Short-term variability in euphotic zone biogeochemistry and primary productivity at
Station ALOHA: A case study of summer 2012


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KEY POINTS

Biogeochemistry of oligotrophic gyres can vary on time-scales from days to weeks

A period of sustained net heterotrophy was observed during August 2012

A low surface salinity feature propagated through the field site
Abstract

Time-series observations are critical to understanding the structure, function, and dynamics of marine ecosystems. The Hawaii Ocean Time-series (HOT) program has maintained near-monthly sampling at Station ALOHA (22° 45′N, 158° 00′W) in the oligotrophic North Pacific Subtropical Gyre (NPSG) since 1988 and identified ecosystem variability over seasonal to interannual time-scales. To further extend the temporal resolution of these near-monthly time-series observations, an extensive field campaign was conducted during July-September 2012 at Station ALOHA with near-daily sampling of upper water-column biogeochemistry, phytoplankton abundance, and activity. The resulting dataset provides biogeochemical measurements at high temporal resolution and documented two important events at Station ALOHA: (1) a prolonged period of low productivity when net community production in the mixed layer shifted to a net heterotrophic state and (2) 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. The shipboard observations during July-September 2012 were supplemented with in situ measurements provided by Seagliders, profiling floats, and remote satellite observations that together revealed the extent of the low productivity and the sea-surface salinity minimum feature in the NPSG.
1. Introduction

Understanding ocean ecosystems requires the collection of long-term, ecological time-series data at multiple locations in the world’s oceans. The Hawaii Ocean Time-series (HOT) program [Karl and Lukas, 1996] has been sampling Station (Stn) ALOHA, situated in the North Pacific Subtropical Gyre (NPSG) at 22° 45′N, 158° 00′W, since October 1988, maintaining the original research objectives to observe and interpret physical and biogeochemical variability in the NPSG ecosystem [Church et al., 2013]. The scientific rationale and foresight to situate an oceanographic time-series program in the relatively stable oligotrophic gyre ecosystem to observe changes over seasonal and decadal timescales has proven to be valuable [Venrick, 1995].

Near-monthly hydrographic and biogeochemical observations have documented ecosystem variability over timescales ranging from interannual e.g. increasing oceanic CO\textsubscript{2} inventories [Keeling et al., 2004; Dore et al., 2009], climate-related biological changes [Corno et al., 2007; Bidigare et al., 2009] to seasonal cycles of phytoplankton productivity [Letelier et al., 1996; Quay et al., 2010], nitrogen fixation [Church et al., 2009], and the downward flux of particulate organic matter [Karl et al., 2012].

Augmentation of shipboard time-series observations with higher resolution in situ observations and experimentation has provided new insight into spatiotemporal variability in the open ocean. Recent oceanographic fieldwork in the oligotrophic NPSG has identified pelagic ecosystem variability not captured by the monthly sampling maintained by the HOT program. Recent examples of such field-based research include characterization of phytoplankton blooms [Fong et al., 2008; Villareal et al., 2012], eddy-driven export of plankton biomass [Guidi et al., 2012], and the vertical entrainment of nutrients into the lower regions of euphotic zone [Johnson et al., 2010; Ascani et al., 2013]. However these oceanographic measurements differ from the
Eulerian sampling strategy of the upper water-column maintained by the HOT program and until now high-resolution fixed-point observations of hydrographic and biogeochemical parameters during an entire season has not been achieved. Accomplishing this goal would help resolve the connections between biological and physical variability and identify the propagation of individual features and their associated biogeochemical properties through the study site which may otherwise be misinterpreted as temporal variability [McGillicuddy, 2001; Karl, et al., 2002; Martin, 2003].

In summer 2012, an extensive field campaign designed to improve the temporal resolution of upper water-column hydrographic and biogeochemical measurements in the NPSG was conducted by the Center for Microbial Oceanography: Research and Education (C-MORE). The upper ocean during the summer months, which vary in definition but broadly extend from June to September, is characterized by relatively shallow mixed layers, elevated daily light flux, low nutrient inventories, and episodic phytoplankton blooms that include diatoms in conjunction with nitrogen (N$_2$)-fixing cyanobacteria or solely N$_2$-fixing microorganisms (e.g. Trichodesmium spp.) [Dore et al., 2008; Church et al., 2009; Wilson et al., 2013]. It is during the summer period that an export pulse of sinking particulate material from the euphotic zone usually occurs [Karl et al., 2012] indicating a transient disconnect between production and consumption mechanisms. In the oligotrophic gyres, photosynthesis and respiration are generally tightly coupled with a resulting net metabolic balance slightly in favor of autotrophic [Williams et al., 2013] although net heterotrophic conditions have also been inferred [Duarte et al., 2013]. The metabolic balance, in terms of oxygen (O$_2$) and carbon (C), is represented by the residual between gross primary production (GPP) and community respiration (CR), referred to as net community
production (NCP). NCP is a small, yet critical term in the global carbon cycle as it represents the biologically produced carbon available for export from the upper ocean [Emerson, 2014].

This paper reports the hydrographic and biogeochemical conditions of the upper water-column at Stn ALOHA between July-September 2012. A striking observation during this period was the absence of any prolonged increase in phytoplankton biomass or bloom activity that is often observed during the summer time in the NPSG. Instead, anomalously low values of phytoplankton abundance and a period of net heterotrophy were recorded. In the absence of local or regional physical forcing mechanisms, we have identified several indicators of ecosystem-scale forcing which potentially contributed to this period of net heterotrophy. A separate hydrographic phenomenon, described as a ‘sea-surface salinity minimum’ was also observed and characterized. The low salinity water was associated with anomalously low concentrations of particulate material and phytoplankton. The daily measurements collected in this study are placed within the context of the 1988–2011 time-series climatology provided by the HOT program’s measurements at Stn ALOHA. Ultimately the high-resolution Eulerian observations revealed the day-to-day biogeochemical variability of the upper water-column and identified hydrographic features that impact this open ocean oligotrophic habitat.

2. Materials and methods

2.1 Field operations and sampling

During 2012, a series of C-MORE-sponsored oceanographic expeditions collectively known as Hawaii Ocean Experiment: DYnamics of Light And Nutrients (HOE DYLAN) conducted operations at Stn ALOHA onboard the R/V Kilo Moana (Table 1). Three major expeditions covered a period from 8–28 July (KM1215), 5–14 August (KM1217), and 22 August to 11
September 2012 (KM1219). These C-MORE cruises were interspersed with monthly HOT program cruises (Table 1).

To characterize the upper water-column, vertical profiles of hydrographic parameters were conducted every 4 h during the three major cruises, typically to a depth of 400 m with a deeper cast extending to 1000 m conducted at 0800 hrs daily. The conductivity-temperature-depth (CTD) package (SBE 911Plus, SeaBird) was attached to a 24 x 12 L Niskin bottle rosette that also incorporated fluorescence, oxygen (O$_2$), and in situ ultraviolet spectrophotometer (ISUS, version 3, Satlantic) sensors. The conductivity, fluorescence, and O$_2$ sensors were calibrated using discrete measurements of salinity [Bingham and Lukas, 1996], fluorometric analysis of chlorophyll $a$ and phaeopigments [Strickland and Parsons, 1972], and dissolved O$_2$ [Carritt and Carpenter, 1966], respectively. The mixed layer depth (MLD) was calculated based on a seawater density anomaly of 0.125 kg m$^{-3}$ from the sea-surface.

