islands during winter 2004–2005, we examined the relationship between photosynthesis and irradiance (P vs. E) in surface waters inside and outside of two cold-core, cyclonic eddies, and conducted five incubation experiments to examine the metabolic response of mixed-layer plankton communities to nutrient-rich deep-sea water additions. Our results showed that in the mixed layer, maximum rates of light-saturated photosynthesis, derived from photosynthesis–irradiance experiments were not significantly different inside vs. outside the eddies ($p = 0.35$ and 0.44 for E-Flux I and E-Flux III, respectively). Addition of nutrients to mixed-layer water showed that (1) gross primary production (GPP) became decoupled from a more constant rate of respiration and (2) net system metabolism shifted from approximate balance, or slight net heterotrophy, to a demonstrably net autotrophic system. From these results, we determined that the threshold GPP for net autotrophic production for the mixed layer of the study region was 1.65 mmol O_2 m^{-3} d^{-1}, which is consistent with previous estimates for the oligotrophic open ocean.

Published by Elsevier Ltd.

1. Introduction

Net community production (NCP) is the balance between gross primary production (GPP) and community respiration (R). When GPP < R, the ecosystem is in a state of net heterotrophy, and when GPP > R, the ecosystem is net autotrophic. Our conceptual paradigm of the open ocean (far removed from the influence of land) on time scales of months and longer is one of a net autotrophic ecosystem that exports organic carbon to depth and produces more oxygen then it consumes (Karl, 2007). Several studies have determined that oligotrophic open ocean ecosystems are net heterotrophic (del Giorgio et al., 1997; Duarte and Agusti, 1998; Williams et al., 2004), and others suggest regional (Serret et al., 2001, 2002; Aristegui and Harrison, 2002) or seasonal (Sherr and Sherr, 1996; Serret et al., 1999; Maixandeau, 2005a, b) variability in ocean ecosystem metabolism. One hypothesis to explain the apparent variability is that extended periods of net heterotrophic production are supported by aperiodic, short-term net autotrophic events (Karl et al., 2003), resulting in a complex time-space mosaic of system metabolism.

The addition of nutrients to oligotrophic surface waters has been shown to alter the metabolic balance on short (5–7 d) time scales (McAndrew et al., 2007). Mixing or other processes that introduce nutrients to the mixed layer could therefore have an important role in the metabolic balance of ocean ecosystems. Physical processes that could introduce nutrients to the upper ocean include mesoscale instabilities such as eddies (Falkowski et al., 1991; Harris et al., 1997; McGillicuddy et al., 1998; Letelier et al., 2000; Gonzalez et al., 2001; Seki et al., 2001; Bidigare et al., 2003; Sweeney et al., 2003; Vaillancourt et al., 2003), internal waves (Garrett, 2003; Gregg et al., 2003), Rossby waves (Uz et al., 2001; Sakamoto et al., 2004) and fronts (Gonzalez et al., 2001).

Both cyclonic and anticyclonic eddies occur frequently in the lee of the Hawaiian Islands (Lumpkin, 1998). They have been associated with elevated nutrient concentrations (Seki et al., 2001), increased primary production (Falkowski et al., 1991; Allen

* Corresponding author. Tel.: +1 808 781 8823; fax: +1 808 956 9516.
E-mail address: pmcandre@hawaii.edu (P.M. McAndrew).

0967-0645/$ - see front matter Published by Elsevier Ltd.
doi:10.1016/j.dsr2.2008.01.004

et al., 1996; Seki et al., 2001), changes in plankton community structure and export (Bidigare et al., 2003; Sweeney et al., 2003; Vaillancourt et al., 2003) and enhanced local fisheries (Seki et al., 2004). Moreover, systematic spatial mapping has shown differences in the net metabolic balance between water inside eddies and the surrounding waters (Gonzalez et al., 2001; Maixandeau, 2005a, b).

One of the central goals of the E-Flux project was to better understand the physical, chemical and biological evolution of cyclonic Hawaiian lee eddies (Benitez-Nelson et al., 2007). The present study examined the influence of mesoscale cyclonic eddies on rates of primary production and the net metabolic balance of the upper ocean during the three 18-day E-Flux cruises in the winter of 2004–2005. Phytoplankton physiological parameters were determined from photosynthesis vs. irradiance experiments, and five incubation experiments were conducted to measure the metabolic response of upper mixed-layer plankton communities inside and outside of lee eddies to nutrient additions. Experiments were sampled daily for measurements of GPP, NCP, R, nutrients and chlorophyll *a* concentrations. The resulting production and respiration measurements were used to determine a threshold GPP for net autotrophic metabolism for this region.

2. Methods

2.1. Study location and eddy characteristics

Experiments were conducted in the lee of the Hawaiian Islands in winter 2004–2005 as part of the E-Flux program (Benitez-Nelson et al., 2007; Dickey et al., 2008). Two well-developed, cold-core cyclonic eddies were identified through combined use of satellite sea surface temperature (SST) imagery, surface drifters and acoustic Doppler current profiler (ADCP) data (Dickey et al., 2008). The first cruise (E-Flux I; November 2004) focused on an eddy (Cyclone *Noah*) in its latter phases (Kuwahara et al., 2008), while the third cruise (E-Flux III; March 2005) focused on an early to mature eddy (Cyclone *Opal*) (Nencioli et al., 2008). Both features had unique physical, chemical and biological signatures. The physical characteristics of both features were relatively unchanged during the cruises; however, the biological characteristics of Cyclone *Opal* appear to have evolved during the study period (Benitez-Nelson et al., 2007; Dickey et al., 2008; Nencioli et al., 2008). During the second cruise (E-Flux II; January 2005), no significant mesoscale eddies were observed (Dickey et al., 2008). An eddy was described as mature if it had a distinct physical signature, as determined by its size, tangential current speeds and vertical isopycnal displacements, and if the plankton communities were actively accumulating biomass and net production (i.e. blooming). A decaying eddy was characterized by a diminishing physical signature and decreasing biomass and net production.

Samples were taken at the eddy centers (IN) and at the control stations outside (OUT) of the eddies, unless otherwise noted. IN stations were identified using satellite, surface drifter and ADCP data (Dickey et al., 2008; Kuwahara et al., 2008; Nencioli et al., 2008). The OUT stations were considered outside the influence of the eddy based on physical and biological features of the study region and were located at variable distances from the eddies' centers.

2.2. Photosynthesis vs. irradiance (P vs. E) experiments

Water samples were obtained between 15:00 and 16:00 h local time from the 43% and 11% light levels and, for selected experiments, from the DCML (Appendix). For each sample, 600 mL of seawater was inoculated with radioactive bicarbonate ($H^{14}CO_3^-$), mixed and distributed in 20-mL aliquots into 26 scintillation vials, each having a final activity of 11.5 μCi. One vial, serving as a time zero, was filtered immediately, after which the filter was placed in a new scintillation vial and frozen. One vial was wrapped in an aluminum foil (dark sample) and placed in a water bath at *in situ* temperature, while the remaining 24 samples were placed in a photosynthetron (CHPT Mfg Co.) at 1 of 24 different light levels and maintained at *in situ* temperature. Photosynthetrons contained a window between the light source and samples, containing a blue copper sulfate solution to simulate *in situ* spectral light quality. *In situ* temperatures were 25.5–27.2, 25.1–25.5 and 23.8–24.8 °C for the mixed layers of E-Flux I, II and III, respectively, and 21.4–24.2 °C for the DCM in E-Flux III. Samples were incubated for 1 h. To terminate the incubations, samples were vacuum filtered onto 25-mm Whatman glass fiber filters (GF/F) (E-Flux I and E-Flux II) or onto a combination of GF/F 5- and 18-μm polycarbonate filters (E-Flux III). Filters were stored frozen until analyzed. At the shore-based laboratory, filters were acidified using 2 N HCl and vented for 24 h before the addition of 10 mL of Aquasol-2 cocktail for liquid scintillation counting. Samples were counted using a Packard Tri-Carb® liquid scintillation counter; after initial counts, filters were stored in the dark and counted again after 1 month (Letelier et al., 1996; Karl et al., 1998). The final disintegrations per minute (dpm) data were used to calculate carbon assimilation.

Photosynthesis vs. irradiance (*P* vs. *E*) curves were defined using a best-fit solution to the equations described in Platt et al. (1980), which include a photoinhibition term. Phytoplankton physiological parameters were determined from the *P* vs. *E* curves and normalized to chlorophyll *a* concentration to facilitate comparison among experiments and cruises. Parameters evaluated included the maximum light-saturated photosynthetic rate under given conditions (P_s, [mg C mg chl^{-1} h^{-1}]), the maximum light-saturated rate of photosynthesis with photoinhibition (P^B_{max}, [mg C mg chl^{-1} h^{-1}]), the light-limited rate of photosynthesis (α, [(mg C mg Chl^{-1} h^{-1})(μmol quanta m^{-2} s^{-1})$^{-1}$]), the photoinhibition term (β, [(mg C mg Chl^{-1} h^{-1})(μmol quanta m^{-2} s^{-1})$^{-1}$]) and the light-saturation parameter (E_k, [μmol quanta m^{-2} s^{-1}]). Irradiance was measured in each of the photosynthetron's wells using a scalar photosynthetically available radiation (PAR) meter (Biospherical Instruments Inc. QSL-2101). Chlorophyll *a* was measured by high-performance liquid chromatography (HPLC) as described in Bidigare et al. (2005). Comparisons of IN vs. OUT stations and between eddies were assessed using analysis of variance (ANOVA).

2.3. Nutrient addition experiments

Experiments were conducted at the center of the eddy (IN) and outside the eddy (OUT) during E-Flux I and E-Flux III. During E-Flux II, only one experiment was conducted. Nutrient-replete deep seawater (DSW) obtained from 700 m was filtered through a 47-mm GF/F filter and added to unfiltered, nutrient-depleted mixed-layer seawater obtained from ~30 m to yield a final concentration of 5% DSW by volume. The DSW depth was chosen for its location well below the mixed layer and for its macro- and trace-nutrient concentrations. For the control, mixed-layer seawater (MLSW) was filtered through a 47-mm GF/F filter and added to unfiltered MLSW to a final concentration of 5% MLSW by volume. Five 10-L carboys were filled for each treatment; one carboy was sampled immediately as a time zero, while the other four carboys were placed in an on-deck incubator, which was at sea surface temperature and shaded to the ~30% light level with

blue plexiglass filters (#2069, Rohm and Haas Co., Philadelphia, PA) to simulate *in situ* light conditions. One carboy for each treatment was removed from the incubator every 24 h for sampling. At each sampling time point, measurements were taken for primary production and respiration and for concentrations of chlorophyll *a* and nutrients.

Primary production and respiration rates were measured using the oxygen light/dark bottle technique. At each sampling time point 15 ground-glass stoppered borosilicate bottles with a nominal volume of 125 mL were filled with seawater. Five sample bottles were fixed immediately (time-zero samples) for Winkler titrations (Carritt and Carpenter, 1966). Five bottles were placed in an incubator on deck for 24 h (light samples) and the remaining five bottles were placed in an opaque bag and incubated for 24 h (dark samples) in the same incubator. At the end of the 24-h incubation, samples were fixed (as above) and stored submerged in water until analysis. Winkler titrations were performed using a computer-controlled photometric endpoint detector (Williams and Jenkinson, 1982). R (mmol $O_2\,m^{-3}\,d^{-1}$) was calculated as the difference between the oxygen concentrations in the dark bottle ($[O_2]_{dark}$) after a 24-h incubation and in the time-zero bottle ($[O_2]_{t0}$). NCP (mmol $O_2\,m^{-3}\,d^{-1}$) is the difference between $[O_2]_{t0}$ and the oxygen concentration in the light bottle ($[O_2]_{light}$) after a 24-h incubation. GPP (mmol $O_2\,m^{-3}\,d^{-1}$) was calculated by adding the values of NCP and R. It should be noted that this technique does not account for potential enhancement of respiration rates in the light (Bender et al., 1987), which would underestimate GPP and R but would not be expected to alter the GPP:R ratio (Pringault et al., 2007).

Silicic acid concentrations were measured using a Bran & Lubbe (AA-3) continuous flow system, and soluble reactive phosphorus (SRP) concentrations were measured using the high-sensitivity MAGIC method (Karl and Tien, 1992). Three 125-mL samples were filtered onto GF/F filters at each time point for chlorophyll *a* analyses. Pigments were extracted from the filters using 100% HPLC-grade acetone, and concentrations were measured, following 24- and 48-h sample extraction, on a Turner Designs TD-700 fluorometer (Strickland and Parsons, 1972; Welschmeyer, 1994). Chlorophyll *a* concentrations were also determined using a Turner Designs 10-AU fluorometer upon return to shore (Holm-Hansen et al., 1965).

3. Results

3.1. Photosynthesis vs. irradiance experiments

The *r*-squared values for the relationship between the *P* vs. *E* experiments and the Platt et al. (1980) model ranged from −0.43 to 0.98. A histogram of the r^2 values (not shown) indicated a gap between $r^2 > 0.40$ and $r^2 < 0.40$. Approximately 73% of the 44 curves constructed had $r^2 > 0.40$ with most between $r^2 = 0.60$ and $r^2 > 0.90$ (see below). Those data with $r^2 < 0.40$ compared to the Platt et al. (1980) model are therefore described as having low correlation with the model relative to other data in this study and are not discussed further.

During E-Flux I, four of the experiments conducted had low correlation with the Platt et al. (1980) model. The remaining 10 experiments had an average $r^2 = 0.69 \pm 0.11$. In E-Flux II, seven experiments had $r^2 < 0.40$ with the Platt et al. (1980) model. The remaining three experiments had an average $r^2 = 0.64 \pm 0.04$. Finally, during E-Flux III, one experiment had $r^2 < 0.40$. The average r^2 for the remaining 19 experiment was 0.81 ± 0.17. Table 1 contains a summary of the average phytoplankton physiological parameters and r^2 values for all experiments for each cruise (see Appendix for complete dataset).

Table 1
Summary of P vs. E experiments and results

Cruise	Location	Dates	Chlorophyll *a*	Filter type(s)	Depth range	Light levels	P_s	P^B_{max}	α	β	E_k	r^2	
E-Flux I	6 IN, 3 OUT	11/5/2004–11/19/2004	0.075–0.188	GFF	15–72	11%, 43%	2.97 ± 1.59	2.45 ± 1.39	0.86 ± 2.67	< 0.001	148 ± 205	(−)0.32–0.84	
E-Flux II	1 IN, 2 OUT	1/22/2005–1/25/2005	0.081–0.150	GFF	16–70	11%, 43%	10.00 ± 7017	3.60 ± 2.59	1.95 ± 3.78	2.08 ± 4.47	79 ± 91	(−)0.43–0.66	
E-Flux III	13 IN, 6 OUT	3/16/2005–3/25/2005	0.010–0.743	5 μm, 18 μm, GFF	12–145	0.5%, 11%, 43%, DCM	2.78 ± 1.06	2.70 ± 1.09	0.16 ± 0.25	< 0.001	45 ± 31	0.32–0.98	

Values are averages for all experiments. Units for P^B_{max}, alpha (α), beta (β) and E_k are (mg C mg $Chl^{-1}\,h^{-1}$), (mg C mg $Chl^{-1}\,h^{-1}$)(μmol quanta $m^{-2}\,s^{-1})^{-1}$, (mg C mg $Chl^{-1}\,h^{-1}$)(μmol quanta $m^{-2}\,s^{-1})^{-1}$ and (μmol quanta $m^{-2}\,s^{-1}$), respectively.

3.2. Nutrient addition experiments

During E-Flux I Experiment 1, GPP increased rapidly after 48 h (3.50 ± 1.08 mmol O_2 m^{-3} d^{-1} at 48 h to 12.35 ± 0.39 mmol O_2 m^{-3} d^{-1} at 72 h) in the DSW treatment and then continued to increase, though less rapidly, through the end of the 96-h incubation (Fig. 1). Between 72 and 96 h, GPP in the MLSW control increased notably (0.10 ± 1.25 to 3.85 ± 2.17 mmol O_2 m^{-3} d^{-1}) and it doubled in the DSW treatment (12.35 ± 0.39 to 26.35 ± 0.46 mmol O_2 m^{-3} d^{-1}). Chlorophyll *a* concentrations remained constant throughout the experiment in the MLSW treatment, but increased more than an order of magnitude in the DSW treatment (Fig. 2). SRP drawdown in both the MLSW and DSW treatments was less than 1 μmol m^{-3} d^{-1} (detection limit of SRP analysis is ± 1 μmol m^{-3}) (Fig. 3). In E-Flux I Experiment II, inclement weather prohibited sampling at the 72- and 96-h time points. GPP in the DSW treatment increased > 10 mmol O_2 m^{-3} d^{-1} between 48 and 120 h (4.18 ± 1.01 to 16.17 ± 2.04 mmol O_2 m^{-3} d^{-1}), whereas GPP in the MLSW treatment decreased between these time points (4.34 ± 1.20 to -0.08 ± 1.22 mmol O_2 m^{-3} d^{-1}). Chlorophyll *a* concentration remained constant in the MLSW treatment, and increased by more than order of magnitude in the DSW treatment (Fig. 2). SRP and Si drawdown were within the error of the measurements (Figs. 3 and 4). During E-Flux II, there was no significant response in GPP in the DSW treatment compared to the MLSW control ($p = 0.89$), and rates of R were greater in the MLSW control than the DSW treatment ($p = 0.06$). Chlorophyll *a* concentrations remained constant in the MLSW treatment, and doubled in the DSW treatment (Fig. 2).