During May through October 2012, a continuous traverse of a 50 km by 50 km ‘bowtie’-shaped formation which extended from Stn ALOHA to the northeast was maintained by Seaglider operations. Each Seaglider cycle reached a maximum depth of 800 m, lasted approximately 6 h, and extended a horizontal distance of 3–5 km between surfacing. The bowtie formation was completed approximately every 2 weeks, allowing for calibration with shipboard measurements when the Seaglider traversed through Stn ALOHA. The Seaglider was equipped with a CTD package (Seabird) and sensors for O$_2$ (Seabird SBE-43 and Aanderaa Optode 3830), fluorescence, and optical backscatter (WET Labs) [Eriksen et al., 2001].

2.2 Biogeochemical analyses
The CTD casts conducted every 4 h were sampled systematically to determine the hydrographic and biogeochemical properties of the water-column. The biogeochemical properties of the water-column (nutrients, particulates, pigments) were sampled by conducting vertical profiles at least every 3 days from discrete depths of 5, 25, 45, 75, 100, 125, 150 and 175 m. The vertical profiles were supplemented by higher temporal resolution sampling at targeted depth horizons, e.g. at 25 m within the mixed layer. To ensure consistency of measurements at Stn ALOHA, the majority of sampling and analytical protocols were identical to those employed by the HOT program (http://hahana.soest.hawaii.edu/index.html). In brief, nutrient analysis which included nitrite (NO$_2^-$) plus nitrate (NO$_3^-$) and phosphate was performed on land using a Bran+Luebbe Autoanalyzer III. NO$_2^-$ + NO$_3^-$ was also determined using the chemiluminescence method for samples collected from 0–175 m as this method has an improved detection limit of 1 nmol L$^{-1}$ [Dore and Karl, 1996]. Seawater samples for particulate carbon (PC) and particulate nitrogen (PN) were collected onto combusted 25 mm diameter Whatman glass fiber filters (GF/F). The filters were stored frozen until analyzed using an Exeter CE-440 CHN elemental analyzer (Exeter Analytical, UK).

Phytoplankton pigments were analyzed using high performance liquid chromatography (HPLC) as described by Bidigare et al., [2005]. Six diagnostic biomarker pigments representative of the major phytoplankton taxa are reported which include fucoxanthin, 19′-hexanoyloxyfucoxanthin, 19′-butanoyloxyfucoxanthin, zeaxanthin, divinylchlorophyll a, and monovinylchlorophyll a. Sample volumes consisted of 2–4 L captured onto Whatman GF/F filters, wrapped in foil, flash frozen and stored at -80°C. Pigments were extracted in 3 ml of 100% acetone in the dark at 4°C for 12 h followed by vortexing, centrifugation, and subsequent analysis using a Varian 9012 HPLC system.
To characterize the N\textsubscript{2}-fixing microorganisms, the \textit{nifH} gene which encodes a subunit of the nitrogenase enzyme was quantified using quantitative PCR (qPCR). The groups of diazotrophs targeted included UCYN-A, \textit{Crocosphaera} spp., \textit{Trichodesmium} spp., and two types of heterocystous cyanobacteria that form symbioses with diatoms. Discrete seawater samples (2–4 L) were collected using the CTD-rosette, filtered using a peristaltic pump onto 10 \(\mu\)m polyester (GE Osmotics, Minnetonka, MN) and 0.2 \(\mu\)m Supor (Cole Parmer, Vernon Hills, IL) filters in series, frozen in liquid nitrogen, and stored at -80°C until processed. The DNA extraction was conducted using published protocols [Moisander \textit{et al.}, 2008] and the qPCR analyses conducted as previously described [Goebel \textit{et al.}, 2010].

Four independent shipboard measurements of productivity were conducted during July-September, although not all measurements extended for the entire period. Productivity measurements included the assimilation of \({}^{14}\text{C}\)-labeled bicarbonate (NaH\(^{14}\text{CO}_3\)) into particulate matter [Letelier \textit{et al.}, 1996], active fluorescence using fast repetition rate fluorometry (FRRF) [Kolber and Falkowski, 1993], and two dissolved gas measurements: triple O\(_2\) isotope (\(^{17}\Delta\)) abundance to derive gross primary production [Luz and Barkan, 2000] and ratios of O\(_2\)/Ar to derive Net Community Production (NCP) [Kaiser \textit{et al.}, 2005]. Seawater samples for \({}^{14}\text{C}\) assimilation were collected pre-dawn at 0400 hrs, dissolved O\(_2\)/Argon (O\(_2\)/Ar) and triple O\(_2\) isotope (\(^{17}\Delta\)) were collected at 0800 hrs, and FRRF was collected at 1600 hrs. Due to the diel variability in O\(_2\) concentrations resulting from biological activity [Hamme \textit{et al.}, 2012; Tortell \textit{et al.}, 2014], calculation of NCP from instantaneous measurements of O\(_2\)/Ar in the early morning may result in an underestimation of NCP at Stn ALOHA by up to 20% compared to the daily mean rate [Ferrón \textit{et al.}, 2015]. Since our samples for O\(_2\)/Ar analysis were collected at 0800 hrs when rates of NCP are at their lowest, our measurements represent a lower estimate of NCP.
For the measurements of $^{14}\text{C}$ incorporation, seawater was collected at 0400 hrs from a depth of 25 m into 500 ml acid-washed polycarbonate bottles in triplicate, spiked with NaH$^{14}\text{CO}_3$, and incubated on-deck over the full daylight period [Letelier et al., 1996]. The on-deck incubators were screened to the light levels equivalent to a depth of 25 m in the water-column using blue acrylic shielding and flow-through surface seawater to maintain temperature. Sampling protocols for $^{14}\text{C}$ assimilation measurements were identical for HOT and C-MORE cruises, except the sample incubations were conducted in situ during the HOT expeditions rather than on-deck incubators. To quantify $^{14}\text{C}$ assimilation, seawater was filtered onto 25 mm diameter Whatman GF/F filters and placed into scintillation vials. After acidifying with 1 mL of 2 M HCl and venting for 24 h to remove inorganic $^{14}\text{C}$, 10 mL of scintillation cocktail (UltimaGold LLT, PerkinElmer) was added to each vial and the radioactivity counted on a Packard liquid scintillation counter (TriCarb2770TR/LT) and quench corrected using internal protocols. Rates of $^{14}\text{C}$ incorporation ($^{14}\text{C}$-PP) are reported per day and represent the net incorporation of carbon into particulate matter during the daylight period.

FRRF measurements were conducted on the ship’s underway seawater system and from vertical CTD-hydrocasts conducted daily at noon. The FRRF instrument was operated with a broad-band excitation source in the 430–545 nm range. The FRRF-based estimates of primary production (FRRF-PP) rates were calculated at time intervals of 15 min using the deckboard PAR data, with the light propagation along the water-column based on light attenuation coefficient provided by daily measurements of a hyperspectral radiometer (Satlantic). These rates were integrated over a 24 h period using first-order interpolation to provide daily rates of FRRF-PP. The rates of FRRF-PP were calculated according to Suggett et al. [2003] assuming 8
mole of quanta/mole O₂, and an average size of the photosynthetic unit of 500
(chlorophyll:reaction center).

The O₂/Ar measurements were conducted by filling 12 mL vials (Exetainer, Labco Ltd),
preserving with mercuric chloride (HgCl₂), and analyzing the O₂/Ar ratios using a membrane
inlet mass spectrometer (MIMS) [Kana et al., 1994]. Reference measurements consisted of
filtered (0.2 µm) surface seawater and the analytical temperature for reference seawater and
samples was maintained at 23°C by immersing the 1/16" stainless steel inlet tubing inside a
water bath. Gases were extracted through a semi-permeable silicone membrane connected to a
vacuum system, and passed through a liquid nitrogen U-tube bath to extract water vapor before
entering a quadruple mass spectrometer (Peiffer HiCube).