Experiment I from E-Flux III was taken from the center of the eddy, above a large bloom of diatoms (Benitez-Nelson et al., 2007; Landry et al., 2008). A rapid increase in GPP was observed during the initial 24 h of the experiment in the DSW treatment (3.54 ± 2.30 to 10.09 ± 0.18 mmol O_2 m^{-3} d^{-1}), while R remained approximately constant (1.53 ± 2.25 to 1.11 ± 0.18 mmol O_2 m^{-3} d^{-1}). Rates of R doubled during each of the subsequent 24-h periods (1.11 ± 0.18 to 2.71 ± 0.78 to 6.32 ± 0.13 mmol O_2 m^{-3} d^{-1}). Between 72 and 96 h, both GPP and chlorophyll *a* concentrations decreased (19.95 ± 0.84 to 12.67 ± 0.89 mmol O_2 m^{-3} d^{-1} and 3.11 ± 0.16 to 2.34 ± 0.07 μg l^{-1}, respectively). Chlorophyll *a* increased by more than an order of magnitude in the DSW treatment and decreased slightly in the MLSW control (Fig. 2).

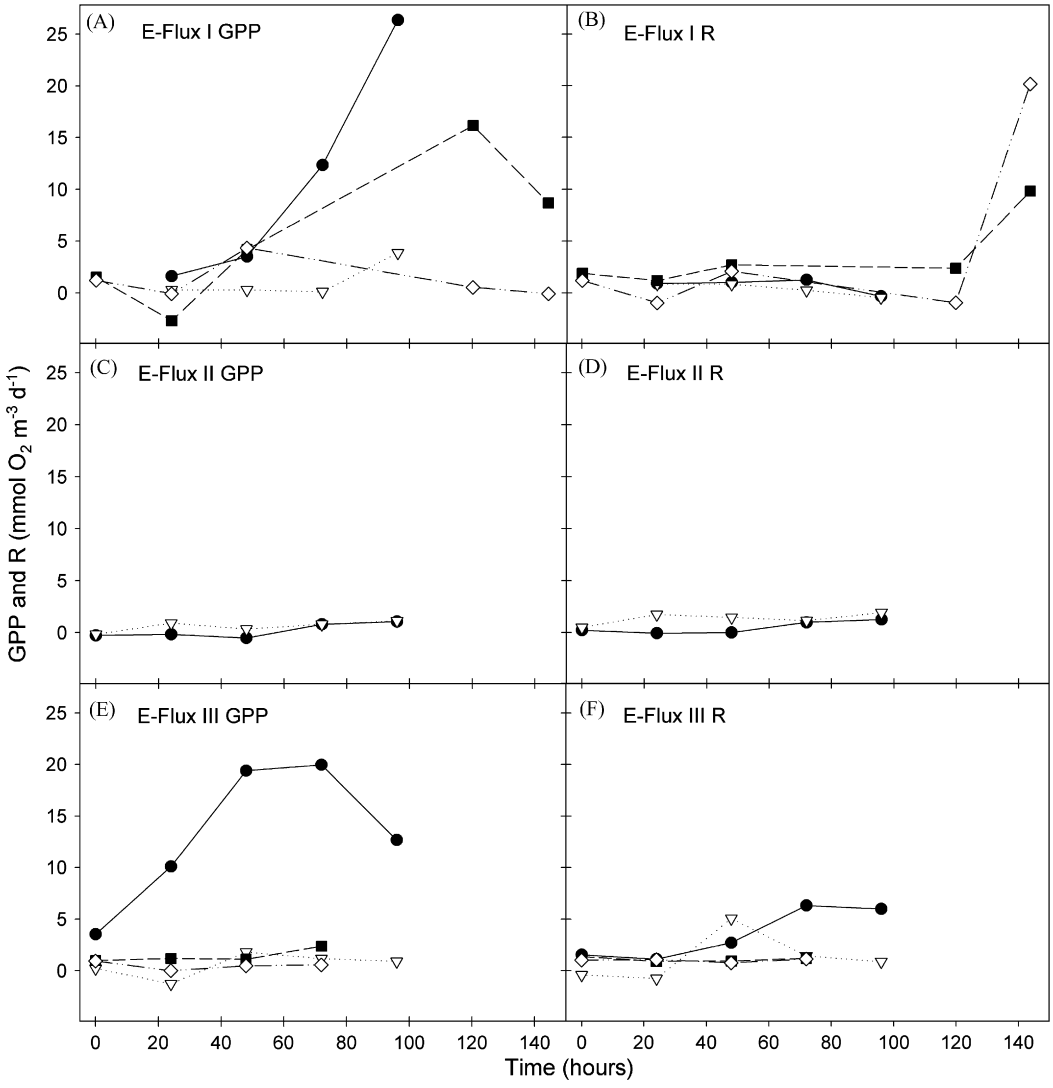


Fig. 1. Gross primary production (GPP) and respiration (R) from nutrient-loading experiments during E-Flux I (A and B), E-Flux II (C and D) and E-Flux III (E and F). Circles and triangles indicate the deep seawater (DSW) and mixed-layer seawater (MLSW) results from the first experiment in each cruise, respectively. Squares and diamonds indicate the DSW and MLSW results from the second experiment in each cruise, respectively. Only one experiment was conducted during E-Flux II.

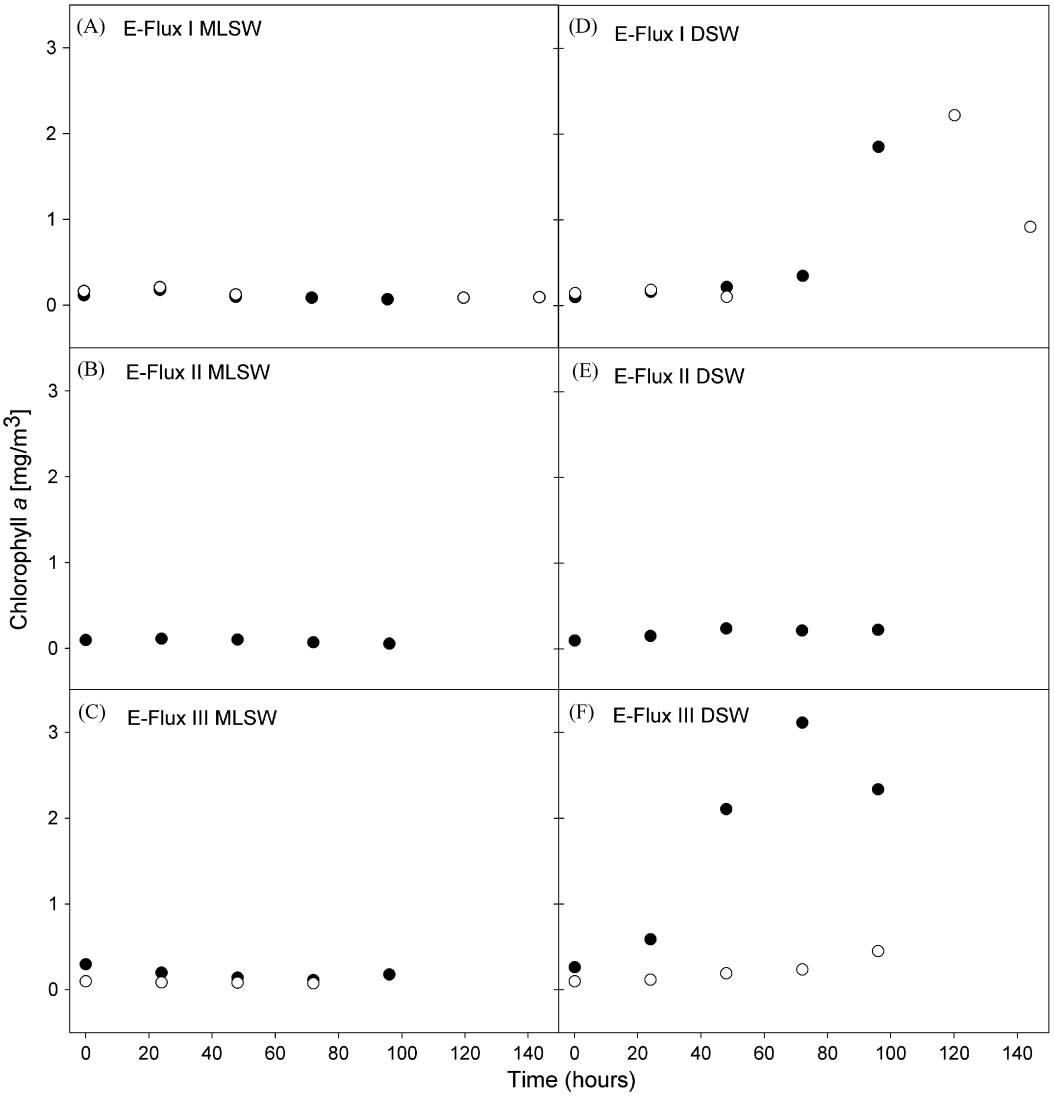


Fig. 2. Chlorophyll concentrations from nutrient-addition experiments conducted during the E-Flux project. Panels (A), (B) and (C) show chlorophyll *a* in the control, or mixed layer seawater (MLSW) additions in E-Flux I, II and III, respectively, and (D), (E) and (F) show chlorophyll *a* in the deep-seawater (DSW) additions in E-Flux I, II and III, respectively. Solid black circles represent the first experiment and the open circles the second experiment for a given cruise.

SRP drawdown was $<1\,\mu mol\,m^{-3}\,d^{-1}$ in the MLSW treatment and $1.7\,\mu mol\,m^{-3}\,d^{-1}$ in the DSW treatment (Fig. 3). Si drawdown was within the error of the measurement for both the MLSW and DSW treatments (Fig. 4). In E-Flux III Experiment II, GPP in the MLSW treatment remained constant for the duration of the experiment, while rates of GPP doubled in the DSW treatment (0.98 ± 0.20 to $2.36\pm0.51\,mmol\,O_2\,m^{-3}\,d^{-1}$; Fig. 1). Chlorophyll *a* concentration increased four-fold in the DSW treatment and remained constant in the MLSW control throughout the experiment (Fig. 2). SRP drawdown was $<1\,\mu mol\,m^{-3}\,d^{-1}$ in both the MLSW and DSW treatments (Fig. 3), and Si drawdown was an order of magnitude larger in the DSW vs. MLSW treatment (2.3 and $31.8\,\mu mol\,m^{-3}\,d^{-1}$, respectively), though both were within the error of the measurement (Fig. 4).

Comparing the results of all time points from the five nutrient addition experiments, Chi-squared analysis showed that GPP of the DSW treatment was independent of GPP of the MLSW control ($p<0.01$) and R was not ($p=0.08$) at the $\alpha=0.05$ significance level. Paired *t*-tests showed that rates of GPP in the DSW treatment for all time points of the five experiments were greater than those in the control samples ($p<0.01$) whereas rates of R were not statistically different ($p=0.27$).

4. Discussion

This study sought fundamental information on the relationship between nutrient addition events and changes in metabolic balance of the oligotrophic open ocean. The cyclonic eddies studied here caused doming of isopycnal surfaces and increased nutrient concentrations at shallower depths. As such, they served as natural, large-scale nutrient addition experiments for us to examine. Our analysis took a three-pronged approach to analyzing metabolic balance in the eddy by (1) measuring primary production inside and outside of the eddies (*P* vs. *E* experiments), (2) incubating mixed-layer water after addition of nutrients, and (3) calculating a threshold for net autotrophic production. In this way, we were able to assess primary production and metabolism in the eddy directly and through incubation experiments. Our results had three important outcomes: (1) maximum rates of photosynthesis in the mixed-layer inside and outside of the eddies studied were not significantly different, (2) metabolic balance of mixed layer water could be altered following addition of nutrients, and (3) our calculated threshold for net autotrophic production was similar to previous estimates of open-ocean ecosystems.

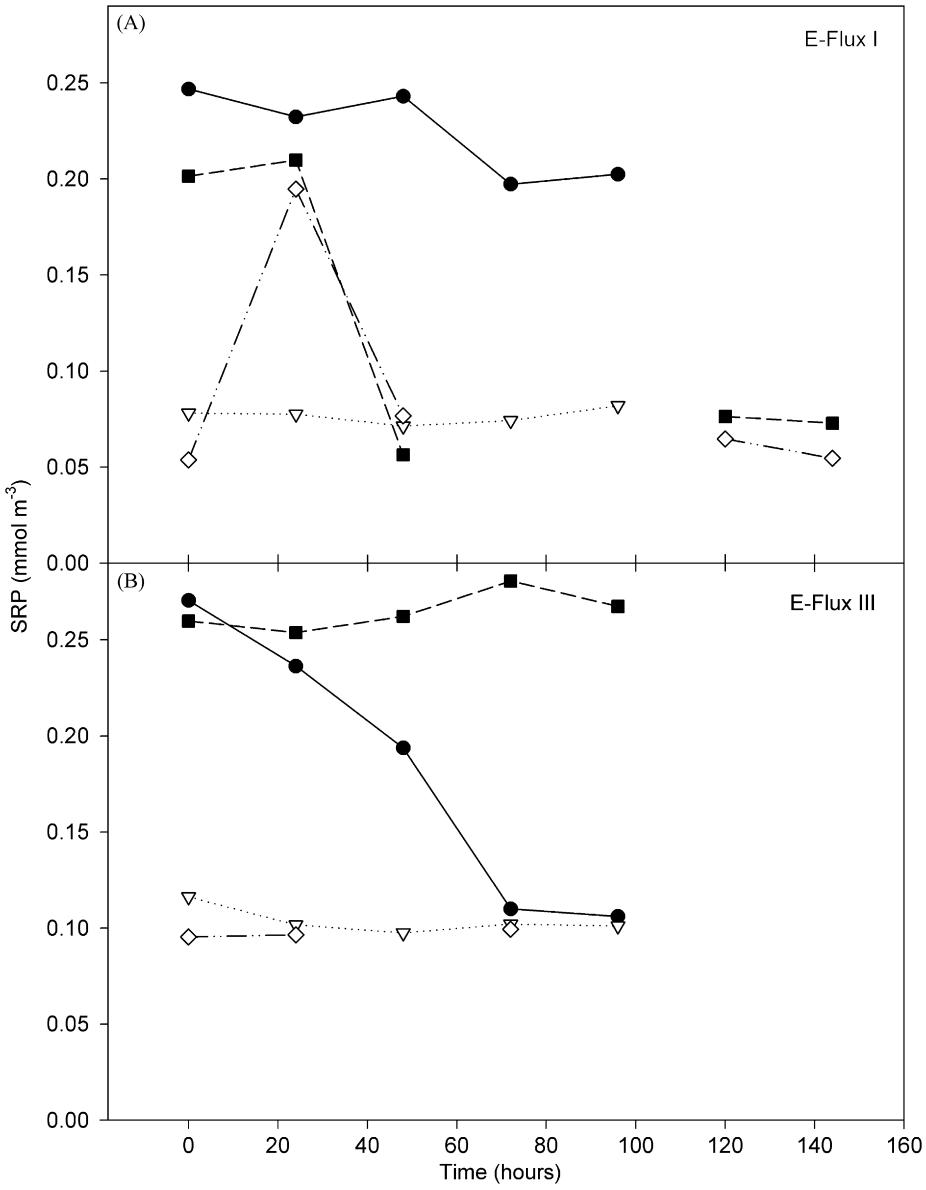


Fig. 3. Soluble reactive phosphorus (SRP) concentrations from the nutrient-loading experiments. Circles and triangles indicate results of the deep-seawater (DSW) and mixed-layer sweater (MLSW) treatments from the first experiment of each cruise, respectively, and squares and diamonds indicate the results of the DSW and MLSW treatments from the second experiment of each cruise, respectively.

4.1. *P vs. E experiments*

While approximately 75% of our data were explained well by the Platt et al. (1980) model, the wide range of r^2 values obtained fitting the model to the *P* vs. *E* data indicated that the model may not adequately explain the relationship of primary production and light in all of our samples. In those samples with low r^2 it is likely that rates of production were influenced by a factor other than light, such as nutrient availability, community composition or grazing. P^B_{max} and P_s values were significantly different among experiments ($p<0.05$), indicating that photoinhibition had a significant effect on maximum rates of photosynthetic production. P^B_{max} estimates from *P* vs. *E* curves were consistent with other estimates of primary production from the E-Flux program, when converted to appropriate units ($mg\,C\,m^{-3}\,d^{-1}$) (Landry et al., 2008). We predicted that we would see differences in P^B_{max} IN vs. OUT of eddies as we regularly observe enhanced chlorophyll concentrations inside cyclonic eddies in the lee of Hawaii using satellites. We further assumed that the higher chlorophyll concentrations coincided with net autotrophic production. However, there was no statistical difference between P^B_{max} ($mg\,C\,mg\,Chl^{-1}\,h^{-1}$) in the mixed layer between the IN and OUT stations ($p=0.35$ and 0.44 for E-Flux I and E-Flux III, respectively). Gonzalez et al. (2001) observed that differences in metabolism inside and outside a cyclonic eddy were not due to enhanced production inside the eddy compared to outside but to decreased rates of R inside vs. outside. As such, the lack of discrepancy inside vs. outside the eddies in this study is likely not anomalous. In addition, if plankton communities in the surface water sampled were growing at close to P^B_{max}, any additional nutrients introduced by the eddy may not have enhanced the production rate per unit biomass.