Net Community Production (NCP) was calculated using two methods as described in Hamme
et al., [2012]. The more traditional approach assumes that the water-column is in steady state
and that vertical and lateral mixing are negligible. Therefore the net biological production or
consumption of O₂ in the mixed layer can be estimated from the gas-exchange of biological O₂
[Kaiser et al., 2005] as:

\[
NCP = k_w \times O_{2eq} \times \Delta(O_2/Ar)
\]

where \(k_w\) is the weighted gas transfer velocity for O₂ (m d⁻¹), \(O_{2eq}\) is the equilibrium
concentration of dissolved O₂ (mmol m⁻³) in the mixed layer, and \(\Delta(O_2/Ar)\) is the deviation of
O₂/Ar from equilibrium, calculated as:

\[
\Delta(O_2/Ar) = \left[ \frac{(O_2/Ar)_{sample}}{(O_2/Ar)_{sat}} - 1 \right]
\]

where \((O_2/Ar)_{sample}\) is the measured ratio in the sample, and \((O_2/Ar)_{sat}\) is the ratio expected at
saturation equilibrium, calculated using the solubility equations of Garcia and Gordon [1992]
for O₂ and Hamme and Emerson [2004] for Ar. The gas transfer velocity used in equation (1)
was estimated from the wind speeds recorded at the WHOTS buoy using the wind-speed
parameterization and Schmidt numbers from Wanninkhof [2014] and a 20-day weighting
algorithm following Reuer et al. [2007] to account for wind speed variability prior to the
measurement (Table S1). We refer to NCP derived from equation 1 as ‘prior O$_2$/Ar-NCP’ as it
averages over a time period prior to the measurements. An alternative approach to calculate
NCP is from the rate of change of Δ(O$_2$/Ar) during the expedition by fitting a linear regression to
Δ(O$_2$/Ar) with time [Hamme et al., 2012].

\[
NCP = k_{O2} \times O_{2eq} \times \Delta(O_2/Ar) + MLD \frac{d(\Delta(O_2/Ar))}{dt} \times O_{2eq}
\]

where $k_{O2}$ is the non-weighted gas transfer velocity for O$_2$, $MLD$ is the average mixed layer
depth, and the rate of change of Δ(O$_2$/Ar) was calculated by fitting a linear regression to the
daily Δ(O$_2$/Ar) values. This method has previously been reported for NCP over timescales of
hours to days [Hamme et al., 2012; Tortell et al., 2014] and is hereafter referred to as ‘real-time
O$_2$/Ar-NCP’, as it averages over the period of time when the measurements were taken.

Samples for triple O$_2$ isotope (17Δ) analysis were collected during the third major expedition.
Measurements were made daily from a depth of 25 m at 0800 hrs from 23 August to 7 September
and also at 4 h intervals between 31 August and 1 September. The same sampling and analytical
protocols were followed as reported by Juranek and Quay [2005]. Samples were collected from
Niskin bottles into pre-evacuated, HgCl$_2$ poisoned, 200 mL glass flasks to limit atmospheric
contamination. Samples were analyzed at Oregon State University using the same mass
spectrometer measurement procedure as described in Juranek and Quay [2005]. Rates of gross
primary production (17Δ-GPP) were determined as per the method of Luz and Barkan [2000]
using the water-column parameters, MLD, wind speeds, and gas transfer velocity as described
for determining NCP from O$_2$/Ar analysis [Table S1].
A comparison of the four productivity measurements is provided in Table 2 based on MLD-integrated production in units of \( \text{O}_2 \). The volumetric rates of \(^{14}\text{C}-\text{PP}\) and FRRF-PP were converted to MLD-integrated values assuming the 25 m sampling depth was representative of the mixed layer. The \(^{14}\text{C}-\text{PP}\) measurements were converted to equivalent units of \( \text{O}_2 \) using a photosynthetic quotient (PQ) of 1.1 which is suitable for regenerated production in the oligotrophic gyre ecosystem [Laws, 1991]. To identify differences between rates of production for the separate expeditions a two-way analysis of variance (two-way ANOVA) and two-sample t-test was utilized after checking data for heterogeneity of variance.

2.3 Additional datasets used

The online Global Marine Argo Atlas dataset was used to help analyze Argo float datasets for sea-surface salinity in the vicinity of Stn ALOHA during July-September 2012 [Roemmich and Gilson, 2009]. In particular, vertical profiles of pressure, temperature, and conductivity were retrieved from three Webb Research APEX profiling floats (Float IDs #5903888, 5903273, 5902241) that were in the vicinity of Stn ALOHA during July-September 2012. The profiles were conducted between the surface and 1000 m every 2-, 5-, and 10-day intervals for the three floats, respectively.

Meteorological measurements were provided by the WHOTS buoy situated at Stn ALOHA from June 2012 to July 2013 (http://uop.whoi.edu/projects/WHOTS/whotsdata.htm). Downwelling irradiance above the sea-surface in the PAR spectral region was measured using a cosine sensor (LI-COR LI-192) mounted on the top deck of the R/V Kilo Moana. Measurements of horizontal velocity in the upper water column were obtained using a hull-mounted Acoustic Doppler Current Profiler (ADCP) (RDI Ocean Surveyor 300-kHz). To place the shipboard
measurements in a wider spatial-temporal context, the surface flow within the Hawaii regional
domain (15–27°N, 150–160°W) was analyzed using the Hybrid Coordinate Ocean Model
(HYCOM) which is run in real-time at the Naval Oceanographic Office at 1/12 degree resolution
[Chassignet et al., 2009]. Satellite observations of regional ocean color (2002-2012, 8 day
averages) for the NPSG were analyzed using images from Moderate Resolution Imaging
Spectroradiometer (MODIS) obtained from the Ocean Biology Processing Group (OBPG;
http://oceancolor.nasa.gov). Data for a 25x25 km region surrounding Station ALOHA were
binned to generate the average and standard deviation at 8-day intervals (e.g. mean of day 1-8
over 2002-2012). Monthly composites were generated for the North Pacific. Anomaly time-
series were calculated by difference of 2012 data relative to spatial or temporal averages. Sea
Surface Height Anomaly (SSHA) was assessed using animations of satellite altimetry covering
15–30°N 148–170°W and produced from Archiving, Validation, and Interpretation of Satellite
Oceanographic data (AVISO).

3. Results

3.1 Hydrographic conditions

During July-September 2012 hydrographic conditions in the upper water-column (0–200 m)
showed both the expected seasonal characteristics of the oligotrophic gyre ecosystem based on
the 1989-2011 climatology at Stn ALOHA and evidence of high day-to-day variability (Figure
1). At the beginning of the field campaign, during 10-20 July, the mean near-surface (0–25 m)
seawater temperature was 24.7 ± 0.1 (standard deviation; SD) °C (Figure 1a). During the
following 5 weeks from 20 July to 28 August the 0–25 m seawater temperature increased
steadily to a maximum of 25.6°C and then subsequently decreased during the remainder of the
campaign (Figure 1b-e). For the overall period during July-September 2012, the near-surface (0–25 m) seawater temperature was 0.7–0.9°C lower than the respective monthly averages from the 1989–2011 climatology at Stn ALOHA, reflecting a long-term interannual anomaly. The near-surface salinity ranged from 35.1–35.4 between July and mid-August 2012 (Figure 1f-i). However initially during 17–18 August and then more consistently from 26 August onwards, salinity decreased coincident with the passage of an upper ocean salinity minimum feature at Stn ALOHA. The mean salinity of the near-surface ocean during 17–18 August was 35.0 and from 6 September onwards was 35.0 which represented a mean decrease of 0.3 compared to the salinity measured during July 2012 (Figure 1f-i). The feature was restricted to the near-surface of the water-column with salinity increasing to ~35.2 by a depth of 50 m. Dissolved O\textsubscript{2} concentrations in 0–25 m of the water-column ranged from 209–218 µmol kg\textsuperscript{-1} (represented by the 5 and 95 percentile, respectively) with an overall mean of 212 ± 0.1 (SD) µmol kg\textsuperscript{-1} (Figure 1k-o). Between depths of 50–100 m, a subsurface O\textsubscript{2} maximum was present with mean O\textsubscript{2} concentrations of 220 ± 3 (SD) µmol kg\textsuperscript{-1}. The deep chlorophyll maximum (DCM) was consistently present at depths between 100–150 m (Figure 1p-t).