Similarly, we found no significant differences in α, β or E_k inside vs. outside of the eddies. Sampling depths were chosen based on light-level as percent of incident irradiance, and if the same organisms are present inside and outside of an eddy feature at the

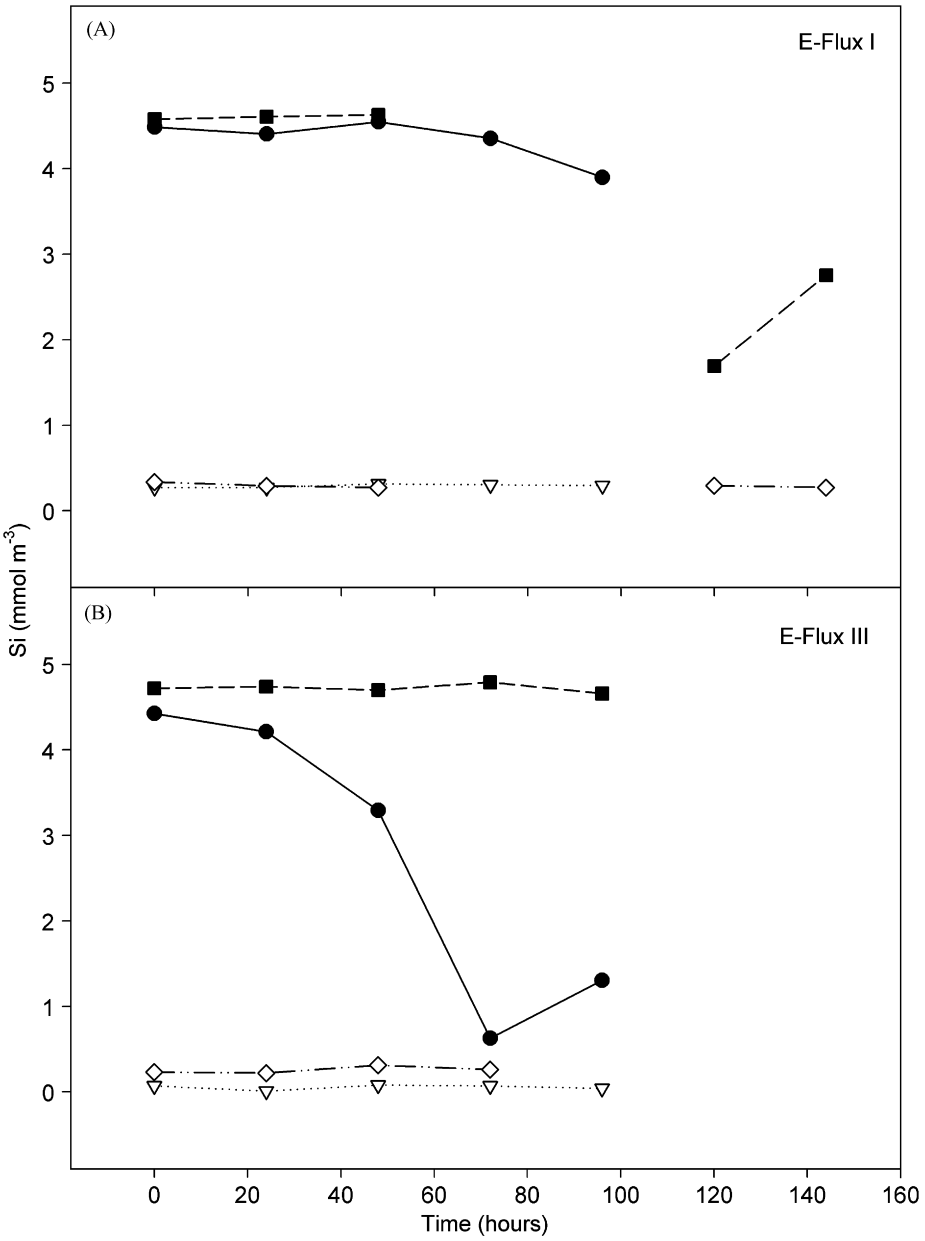


Fig. 4. Silicate concentrations from nutrient-loading experiments, as in Fig. 3.

same light-level this would account for the lack of difference in phytoplankton physiological parameters IN vs. OUT. In E-Flux III, α of the larger size fractions (>5 and $>18\,\mu m$) in the DCML at the eddy center was statistically different from that of the total community at those stations ($p<0.05$), indicating that those size fractions were more light-limited than the rest of the community. A diatom bloom was present in the DCML at the eddy center with a layer of senescent diatoms shallow to it (Benitez-Nelson et al., 2007), which may have shaded the DCML.

4.2. Nutrient-addition experiments

The nutrient-addition experiments conducted in this study enabled us to resolve daily changes in community metabolism on 5- to 7-d time scales. As previous work (McAndrew et al., 2007) suggested, rates of GPP increased following nutrient addition more rapidly and to a higher final rate than that of R. The length of time it took rates of GPP to respond varied between 24 and 72 h. In both experiments from E-Flux I, for example, GPP increased most rapidly after more than 24 h of incubation, whereas GPP in E-Flux III Experiment I increased rapidly within 24 h of the start of the experiment. E-Flux III Experiment I was unique in that it was conducted with water from the mixed layer of Cyclone *Opal* and contained time-zero chlorophyll and phosphate concentrations that were approximately twice as great as those in the other four experiments (Figs. 2 and 3). In essence, it appears to have been a nutrient addition experiment already begun, which may partially explain the more rapid response time of GPP following nutrient addition compared to the other experiments. These results support the conceptual model proposed by Sweeney et al. (2003) on the effects of cyclonic eddies on upper-ocean ecosystems. In this model a "nutrient injection" period is followed after some time by a biological response. Our incubation experiments imply that the lag time between the injection and response could vary on the order of days, if it is assumed

the injection is rapid as in the incubations. Our results also suggest that if nutrients are added after a bloom is initiated, then the response time to increase GPP would be faster than in non-bloom conditions. As there is a larger plankton population accumulating biomass, this seems logical. It could also explain the rapid drawdown of nutrients in the corresponding nutrient addition experiment (E-Flux III Experiment I, Figs. 3 and 4).

Nutrient drawdown was not consistent with the magnitude of increase in GPP in our incubation experiments. Again, in E-Flux III Experiment I (from Cyclone *Opal*), there was a rapid drawdown in SRP and Si to approximately pre-nutrient addition concentrations (Figs. 3 and 4), and this coincided with an increase in GPP to $\sim$20 mmol O_2 m^{-3} d^{-1} (Fig. 1). In E-Flux I Experiment I, GPP increased to $>$25 mmol O_2 m^{-3} d^{-1}; however, the nutrient drawdown was approximately one-third that of E-Flux III Experiment I. One possible explanation for the observed differences in response is that the seed community composition differed between experiments, thereby resulting in different responses to nutrient addition. Also, because ambient nutrient concentrations are the result of net rates of uptake and remineralization, variations in nutrient turnover among the various experiments cannot be ruled out.

Because it is the difference between rates of GPP and R that determine net metabolism, however, understanding GPP dynamics alone is not sufficient. As mentioned above, R did not respond as rapidly as GPP to the nutrient addition. Rates of R in the DSW treatment were not significantly different from the control in four of the five experiments, indicating that R does not respond to nutrient addition on the time scales studied. The result of this was rapid decoupling of GPP and R in the first few days of our experiments. In both our experiments and in eddy systems, the excess production during this decoupling period may be a source of organic carbon to fuel heterotrophic metabolism in the oligotrophic open ocean. In the last 2 days (72 and 96 h) of the E-Flux III Experiment I (Cyclone *Opal*) DSW treatment, however, rates of R were significantly different from their control ($p = 0.01$; Fig. 1). By these two time points, nutrients had decreased (Figs. 3 and 4); therefore, increased nutrient concentrations likely did not promote these increases in R.

The length of time in which increased GPP was observed following the addition of nutrients was also not consistent. Measuring GPP at only the starting time and at 96 h as in previous work (see McAndrew et al., 2007) could be misleading if trying to assess the time-integrated impact of GPP response. In E-Flux III Experiment I (Fig. 1E), for example, the highest rate of GPP was observed at 72 h and decreased by 96 h, whereas in E-Flux I Experiment I (Fig. 1A), GPP was greatest at 96 h. It is possible that the E-Flux III experiment was already experiencing a bloom and responded rapidly because there were more organisms there to consume nutrients and grow.

4.3. Net autotrophic metabolic threshold for the lee of Hawaii

Model II regression analysis was used to determine the relationship between NCP and GPP measured using the oxygen light/dark bottle technique from the nutrient-amendment experiments (Fig. 5), and it yielded an estimate for the threshold for net autotrophic production of 1.65 mmol O_2 m^{-3} d^{-1} ($r^2 = 0.94$). This is similar to a global threshold of 1.3 mmol O_2 m^{-3} d^{-1}, which can be calculated from the regression analysis of Robinson and Williams (2005), and with a previous estimate for the open ocean of 1.1 mmol O_2 m^{-3} d^{-1} by Duarte and Agusti (1998). It is less than estimates for more productive areas such as the Mediterranean littoral (3.95 mmol O_2 m^{-3} d^{-1}) (Duarte et al., 2004) and Antarctic coastal waters during austral summer (2.05–2.2 mmol O_2 m^{-3} d^{-1}) (Agusti et al., 2004; Agusti and Duarte, 2005).

To examine the reliability of the threshold calculated, we compared it to data from a study on metabolic balance conducted at Station ALOHA by Williams et al. (2004) over a 1-year period using the oxygen light/dark bottle technique. Fig. 6 shows rates of GPP from that study compared to the threshold calculated in the present one. Rates of GPP greater than 1.65 mmol O_2 m^{-3} d^{-1} indicate net autotrophy, and those that are less indicate net heterotrophy. As the threshold in this study was calculated with water from 30 m in the mixed layer, the rates of GPP at 25 and 45 m in Fig. 6 are particularly noteworthy for comparisons. All data indicate net heterotrophic metabolism, which is consistent with the results published by Williams et al. (2004). To obtain a rate of GPP higher than 1.65 mmol O_2 m^{-3} d^{-1} would, therefore, require an event to enhance total primary production. The nutrient loading experiments conducted in this study demonstrated that nutrient addition may be one method for enhancing GPP above the threshold (Fig. 1). The feasibility of achieving nutrient additions of the magnitude used in the experiments in

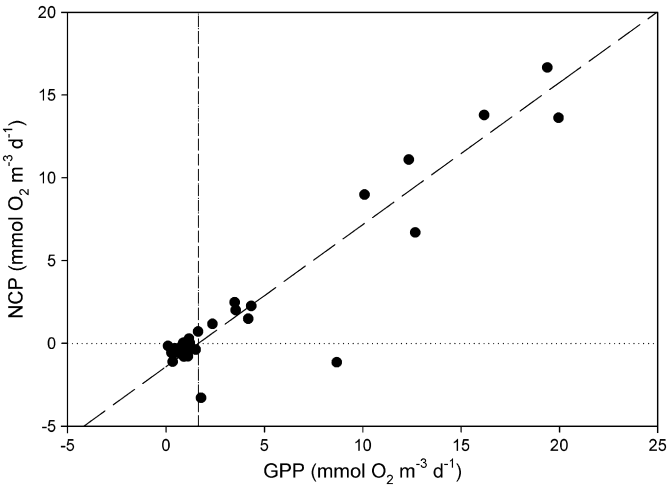


Fig. 5. Net community production (NCP) vs. gross primary production (GPP) from nutrient-addition experiments. The dotted line is the Model II regression NCP = 0.86 × GPP−1.41, $r^2 = 0.94$. The threshold for net autotrophic production is 1.65 mmol O_2 m^{-3} d^{-1} (vertical line). Net metabolic balance (NCP = 0) is shown by the horizontal dotted line.

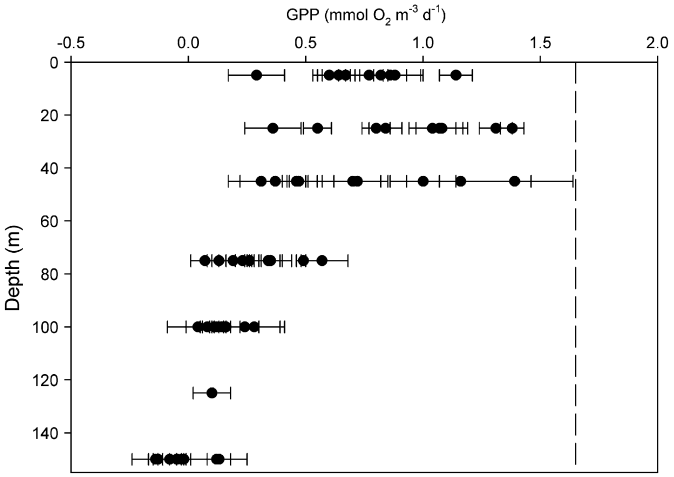


Fig. 6. Gross primary production from Williams et al. (2004) study on metabolic balance at Station ALOHA compared to the threshold for net autotrophic production calculated in this study.

the environment has been discussed elsewhere (see McAndrew et al., 2007).

5. Conclusions

No significant differences in maximum, biomass-normalized, light-saturated rates of photosynthesis or related phytoplankton physiological parameters were observed between the mixed layer inside and outside of the Hawaii lee eddies studied despite an uncommon diatom bloom. Nutrient addition experiments indicated that total plankton production in the mixed layer inside the eddies studied could be enhanced with the addition of nutrients via phytoplankton biomass accumulation, resulting in a switch from net heterotrophy to net autotrophy for the planktonic microbial assemblage as a whole. These results indicate that nutrients could be controlling net metabolism in open-ocean ecosystems.

Acknowledgments

We thank the participants of the E-Flux cruises and the captain and crew of the R/V *Kaimikai-O-Kanaloa* and R/V *Wecoma*. We also thank the Gordon and Betty Moore Foundation and the National Science Foundation for financial support.

Appendix

Summary of P vs. E experiments and results. Units for P^B_{max}, alpha (α), beta (β) and E_k are (mg C mg Chl^{-1} h^{-1}), (mg C mg Chl^{-1} h^{-1}), (mg C mg Chl^{-1} h^{-1})(μmol quanta m^{-2} s^{-1})$^{-1}$, (mg C mg Chl^{-1} h^{-1})(μmol quanta m^{-2} s^{-1})$^{-1}$ and (μmol quanta m^{-2} s^{-1}), respectively (Table A.1).