The mean MLD during 8–20 July 2012 was 66 ± 13 (SD) m, with a maximum depth of 86 m (Figure 1). For the remainder of the study period (20 July to 9 September) the MLD was shallower, with a mean depth of 51 ± 12 (SD) m. The prolonged period of deeper mixing in early July is unusual for the period of July-September at Stn ALOHA (the mean depth based on the 1988-2011 climatology is 49 ± 11 (SD) m). Shipboard observations at Stn ALOHA between 1989 and 2011 reveal five occurrences when the cruise-averaged-MLD exceeded 60 m during June-September based on a potential density anomaly of 0.125.
Satellite derived SSHA in the ALOHA region between July and September 2012 suggested relatively modest eddy activity, with SSHA varying between -3.09 cm and 8.53 cm. The largest excursions in SSHA occurred in early July and September due to the westward advection of eddies approximately 180 km to the north of Stn ALOHA.

3.2 Sea-surface salinity minimum at Stn ALOHA in August-September 2012

In addition to the shipboard CTD measurements (Figure 1), vertical profiles of salinity, temperature, and O2 were collected by Seagliders (Figure 2) and Argo floats (Figure 3). These in situ observations provided an estimate of the temporal extent of the sea-surface salinity minimum feature observed in August-September (Figure 1f). The Seaglider traversed an area approximately 2500 km² in size and the sea-surface salinity minimum feature was observed at Stn ALOHA until late September (0–25 m mean ± SD salinity of 35.1 ± 0.2), after which time salinity in the near-surface ocean returned to values more typical of late summer and early fall based on the HOT program climatology. Argo floats also detected the sea-surface salinity minimum both in September and prior to its arrival at Stn ALOHA in August (Figure 3). The sea-surface salinity minimum was most evident in the salinity profiles recorded by Argo float #5903888 (0–25 m depth-averaged salinity mean ± SD of 35.0 ± 0.03 during 12 September to 7 October), which profiled at 2 day intervals and was drifting clockwise around Stn ALOHA during July to December 2012 (Figure 3a). The two other Argo floats were located 200-300 km south-east of Stn ALOHA and recorded mean 0–25 m depth-averaged salinity of 35.0 ± 0.1 (SD) during 11 June and 25 September (Float #5903273; Figure 3b) and 35.0 ± 0.1 (SD) during 7 July and 25 September (Float #5902241; Figure 3c). Similar to the Seaglider, the three Argo floats did not continue to detect the sea-surface salinity minimum in October indicating that it had
dissipated or propagated elsewhere undetected. Analysis of the Argo float data to the west and north of Stn ALOHA during September to December 2012 did not reveal any surface salinity minimum features. It is also noteworthy that neither the Argo floats or the Seaglider detected the sea-surface salinity minimum on 17–18 August when it was sampled by the shipboard CTD, indicating the feature was initially irregular and hard to detect.

Efforts to determine the size and origin of the sea-surface salinity minimum proved difficult since it was not evident in satellite-derived measurements of salinity and there were no changes in SSHA associated with the sea-surface salinity minimum. Analysis of circulation patterns generated by the HYCOM model revealed a mean sea-surface flow from the south-east during August to September 2012 (data not shown) and Argo-derived salinity profiles indicated decreased near-surface salinity south-east of Stn ALOHA prior to September 2012 (Figure 3d-e). Using the Argo float monthly-averaged 0–100 m salinity during 2004–2014 for September, a northwest latitudinal shift of the mean salinity field by ~500 km would bring seawater with salinity of 35.0 to Stn ALOHA.

3.3 Water-column particulate material and nutrients

Water-column nutrients and particulate material were sampled at 3 day intervals or greater between depths of 0–175 m during July-September 2012. Depth-averaged (5–25 m) phosphate concentrations ranged from 0.07–0.14 µmol L⁻¹ during July-September 2012 (Figure 4a). The phosphate concentrations during July-September are consistent with the 5–25 m depth-averaged values observed throughout 2012 (mean ± SD of 0.1 ± 0.02 µmol L⁻¹); however, the phosphate concentrations in 2012 are high compared to the overall mean of 0.06 ± 0.03 (SD) µmol L⁻¹ for 1989-2011 climatological record. Hence the elevated concentrations of phosphate in 2012
appear indicative of interannual variability, rather than short-term (monthly) variability.

Concentrations of $\text{NO}_2^- + \text{NO}_3^-$ (not shown in Figure 4) were consistently low in the near-surface water-column during July-September 2012. An increase in $\text{NO}_2^- + \text{NO}_3^-$ concentrations to 6–8 nmol L$^{-1}$ (5–25 m depth-averaged) was recorded by the HOT program during July-August (http://hahana.soest.hawaii.edu/hot/hot-dogs), but not captured during the longer C-MORE expeditions which reported consistently low (2–5 nmol L$^{-1}$) concentrations.

During the period of study, the mean depth-averaged (5–25 m) concentration of PC was 2.3 ± 0.3 (SD) µmol L$^{-1}$ (Figure 4b). The most distinct trend was observed during August-September as a persistent decrease in PC concentrations associated with the sea-surface salinity minimum. The lowest PC concentration of 1.7 ± 0.01 µmol L$^{-1}$ was observed on 5 September. This is at the lower end of the long-term PC concentrations at Stn ALOHA for July-September, which range from 1.1–3.8 µmol L$^{-1}$ (mean ± SD of 2.3 ± 0.5 µmol L$^{-1}$) based on the 1989-2011 HOT climatology. In comparison, the mean 5–25 m depth-averaged concentration of PN for July-September was 0.32 ± 0.06 (SD) µmol L$^{-1}$ (Figure 4c). A similar decreasing trend was observed in PN concentrations compared to PC toward the end of the campaign with the lowest PN concentration (0.24 µmol L$^{-1}$) measured on 5 September 2012 (Figure 4c).

### 3.4 Phytoplankton community composition

The abundance of flow cytometry enumerated populations of phytoplankton and heterotrophic picoplankton (bacteria and archaea) in the upper water-column showed a coherent and collective spatial and temporal pattern during July-September 2012 (Figure 5). The 5–25 m depth-averaged mean abundance of *Prochlorococcus* during the overall period from July-September was $1.6 \pm 0.3$ (SD) x $10^5$ cells mL$^{-1}$. An approximate 17% decrease in 5–25 m depth-
averaged mean cell abundance was observed during 1–7 September (1.4 ± 0.3 (mean ± SD) x 10^5 cells mL\(^{-1}\)), coincident with the presence of the sea-surface salinity minimum (Figure 5a-c). Variability was also evident in the vertical distribution of *Prochlorococcus* with maximum cell abundances occurred at 75 m where concentrations averaged 2.1 ± 0.3 (mean ± SD) x 10^5 cells mL\(^{-1}\) during July-September. The abundance of *Prochlorococcus* decreased rapidly with depth below 75 m and cell concentrations were ~25% of the maximum abundance at 125 m. 