Table A.1

Cruise	Location	Date	Chlorophyll *a*	Filter	Depth	Light level (%)	P_s	P^B_{max}	α	β	E_k	r^2
E-Flux I	OUT	11/5/2004	0.13	GF/F	25	43	4.63±1.97	3.36±0.47	0.03±0.01	<0.01±<0.01	96±176	0.63
E-Flux I	OUT	11/5/2004	0.168	GF/F	60	11	1.49±0.27	1.48±0.24	0.18±0.19	<0.01±<0.01	8±10	0.37
E-Flux I	IN	11/11/2004	0.117	GF/F	15	43	3.97±1.01	3.97±0.99	10.00±>1e3	<0.01±<0.01	0±>1e3	−0.32
E-Flux I	IN	11/11/2004	0.143	GF/F	39	11	3.18±0.95	2.41±0.22	0.02±0.00	<0.01±<0.01	112±100	0.84
E-Flux I	IN	11/13/2004	0.144	GF/F	16	43	1.76±0.33	1.76±0.33	0.04±0.02	<0.01±<0.01	44±21	0.52
E-Flux I	IN	11/13/2004	0.175	GF/F	39	11	1.77±0.13	1.77±0.13	1.65±1.14	<0.01±<0.01	1±1	0.35
E-Flux I	IN	11/14/2004	0.13	GF/F	16	43	1.61±0.86	1.36±0.28	0.01±0.00	<0.01±<0.01	190±127	0.76
E-Flux I	IN	11/14/2004	0.075	GF/F	44	11	5.85±1.02	5.55±0.41	0.07±0.02	<0.01±<0.01	77±84	0.77
E-Flux I	IN	11/17/2004	0.156	GF/F	26	43	4.65±5.78	2.79±2.24	0.02±0.01	<0.01±0.01	185±909	0.63
E-Flux I	IN	11/17/2004	0.188	GF/F	72	11	4.25±2.36	2.54±0.91	0.01±0.00	<0.01±<0.01	181±361	0.83
E-Flux I	OUT	11/18/2004	0.107	GF/F	18	43	4.20±49.74	4.20±452.10	0.01±0.01	<0.01±0.02	821±>1e3	0.62
E-Flux I	OUT	11/18/2004	0.167	GF/F	50	11	0.78±0.25	0.70±0.08	0.01±0.00	<0.01±<0.01	81±36	0.59
E-Flux I	OUT	11/19/2004	0.103	GF/F	16	43	1.50±0.88	1.50±3.29	0.01±0.01	<0.01±<0.01	150±226	0.64
E-Flux I	OUT	11/19/2004	0.163	GF/F	43	11	2.00±3.77	0.92±1.49	0.01±0.00	<0.01±0.01	131±310	0.28
Mean							2.97	2.45		0.86	148	0.54
σ							1.59	1.39		2.67	205	0.30
E-Flux II	IN	1/16/2005	0.096	GF/F	18	43	10.28±596.12	4.14±301.35	8.06±>1e3	3.71±300.71	1±319	0.19
E-Flux II	IN	1/16/2005	0.109	GF/F	47	11	6.10±1.02	5.98±0.79	1.16±1.12	<0.01±0.01	5±8	0.00
E-Flux II	IN	1/17/2005	0.084	GF/F	20	43	20.54±>1e3	3.98±>1e3	10.00±>1e3	14.21±>1e3	0±>1e3	0.11
E-Flux II	IN	1/17/2005	0.116	GF/F	50	11	18.51±>1e3	2.09±377.06	0.05±0.06	0.13±15.80	45±>1e3	0.13
E-Flux II	IN	1/20/2005	0.082	GF/F	16	43	19.37±>1e3	1.69±>1e3	0.01±0.02	0.04±13.97	169±>1e3	0.30
E-Flux II	IN	1/20/2005	0.098	GF/F	41	11	0.70±0.00	0.00±>1e3	0.02±>1e3	2.68±<0.01	0±>1e3	−0.43
E-Flux II	IN	1/22/2005	0.081	GF/F	22	43	1.88±4.74	1.53±1.15	0.02±0.06	<0.01±0.01	62±312	0.35
E-Flux II	IN	1/22/2005	0.112	GF/F	57	11	9.17±2.45	9.17±9.12	0.15±0.05	<0.01±0.01	62±106	0.60
E-Flux II	OUT	1/25/2005	0.099	GF/F	27	43	5.87±19.30	3.86±9.53	0.02±0.01	<0.01±0.02	247±>1e3	0.66
E-Flux II	OUT	1/25/2005	0.15	GF/F	70	11	7.59±44.36	3.50±21.33	0.02±0.01	<0.01±0.08	193±>1e3	0.66
Mean							10.00	3.60	1.95		79	0.26
σ							7.17	2.59	3.78		91	0.34
E-Flux III	IN	3/16/2005	0.114	GF/F	12	43.0	4.12±0.76	4.12±2.33	0.09±0.03	<0.01±<0.01	47±24	0.68
E-Flux III	IN	3/16/2005	0.118	GF/F	33	11.0	3.62±0.43	3.62±0.29	0.41±0.17	<0.01±<0.01	9±6	0.53
E-Flux III	IN	3/18/2005	0.209	18 μm	64	DCML	4.85±1.59	4.85±8.63	0.05±0.01	<0.01±<0.01	101±60	0.91
E-Flux III	IN	3/18/2005	0.601	GF/F	64	DCML	4.18±0.32	3.86±0.11	0.07±0.01	<0.01±<0.01	54±18	0.96
E-Flux III	IN	3/19/2005	0.191	5 μm	65	DCML	1.95±0.99	1.95±5.48	0.02±0.01	<0.01±<0.01	100±198	0.85
E-Flux III	IN	3/19/2005	0.743	GF/F	65	DCML	2.28±0.17	2.04±0.05	0.04±0.00	<0.01±<0.01	57±10	0.97
E-Flux III	IN	3/20/2005	0.1	5 μm	80	0.5	1.86±0.66	1.86±2.25	0.04±0.01	<0.01±<0.01	53±42	0.68
E-Flux III	IN	3/20/2005	0.376	GF/F	80	0.5	1.80±0.08	1.68±0.04	0.08±0.01	<0.01±<0.01	21±3	0.94
E-Flux III	IN	3/22/2005	0.174	5 μm	82	DCML	2.03±0.34	1.47±0.10	0.02±0.00	<0.01±<0.01	64±17	0.97
E-Flux III	IN	3/22/2005	0.683	GF/F	82	DCML	1.99±0.12	1.74±0.04	0.04±0.00	<0.01±<0.01	44±6	0.97
E-Flux III	IN	3/22/2005	0.01	5 μm	110	DCML	2.91±0.18	2.91±0.14	1.04±0.44	<0.01±<0.01	3±1	0.45
E-Flux III	IN	3/22/2005	0.354	GF/F	110	DCML	1.13±0.07	1.12±0.04	0.06±0.01	<0.01±<0.01	20±4	0.85
E-Flux III	IN	3/23/2005	0.34	GF/F	125	DCML	1.20±0.09	1.20±0.08	0.28±0.11	<0.01±<0.01	4±2	0.62
E-Flux III	OUT	3/23/2005	0.01	5 μm	145	DCML	2.91±0.35	2.91±0.30	0.57±0.34	<0.01±<0.01	5±4	0.32
E-Flux III	OUT	3/23/2005	0.202	GF/F	145	DCML	2.27±0.55	2.27±2.17	0.07±0.02	<0.01±<0.01	34±18	0.98
E-Flux III	OUT	3/23/2005	0.202	GF/F	145	DCML	2.46±0.12	2.33±0.06	0.11±0.01	<0.01±<0.01	21±4	0.93
E-Flux III	OUT	3/24/2005	0.096	GF/F	22	43.0	3.20±0.70	3.20±1.93	0.08±0.02	<0.01±<0.01	40±18	0.71
E-Flux III	OUT	3/24/2005	0.119	GF/F	56	11.0	3.43±0.75	3.43±3.19	0.04±0.01	<0.01±<0.01	85±38	0.87
E-Flux III	OUT	3/25/2005	0.081	GF/F	19	43.0	4.25±1.30	4.25±4.71	0.08±0.03	<0.01±<0.01	51±33	0.66
E-Flux III	OUT	3/25/2005	0.137	GF/F	50	11.0	3.22±0.57	3.22±2.46	0.04±0.01	<0.01±<0.01	85±31	0.94
Mean							2.78	2.70	0.16		45	0.79
σ							1.06	1.09	0.25		31	0.20

References

Agusti, S., Duarte, C.M., 2005. Threshold of gross primary production for planktonic metabolic balance in the Southern Ocean: an experimental test. Limnology and Oceanography 50, 1334–1339.

Agusti, S., Satta, M.P., Mura, M.P., 2004. Summer community respiration and pelagic metabolism in upper surface Antarctic waters. Aquatic Microbial Ecology 35, 197–205.

Allen, C., Kanda, J., Laws, E., 1996. New production and photosynthetic rates within and outside a cyclonic mesoscale eddy in the North Pacific subtropical gyre. Deep-Sea Research I 43, 917–936.

Aristegui, J., Harrison, W.J., 2002. Decoupling of primary production and community respiration in the ocean: implications for regional carbon studies. Aquatic Microbial Ecology 29, 199–209.

Bender, M., Grande, K., Johnson, K., Marra, J., Williams, P.L., Sieburth, J., Pilson, M., Langdon, C., Hitchcock, G., Orchardo, J., Hunt, C., Donaghay, P., Heinemann, K., 1987. A comparison of four methods for determining planktonic community production. Limnology and Oceanography 32, 1085–1098.

Benitez-Nelson, C.R., Bidigare, R.R., Dickey, T.D., Landry, M.R., Leonard, C.L., Brown, S.L., Nencioli, F., Rii, Y.M., Maiti, K., Becker, J.W., Bibby, T.S., Black, W., Cai, W.-J., Carlson, C., Chen, F., Kuwahara, V.S., Mahaffey, C., McAndrew, P.M., Quay, P.D., Rappe, M.S., Selph, K.E., Simmons, M.P., Yang, E., 2007. Mesoscale eddies drive increased silica export in the subtropical Pacific Ocean. Science 316, 1017–1021.

Bidigare, R.R., Benitez-Nelson, C., Leonard, C.L., Quay, P.D., Parsons, M.L., Foley, D.G., Seki, M.P., 2003. Influence of a cyclonic eddy on microheterotroph biomass and carbon export in the lee of Hawaii. Geophysical Research Letters 30, 51-1-4.

Bidigare, R.R., Heukelem, L.V., Trees, C.C., 2005. Analysis of Algal Pigments by High-Performance Liquid Chromotography. Algal Culturing Techniques, Academic Press, pp. 327–345.

Carritt, D.E., Carpenter, J.H., 1966. Comparison and evaluation of currently employed modifications of the Winkler method for determining dissolved oxygen in seawater: a NASCO report. Journal of Marine Research 24, 286–318.

del Giorgio, P.A., Cole, J.J., Cimbleris, A., 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. Nature 385, 148–151.

Dickey, T., Nencioli, F., Kuwahara, V., Leonard, C., Black, W., Bidigare, R., Rii, Y., Zhang, Q., 2008. Physical and bio-optical observations of oceanic cyclones west of the island of Hawai'i. Deep-Sea Research II, doi:10.1016/j.dsr2.2008.01.006 [in press].

Duarte, C.M., Agusti, S., 1998. The CO_2 balance of unproductive aquatic ecosystems. Science 281, 234–236.