*Synechococcus* abundance at 5–25 m depths was 2 orders of magnitude lower than *Prochlorococcus* during July-September, with a mean abundance of 1.2 ± 0.4 (SD) x 10^3 cells mL\(^{-1}\) (Figure 5). Similar to the temporal patterns of *Prochlorococcus*, the population of *Synechococcus* also decreased during 1–7 September by ~28% with a mean cell abundance of 0.8 ± 0.1 (SD) x 10^3 cells mL\(^{-1}\) (Figure 5). The mean abundance of photosynthetic picoeukaryotes between 5–25 m was 0.9 ± 0.3 (SD) x 10^3 cells mL\(^{-1}\) during July-September (Figure 5j-l) and the mean abundance of free-living heterotrophic picoplankton was 5.2 ± 0.7 (SD) x 10^5 cells mL\(^{-1}\) (Figure 5d-e). The effect of the sea-surface salinity minimum was also evident in populations of photosynthetic picoeukaryotes and heterotrophic picoplankton which were 33 and 24 % less abundant between depths of 5–25 m during 1–7 September compared to July-August 2012.

In addition to flow cytometry enumerations of cell abundance, phytoplankton pigments at the 25 m depth horizon were sampled at daily (or more frequent) intervals, in addition to vertical profiles every 3 days (Figure 6). The most abundant pigments analyzed were zeaxanthin (Figure 6a), divinylchlorophyll a (Figure 6b), and monovinylchlorophyll a (Figure 6c). Divinylchlorophyll a, the diagnostic pigment for *Prochlorococcus*, was significantly lower in concentration during 7–14 August with a mean concentration of 31 ± 4 (SD) ng L\(^{-1}\) compared to 7–23 July (mean ±
SD: $46 \pm 10 \, \text{ng L}^{-1}$) and 23 August to 10 September (mean ± SD: $51 \pm 7 \, \text{ng L}^{-1}$) (Figure 6b).

Daily excursions in pigment concentrations were occasionally observed (e.g. 31 August) and coincided with small-scale patterns in local hydrography (Figure 1). Of the three lesser abundant pigments, 19'-hexanoyloxyfucoxanthin and fucoxanthin, diagnostic biomarkers for prymnesiophytes and diatoms respectively, displayed the largest variability during July-September 2012 (Figure 6d, 6e). The highest concentrations of fucoxanthin were observed in July (mean ± SD: $6 \pm 1 \, \text{ng L}^{-1}$) with concentrations subsequently decreasing steadily throughout the summer (Figure 6e).

Depth-averaged (5–25 m) concentrations of nifH gene copies for four major groups of N$_2$ fixing microorganisms are shown in Figure 7. UCYN-A, was the most prominent diazotroph during July-September 2012 with an overall mean abundance of $6.8 \pm 5.0 \, \text{(SD)} \times 10^5$ nifH gene copies L$^{-1}$. *Trichodesmium* increased in abundance during the summer to reach a maximum gene abundance of $4.4 \times 10^4$ nifH gene copies L$^{-1}$ during late August-September. The heterocystous cyanobacteria were most abundant in July with a mean concentration of $7.1 \pm 1.5 \, \text{(SD)} \times 10^3$ nifH gene copies L$^{-1}$ and subsequently decreased in abundance during the summer. *Crocosphaera* was detected throughout July-September with a mean gene abundance of $6.4 \pm 3.4 \, \text{(SD)} \times 10^3$ nifH gene copies L$^{-1}$.

### 3.5 Productivity measurements

Measurements of O$_2$/Ar ratios and $^{14}$C assimilation were conducted during all three major expeditions, while FFRF and $^{17}\Delta$ were limited to fewer measurements (Figure 8; Table 2). The O$_2$/Ar measurements are represented by $\Delta$O$_2$/Ar(%) including the linear regressions used to calculate real-time O$_2$/Ar-NCP (Figure 8a) and prior O$_2$/Ar-NCP in units of mmol O$_2$ m$^{-2}$ d$^{-1}$.
(Figure 8b). Rates of prior O$_2$/Ar-NCP were significantly different (t-test, P<0.01) for each of
the major expeditions and demonstrated a clear change between net autotrophic and net
heterotrophic conditions in the near-surface waters (Figure 8a, Figure 8b). During 9–24 July, the
mean prior O$_2$/Ar-NCP was 6.0 ± 3.2 (SD) mmol O$_2$ m$^{-2}$ d$^{-1}$ while the real-time O$_2$/Ar-NCP was
1.6 ± 2.6 (SD) mmol O$_2$ m$^{-2}$ d$^{-1}$. The decrease in O$_2$/Ar-NCP during July ultimately led to net
heterotrophic conditions being present in the mixed layer by the time daily measurements were
resumed on 5 August. During 5–12 August, the mean MLD-integrated prior O$_2$/Ar-NCP was
7.6 ± 4.2 (SD) mmol O$_2$ m$^{-2}$ d$^{-1}$ while real-time O$_2$/Ar-NCP was positive 3.9 ± 2.2 (SD) mmol O$_2$
m$^{-2}$ d$^{-1}$, indicating the ecosystem had either recovered from the period of net heterotrophy or
there was spatial variability in ΔO$_2$/Ar. While temporal trends on weekly timescales were
present in rates of real-time O$_2$/Ar-NCP during 8–24 July and 5–12 August (Figure 8a), this was
not the case for 22 August to 5 September (Figure 8a). In the absence of temporal trends of
weekly timescales, O$_2$/Ar measurements during 23 August to 6 September were characterized by
high day-to-day variability with a mean MLD-integrated prior O$_2$/Ar-NCP was -0.5 ± 3.1 (SD)
mmol O$_2$ m$^{-2}$ d$^{-1}$. The variability in prior O$_2$/Ar-NCP both pre-empted and coincided with the
arrival of the sea-surface salinity minimum feature and therefore was likely due to high spatial
variability.

Rates of $^{14}$C-PP sampled at 25 m during every major expedition similarly revealed distinct
patterns during July-September 2012 (Figure 8c). The highest rates of $^{14}$C-PP occurred during
9–25 July with a mean of 0.61 ± 0.1 (SD) mmol C m$^{-3}$ d$^{-1}$ (MLD-integrated 36.3 ± 6.5 mmol C
m$^{-2}$ d$^{-1}$). The lowest rates occurred during 6–12 August with a mean value of 0.49 ± 0.1 (SD)
mmol C m$^{-3}$ d$^{-1}$ (MLD-integrated 26.7 ± 5.1 mmol C m$^{-2}$ d$^{-1}$). During 23 August to 8
September, the rates of $^{14}$C assimilation ranged from 0.48–0.72 mg C m$^{-3}$ d$^{-1}$, with an overall
mean of 0.62 ± 0.1 (SD) mmol C m⁻³ d⁻¹ (MLD-integrated 33.1 ± 7.4 mmol C m⁻² d⁻¹). A comparison of the three expeditions revealed significantly lower rates of $^{14}$C assimilation during 7–14 August (t-test, P<0.001), however there was no significant difference between the $^{14}$C assimilation rates during 9–25 July and 23 August to 7 September (t-test, P>0.05; Table 2).

The FRRF-based measurements of productivity (FRRF-PP) were conducted during 9–25 July and 23 August to 8 September (Figure 8d). There was no significant difference (t-test, P>0.05) between the mean values of FRRF-PP measured at a depth of 25 m during the two expeditions which were 0.66 ± 0.13 (SD) mmol C m⁻³ d⁻¹ for 9–25 July and 0.72 ± 0.07 (SD) mmol C m⁻³ d⁻¹ for 23 August to 8 September. A consistent downward trend in FRRF-PP was observed during 23 August to 4 September which coincided with the decreasing concentrations of PC (Figure 4). The values of FRRF-PP are provided in Table 2 as MLD-integrated rates of production, using the MLD values provided in the supporting information.