Duarte, C.M., Agusti, S., Vaque, D., 2004. Controls on planktonic metabolism in the Bay of Blanes, northwestern Mediterranean littoral. Limnology and Oceanography 49, 2162–2170.

Falkowski, P.G., Ziemann, D., Kolber, Z., Bienfang, P.K., 1991. Role of eddy pumping in enhancing primary production in the ocean. Nature 352, 55–58.

Garrett, C., 2003. Mixing with latitude. Nature 422, 477–478.

Gonzalez, N., Anadon, R., Mourino, B., Fernandez, E., Sinha, B., Escanez, J., Armas, D.D., 2001. The metabolic balance of the planktonic community in the North Atlantic Subtropical Gyre: the role of mesoscale instabilities. Limnology and Oceanography 46, 946–952.

Gregg, M.C., Sanford, T.B., Winkel, D.P., 2003. Reduced mixing from the breaking of internal waves in equatorial waters. Nature 422, 513–515.

Harris, R.P., Boyd, P., Harbour, D.S., Head, R.N., Pingree, R.D., Pomroy, A.J., 1997. Physical, chemical and biological features of a cyclonic eddy in the region of 61°10′N 19°50′W in the North Atlantic. Deep-Sea Research I 44, 1815–1839.

Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W., Strickland, J.D.H., 1965. Fluorometric determination of chlorophyll. Journal du Conseil 30, 3–15.

Karl, D., 2007. Microbial oceanography: paradigms, processes and promise. Nature Reviews Microbiology 5, 759–769.

Karl, D.M., Tien, G., 1992. MAGIC: a sensitive and precise method for measuring dissolved phosphorus in aquatic environments. Limnology and Oceanography 37, 105–116.

Karl, D.M., Hebel, D., Bjorkman, K., Letelier, R., 1998. The role of dissolved organic matter release in the productivity of the oligotrophic North Pacific Ocean. Limnology and Oceanography 43, 1270–1286.

Karl, D.M., Laws, E.A., Morris, P., Williams, P.J.L., Emerson, S., 2003. Metabolic balance of the open sea. Nature 426, 32.

Kuwahara, V.S., Nencioli, F., Dickey, T.D., Rii, Y.M., Bidigare, R.R., 2008. Physical dynamics and biological implications of Cyclone *Noah* in the lee of Hawai'i during E-Flux I. Deep-Sea Research II, doi:10.1016/j.dsr2.2008.01.007 [in press].

Landry, M.R., Brown, S.L., Rii, Y.M., Selph, K.E., Bidigare, R.R., Yang, E., Simmons, M.P., 2008. Depth-stratified phytoplankton dynamics in Cylone *Opal*, a subtropical mesoscale eddy. Deep-Sea Research II, doi:10.1016/j.dsr2.2008.02.001 [in press].

Letelier, R.M., Dore, J.E., Winn, C.D., Karl, D.M., 1996. Seasonal and interannual variations in photosynthetic carbon assimilation at Station ALOHA. Deep-Sea Research II 43, 467–490.

Letelier, R.M., Karl, D.M., Abbott, M.R., Flament, P., Freilich, M., Lukas, R., Strub, T., 2000. Role of late winter mesoscale events in the biogeochemical variability of the upper water column of the North Pacific Subtropical Gyre. Journal of Geophysical Research 105, 28723–28739.

Lumpkin, C.F., 1998. Eddies and currents of the Hawaiian Islands. Ph.D. Dissertation, University of Hawaii, Honolulu.

Maixandeau, A., Lefevre, D., Fernandez, I., Sempere, R., Sohrin, R., Ras, J., Van Wambeke, F., Caniaux, G., Queguiner, B., 2005a. Mesoscale and seasonal variability of community production and respiration in the surface waters of the NE Atlantic Ocean. Deep-Sea Research I 52, 1663–1676.

Maixandeau, A., Lefevre, D., Karayanni, H., Christaki, U., Van Wambeke, F., Thyssen, M., Denis, M., Fernandez, C., Uitz, J., Leblanc, K., Queguiner, B., 2005b. Microbial community production, respiration, and structure of the microbial food web of an ecosystem in the northeastern Atlantic ocean. Journal of Geophysical Research 110, C07S17.

McAndrew, P.M., Bjorkman, K.M., Church, M.J., Morris, P.J., Jachowski, N., Williams, P.J.L.B., Karl, D.M., 2007. Metabolic response of oligotrophic plankton communities to deep water nutrient enrichment. Marine Ecology Progress Series 332, 63–75.

McGillicuddy, D.J., Robinson, A.R., Siegel, D.A., Jannasch, H.W., Johnson, R., Dickey, T.D., McNeil, J., Michaels, A.F., Knap, A.H., 1998. Influence of mesoscale eddies on new production in the Sargasso Sea. Nature 394, 263–266.

Nencioli, F., Kuwahara, V.S., Dickey, T.D., Rii, Y.M., Bidigare, R.R., 2008. Physical dynamcis and biological implications of a mesoscale eddy in the lee of Hawai'i: Cyclone *Opal* observations during E-Flux III. Deep-Sea Research II, doi:10.1016/j.dsr2.2008.02.003 [in press].

Platt, T., Gallegos, C.L., Harrison, W.G., 1980. Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. Journal of Marine Research 38, 687–701.

Pringault, O., Tassas, V., Rochelle-Newall, E., 2007. Consequences of respiration in the light on the determination of production in pelagic systems. Biogeosciences 4, 105–114.

Robinson, C., Williams, P.J.L.B., 2005. Respiration and its measurement in surface waters. In: Del Giorgio, P.A., Williams, P.J.L.B. (Eds.), Respiration in Aquatic Ecosystems. Oxford University Press, pp. 147–180.

Sakamoto, C.M., Karl, D.M., Jannasch, H.W., Bidigare, R.R., Letelier, R.M., Walz, P.M., Ryan, J.P., Polito, P.S., Johnson, K.S., 2004. Influence of Rossby waves on nutrient dynamics and the plankton community structure in the North Pacific subtropical gyre. Journal of Geophysical Research 109, C05032.

Seki, M.P., Polovina, J.J., Brainard, R.E., Bidigare, R.R., Leonard, C.L., Foley, D.G., 2001. Biological enhancement at cyclonic eddies tracked with GOES thermal imagery in Hawaiian waters. Geophysical Research Letters 28, 1583–1586.

Seki, M., Lumpkin, R., Flament, P., 2004. Hawaii cyclonic eddies and blue marlin catches: the case study of the 1995 Hawaiian International Billfish Tournament. Journal of Oceanography 58, 739–745.

Serret, P., Fernandez, E., Sostres, J., Anadon, R., 1999. Seasonal compensation of microbial production and respiration in a temperate sea. Marine Ecology Progress Series 187, 43–57.

Serret, P., Robinson, C., Fernandez, E., Teira, E., Tilstone, G., 2001. Latitudinal variation in the balance between plankton photosynthesis and respiration in the eastern Atlantic Ocean. Limnology and Oceanography 46, 1642–1652.

Serret, P., Fernandez, E., Robinson, C., 2002. Biogeographic differences in the net ecosystem metabolism of the open ocean. Ecology 83, 3225–3234.

Sherr, E.B., Sherr, B.F., 1996. Temporal offset in oceanic production and respiration processes implied by seasonal changes in atmospheric oxygen: the role of heterotrophic microbes. Aquatic Microbial Ecology 11, 91–100.

Strickland, J.D.H., Parsons, T.R., 1972. A Practical Handbook of Seawater Analysis. Fisheries Research Board of Canada, Ottawa.

Sweeney, E.N., McGillicuddy Jr., D.J., Buesseler, K.O., 2003. Biogeochemical impacts due to mesoscale eddy activity in the Sargasso Sea as measured at the Bermuda Atlantic Time-series Study (BATS). Deep-Sea Research II 50, 3017–3039.

Uz, B.M., Yoder, J.A., Osychny, V., 2001. Pumping of nutrients to ocean surface waters by the action of propagating planetary waves. Nature 409, 597–600.

Vaillancourt, R.D., Marra, J., Seki, M.P., Parsons, M.L., Bidigare, R.R., 2003. Impact of a cyclonic eddy on phytoplankton community structure and photosynthetic competency in the subtropical North Pacific Ocean. Deep-Sea Research I 50, 829–847.

Welschmeyer, N.A., 1994. Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. Limnology and Oceanography 39, 1985–1992.

Williams, P.J.L.B., Jenkinson, N.W., 1982. A transportable microprocessor-controlled precise Winkler titration suitable for field station and shipboard use. Limnology and Oceanography 27, 576–584.

Williams, P.J.L.B., Morris, P.J., Karl, D.M., 2004. Net community production and metabolic balance at the oligotrophic ocean site, station ALOHA. Deep-Sea Research I 51, 1563–1578.