Measurements of dissolved triple O₂ isotopes to determine GPP ($^{17}$Δ-GPP) were conducted on 22 separate occasions during 23 August to 7 September (Table S2). The mean MLD-integrated $^{17}$Δ-GPP for the 12 day period was 91 ± 35 (SD) mmol O₂ m⁻² d⁻¹ (range of 38–168 mmol O₂ m⁻² d⁻¹). The analysis of duplicate seawater samples on the 28 August yielded a mean ± SD of 51 ± 5 mmol O₂ m⁻² d⁻¹ (Table S2). The $^{17}$Δ-GPP was almost 3-fold higher than MLD-integrated $^{14}$C-PP and 40% higher than MLD-integrated FRRF-PP during 23 August to 7 September (Table 2).

The significant period of low productivity when the upper water-column was in a net heterotrophic state was explored using other datasets including phytoplankton biomarkers, time-series climatological measurements, and satellite-derived TChla. During 7–12 August, the low rates of productivity coincided with low concentrations of TChla, an indicator of photosynthetic
biomass (Figure 8e). The mean concentration of TChl$\alpha$ decreased at the 25 m depth horizon from 82 ± 6 (SD) ng L$^{-1}$ in 9–25 July by 30% to 66 ± 6 (SD) ng L$^{-1}$ in 6–13 August (Figure 8e). The mean concentration of TChl$\alpha$ subsequently increased to an average concentration of 82 ± 7 (SD) ng L$^{-1}$ for 23 August to 7 September (Figure 8e). A comparison of the three expeditions revealed significantly lower concentration of TChl$\alpha$ during 7–12 August (t-test, $P<0.001$), however there was no significance difference between concentration of TChl$\alpha$ during 9–25 July and 23 August to 7 September (t-test, $P>0.05$).

The HOT program’s near-monthly measurements at Stn ALOHA of $^{14}$C assimilation and particle export rates during March-October 2012 are shown in comparison with the 1989-2011 HOT climatology (Figure 9). The monthly time-series measurements support the observation of low productivity occurring during August 2012. The mean depth-averaged (5–25 m) rates of $^{14}$C-PP rates measured on 17 August was 0.44 mmol C m$^{-3}$ d$^{-1}$ (Figure 9a), equivalent to a MLD-integrated rate of $^{14}$C-PP of 20.6 mmol C m$^{-2}$ d$^{-1}$. These rates of $^{14}$C-PP are low for this time of year at Stn ALOHA with a monthly mean for August based on the 1989-2011 HOT climatology of 0.66 ± 0.2 mmol C m$^{-3}$ d$^{-1}$ (Figure 9a). In addition to $^{14}$C assimilation, during 17–18 August 2012, measured downward export of C was 1.5 mmol C m$^{-2}$ d$^{-1}$, almost half of the the mean ± SD (2.9 ± 0.9 mmol C m$^{-2}$ d$^{-1}$) for the month of August during the 1989-2011 Stn ALOHA climatology (Figure 9b).

The spatial and temporal extent for the period of low productivity was further investigated using remote sensing products provided by MODIS. Satellite-derived TChl$\alpha$ concentrations for 2012 are compared with the antecedent 10-year climatology (Figure 9c). The period of low productivity observed during 4–14 August by shipboard measurements is accompanied by a decrease in satellite-derived TChl$\alpha$ relative to the 10-year mean. However there is a temporal
mis-match with the shipboard measurements of TChl\textsubscript{a}, as determined by HPLC and fluorometry, as the satellite data shows the largest TChl\textsubscript{a} anomaly to be in September 2012 when concentrations of TChl\textsubscript{a} are less than the minimum values observed in the 10-year climatology. In contrast, the shipboard observations show August to have the lowest TChl\textsubscript{a} concentrations (Figure 8e). A broader look at the TChl\textsubscript{a} anomaly throughout the NPSG reveals the negative anomaly is evident in August-September, but not earlier in July 2012 (Figure 10). Albeit patchy, the negative TChl\textsubscript{a} anomaly during August-September extended from 22–26°N to 152–160°W, a region of approximately 300,000 km\textsuperscript{2}.

4. Discussion

4.1 Insights from high-resolution sampling in July-September 2012

The NPSG is a characteristic oligotrophic ecosystem with warm, stable conditions aided by strong seasonal stratification. Time-series observations conducted by the HOT program at Stn ALOHA for nearly three decades have characterized the frequently subtle seasonal and interannual variability associated with key physical and biological processes. For example, 0–200 m depth-integrated rates of primary productivity as determined by \textsuperscript{14}C assimilation during 1988–2012 are 1.5 times higher in June-August (mean ± SD: 50.7 ± 11.8 mmol C m\textsuperscript{−2} d\textsuperscript{−1}) compared to December-February (mean ± SD: 34.7 ± 8.5 mmol C m\textsuperscript{−2} d\textsuperscript{−1}). One of the benefits of the long-term time-series observations is the ability to report the monthly or seasonal variability throughout several decades and the mean rate of \textsuperscript{14}C assimilation in the month of August is 52.6 ± 11.1 (SD) mmol C m\textsuperscript{−2} d\textsuperscript{−1}, ranging from 39.8–68.8 mmol C m\textsuperscript{−2} d\textsuperscript{−1} (represented by the 5 and 95 percentile values). This highlights that the variability within a single month can almost equal the variability measured within an entire annual period, suggesting that the short-
term phenomena (e.g. phytoplankton blooms, mesoscale eddies, and wind-driven mixing) play an important role in shaping elemental cycling and phytoplankton growth. Until now however, high-resolution analysis of a single seasonal period using intensive shipboard time-series measurements has not been conducted alongside the HOT program.

During July-September 2012, high temporal-resolution sampling at Stn ALOHA revealed changes in water-column biogeochemical properties over time-scales of days to weeks. Overall, the measurements recorded a period of anomalously low productivity with a prolonged event of net heterotrophy in the upper water-column. Our observation coincided with an absence of mesoscale eddies, a near-ubiquitous feature of the NPSG which advect through Stn ALOHA. While the focus of this study was on the upper ocean productivity and community composition (Section 4.2), an analysis of the longer-term temporal variability and the wider NPSG is required to contextualize the findings from July-September 2012 (Section 4.3).

4.2 Productivity and community structure in July-September 2012

An overall picture of NCP at Stn ALOHA between July-September 2012 is provided by the daily measurements of $\text{O}_2$/Ar ratio. Positive rates of NCP were initially measured in early July, but began to decrease until ultimately net heterotrophic conditions were recorded in early August. It is unfortunate that the transition period occurred in-between the two expeditions, although noteworthy that the changes occurred over timescales of several weeks. Overall it is unusual for such a prolonged period of net heterotrophy to be present during the summer at Station ALOHA [Emerson et al., 1997; Juranek and Quay, 2005; Quay et al., 2010]. The magnitude of the low productivity is apparent when comparing prior $\text{O}_2$/Ar-NCP measured during 6–12 August in units of $\text{O}_2$ (-7.6 ± 4.2 mmol $\text{O}_2$ m$^{-2}$ d$^{-1}$) with the summary of NCP
measurements previously reported for Stn ALOHA based on *in situ* geochemical methods (range from 3–11 mmol O$_2$ m$^{-2}$ d$^{-1}$) [Williams *et al.*, 2013 and references therein]. The mixed layer community subsequently recovered from the period of net heterotrophy although rates of NCP were still comparatively low during 22 August to 6 September which was attributed to the sea-surface salinity minimum. The three cruises are examined chronologically with regards to productivity and biological community composition.

During July the mixed layer depth became progressively more shallow (Figure 1) and from 20 July onwards (for the next 5 weeks) the near-surface seawater (0–25 m) temperature increased by 1°C. During 7–23 July, ΔO$_2$/Ar values were at their maximum recorded during July-September and the mean MLD-integrated prior O$_2$/Ar-NCP was 6.0 ± 3.2 (SD) mmol O$_2$ m$^{-2}$ d$^{-1}$. During this period, although the ΔO$_2$/Ar values were positive, indicating recent net autotrophic production, there was a decrease in ΔO$_2$/Ar values with time, indicating that either the system was not in steady state, or there was some spatial variability in ΔO$_2$/Ar. Estimated real-time O$_2$/Ar-NCP for this period was 1.6 ± 2.6 (SD) mmol O$_2$ m$^{-2}$ d$^{-1}$, four times lower than the mean prior O$_2$/Ar-NCP. During this period, concentrations of fucoxanthin, the diagnostic pigment biomarker for diatoms were at their summer maximum with a mean of 5.7 ± 1.1 (SD) ng L$^{-1}$ (Figure 6e). Furthermore, the combined total *nifH* gene copies for heterocystous cyanobacteria were also at their maximum with an average abundance of 7.1 ± 1.5 (SD) x 10$^3$ gene copies L$^{-1}$ during 10–24 July (Figure 7). We therefore infer that the positive NCP during July was driven by diatoms that host symbiotic diazotroph assemblages. The identity of the heterocystous cyanobacteria determined by gene analysis was the endosymbiont *Richelia intracellularis* which is associated with the diatoms *Rhizosolenia* and *Hemiaulus* [Foster and O'Mullan, 2008]. High abundances of diatom-diazotroph assemblages have been associated with major increases in
surface TChla concentration [Wilson, 2003; Fong et al., 2008; Villareal et al., 2012] and the seasonal pulse of exported material that occurs at Stn ALOHA each year between July and August is thought to be fueled by these symbiotic micro-organisms [Karl et al., 2012]. A separate study on particle distributions in the euphotic zone at Stn ALOHA during July-September 2012 showed a positive correlation ($R^2 = 0.24$, $p<0.05$) between fucoxanthin concentrations and 20-100 µm sized particles [Barone et al., 2015]. Both fucoxanthin and 20-100 µm sized particles have the highest concentrations and the largest variability during July and are most likely the cause of the higher variability observed in the FRRF-derived estimates of productivity during July compared to the 22 August to 11 September expedition (Figure 8d).

By the start of the second leg of the three C-MORE expeditions (4–14 August), the pattern of NCP had changed. $\Delta$O$_2$/Ar values were negative, indicating a recent period of net heterotrophy and prior-O$_2$/Ar-NCP values were also negative with a mean value of $-7.6 \pm 4.2$ mmol O$_2$ m$^{-2}$ d$^{-1}$. However, $\Delta$O$_2$/Ar values during this period showed an increase with time and therefore real-time O$_2$/Ar-NCP was positive, with a mean value of $3.9 \pm 2.2$ mmol O$_2$ m$^{-2}$ d$^{-1}$. Again, this indicates that either the mixed layer was recovering from the period of net heterotrophy or there was spatial variability in $\Delta$O$_2$/Ar. The mismatch between prior and real time NCP has been previously observed [Hamme et al., 2012], whereas in other occasions both approaches agree well [Ferrón et al., 2015]. Rates of $^{14}$C-PP are lowest during 6–12 August (mean ± SD: 26.7 ± 5.1 mmol C m$^{-2}$ d$^{-1}$) and remained low until 18 August when in situ $^{14}$C measurements were conducted by the HOT program (Figure 9). The low productivity period was accompanied by a decrease in concentrations of photosynthetic pigments TChla (Figure 8e), Zeax, and dvchla (Figure 6a and 6b), indicating an accompanying shift in the dominant phytoplankton population. Despite changes in productivity and community composition, there was low variability in the
hydrographic structure of the water-column or nutrient conditions to accompany the rapid change
from net autotrophic to net heterotrophic conditions. During 23 August to 7 September,
measurements of $^{14}$C-PP and O$_2$/Ar-NCP were accompanied by measurements of FRFF-PP and
$^{17}$Δ-GPP. Simultaneous measurements of the four methods of productivity are infrequently
achieved, particularly for a 15-day period in the open ocean, and therefore offer an insight into
the daily variability of these parameters when there was high spatial heterogeneity in the upper
water-column. While MLD-integrated prior O$_2$/Ar-NCP remained low for this period with a
mean of -0.5 ± 3.1 (SD) mmol O$_2$ m$^{-2}$ d$^{-1}$, rates of $^{14}$C-PP had increased from the low values
measured during 6–12 August to a mean of 33.1 ± 7.4 (SD) mmol C m$^{-2}$ d$^{-1}$. Overall MLD-
integrated $^{17}$Δ-GPP averaged 90.7 ± 35.3 mmol O$_2$ m$^{-2}$ d$^{-1}$ for the entire 15 day period and were
comparable with previous measurements at Stn ALOHA in the summertime [Juranek and Quay,
2005; Quay et al., 2010]. The high variability in the MLD-integrated $^{17}$Δ-GPP measurements is
supportive of the observation that there was high lateral heterogeneity in the surface seawater
during this period. The O$_2$-based productivity estimates extrapolate for the residence time of O$_2$
in the mixed layer which sets a boundary on how much they can vary over a 24 h period.
Considerable day-to-day variability was also observed in the O$_2$/Ar measurements with one of
the largest decreases in prior O$_2$/Ar-NCP on 4 September when the near-surface water column
became undersaturated (99.7%) in dissolved O$_2$ (Table S1). This coincided with a strong
decrease in salinity associated with the sea-surface salinity minimum (Figure 1). The most
consistent temporal trend in the different measurements of productivity was evident in FRFF-
derived estimates which decreased continually during the observation period. FRFF-PP is
considered to more closely resemble GPP, however it was ~40% lower than $^{17}$Δ-GPP during 23
August to 7 September 2012. The decrease in FRFF-PP is coincident with decreasing
concentrations of flow cytometry-enumerated phytoplankton abundance (Figure 5) and particulate material (Figure 4). Ultimately the overall broad overview from this period is that the near-surface water-column was recovering from a net heterotrophic state although MLD-integrated prior O₂/Ar-NCP are still comparatively low and the sea-surface salinity minimum was accompanied by substantial spatial variability.

4.3 Further analysis of the low productivity period

It is unusual to observe an intensive period of net heterotrophic conditions during the summer at Stn ALOHA. The pronounced period of net heterotrophy occurred during the 4–14 August expedition, however prior O₂/Ar-NCP during 26 August to 5 September was still relatively low (-0.5 ± 3.1 mmol O₂ m⁻² d⁻¹) (Figure 8). Satellite observations revealed that the low productivity was not localized to Stn ALOHA as an extensive low TChla anomaly was evident from August through to September across the geographic area from 22–26°N to 152–160°W (Figure 10). The prolonged period of anomalous TChla as revealed by MODIS (Figure 10) is somewhat contradictory to the shipboard pigment measurements (Figure 8e) where HPLC-derived TChla increased in September relative to 4–14 August. However it does suggest the low productivity was a regional phenomenon lasting for 1–2 months. In the absence of any local or regional physical forcing identified, wider ecosystem controls on productivity at Stn ALOHA are considered below.

One possible explanation for the low productivity is micro-nutrient limitation which would account for the build-up of phosphate that was at a higher concentration (0–100 m integrated values of 11.3 mmol m⁻²) during 2012 than any other year (range from 3.0 mmol m⁻² in 2003 to 10.0 mmol m⁻² in 1999) since 1988 (http://hahana.soest.hawaii.edu/hot/hot-dogs). The
Identification of the limiting micro-nutrient(s) was not investigated experimentally during this field program, however near-surface concentrations of dissolved iron ranged from 0.14–0.87 nmol kg\(^{-1}\) (mean 0.31± 0.14 nmol kg\(^{-1}\)) throughout the summer and may have been limiting for certain phytoplankton species [Fitzsimmons et al., in revision Geochimica et Cosmochimica Acta, 2015]. Another factor that directly influences growth and metabolism of marine plankton is seawater temperature [Laws et al., 2000] which had a lower annual mean recording (24.5°C) between depths of 0–50 m during 2012 compared to the previous 12 years (24.6–25.4°C) (http://hahana.soest.hawaii.edu/hot/hot-dogs). However the biogeochemical trends present in August 2012 should also be compared with longer timescales and during the past 5 years (2009–2014), 0–100 m depth-integrated \(^{14}\)C-PP has steadily increased (annual mean of 183 g C m\(^{-2}\) d\(^{-1}\) in 2009 compared to 233 g C m\(^{-2}\) d\(^{-1}\) in 2014), while the high phosphate concentrations observed in 2012 subsequently decreased and near-surface seawater temperatures subsequently increased (http://hahana.soest.hawaii.edu/hot/hot-dogs). An additional influence on productivity is near-surface water-column mixing. A ‘typical’ mixed layer depth during the summertime at Stn ALOHA is 50 m and during 2012 the upper water-column did not stratify to this extent until late July. The ramifications of a delay in stratification on the diazotroph community which have been implicated in bloom formation in the NPSG [Dore et al., 2008] are unclear and their abundances during July-September (Figure 7) were at the lower end of their previously reported summertime abundances at Stn ALOHA [Church et al., 2009]. Over longer-term timescales, a strengthening in stratification of the upper ocean is generally expected to cause decreased marine primary productivity in the subtropics, although this was not evident from historical analysis of the Stn ALOHA climatology [Dave and Lozier, 2010].
4.4 Sea-surface salinity minimum

The hydrographic feature which was uniquely described in this study was a sea-surface salinity minimum restricted to the upper water-column and with biogeochemical properties distinct from the surrounding waters. Although it was difficult to track the source of the sea-surface salinity minimum with any certainty, ADCP and Argo float data indicate that it originated southeast of the Hawaiian Islands. This is supported by analysis of circulation patterns generated by the HYCOM model which revealed that the mean sea-surface flow was from the south-east during August to September 2012. The major ocean current to the southeast of the Hawaiian Islands is the North Equatorial Current, which extends from 10 to 20° N [Bondur et al., 2008]. The North Equatorial Current bifurcates to the east of the island of Hawaii and the northern portion then contributes to the North Hawaii Ridge Current (NHRC), a weak predominantly westward flowing current [Qiu et al., 1997; Firing et al., 1999; Bondur et al., 2008]. The magnitude of the NHRC varies considerably, ranging from undetectable to a maximum of 17 cm sec\(^{-1}\) with no identified seasonal pattern in magnitude [Firing, 1996]. Its northern boundary is usually located south of Stn ALOHA although it was detected intermittently at the time-series monitoring station [Firing, 1996].

The sea-surface salinity minimum described in this study provides an important example regarding the effect of discrete features (e.g. mesoscale eddy fields, meandering jets, and eddy dipoles) on biogeochemical variability at the ocean surface [Williams and Follows, 2011]. These features often have isolated water masses in their interiors for extended periods of time, indicative of transport barriers along their edges [Harrison and Glatzmeier, 2010]. For example, the transport of isolated water can provide nutrients into oligotrophic gyres which triggers biological productivity [e.g. Bracco et al., 2000; McGillicuddy et al., 2007]. In this instance
there was no evidence for nutrient injection into the oligotrophic ecosystem and instead the
dominant effect of the isolation associated with sea-surface salinity minimum was a decline in
biomass and productivity.

Ultimately, the community structure and biogeochemical signature associated with the sea-
surface salinity minimum revealed a decreased microbial abundance which may have resulted
from two factors. The first is that its properties are representative of the originating ecosystem
remaining unchanged prior to its detection at Stn ALOHA. This is unlikely as a comparison of
Prochlorococcus, Synechococcus, and heterotrophic bacteria abundance between Stn ALOHA
and the tropical Pacific Ocean (0-10° N, 140° W) do not reveal major abundance differences
[Landry and Kirchman, 2002]. The second explanation is that biological activity (death, cell
lysis, and grazing) caused the decrease in biomass. The cumulative effects of these events would
be quite significant (as is the case) due to the isolation of sea-surface salinity minimum from the
surrounding water masses. In spite of the decrease in biomass an increase in inorganic nutrient
concentrations which might be expected for net remineralization of the organic material was not
observed. Most likely the biological material was exported downwards with some retained at the
base of the sea-surface salinity minimum (at depths of 50–70 m in the water-column) due to the
physical discontinuity resulting from strong stratification.

Although the *in situ* autonomous Seagliders and profiling floats were able to measure the
extent of the sea-surface salinity minimum which continued through September (Figure 2), it is
regrettable that the sampling of the feature was terminated at the end of the campaign. The
decreasing concentrations of key water-column properties including particulate material,
*Prochlorococcus* abundances, and prior O₂/Ar-NCP suggest that the full extent of the
biogeochemical conditions associated with the sea-surface salinity minimum might not have
been evaluated. Increasing deployment of *in situ* sensors to measure O$_2$ [Riser and Johnson 2008], nutrients [Johnson et al., 2010], and even community composition and activity [Robidart et al., 2014] on autonomous vehicles will help attribute biogeochemical variability to discrete hydrographic features in the future.

5. Conclusion

In an oligotrophic gyre setting, where the ecosystem operates at the interface between net autotrophic to net heterotrophic conditions, our study shows that daily measurements are extremely informative when attempting to characterize intra-seasonal variability and identify its drivers. In some instances changes in plankton community could be related to episodic hydrographic features *e.g.* decrease in cell abundance associated with the presence of the sea-surface salinity minimum. However, in other instances, such as the observed shift from net autotrophic to net heterotrophic conditions between July and August 2012, it is harder to explain the causes. Our inability to separate temporal from spatial variability through our Eulerian sampling approach highlights some of the difficulties faced in the study of pelagic microbial assemblages in which generation scales are in the order of days and kilometers. In the absence of local causation mechanisms being identified, larger spatial-temporal influences were investigated including nutrient concentrations, mixed-layer depth, and seawater temperature. Ultimately extensive ship operations lasting nearly 3 months are difficult to accomplish and advances in obtaining sufficient spatial-temporal resolution will require the integration of autonomous, *in situ* instrumentation including floats, Seagliders, and moorings in collaboration with ship-based observations and experimentation.
Acknowledgements

The dataset presented here resulted from the input of over fifty sea-going and shore-based oceanographers who contributed to the success of the field campaigns in 2012. We thank the Hawaii Ocean Time-series (HOT) program, the R/V Kilo Moana captain and crew, L. Fujieki for creating the C-MORE Data System which hosts the C-MORE field data (http://hahana.soest.hawaii.edu/cmoreDS/interface.html), S. Poulos for leading the Seaglider operations (http://hahana.soest.hawaii.edu/seagliders/), and P. Berube, T. Clemente, S. Tozzi for cruise leadership. The WHOTS surface mooring data are provided by R.A. Weller and A. J. Plueddemann (http://www.soest.hawaii.edu/whots/) with funding from the NOAA Climate Observation Division. We thank H. Alexander, D. Böttjer, M. Segura-Noguera, and two anonymous reviewers for critical comments to the manuscript. This research was supported by the National Science Foundation (NSF) Center for Microbial Oceanography: Research and Education (C-MORE) (EF0424599 to D.M.K.), NSF Grant OCE-1153656 (D.M.K) and a Gordon and Betty Moore Foundation Marine Microbiology Investigator award to D.M.K. The HOT program is supported by the NSF (OCE-1260164 to M.J.C, R.R.B., and D.M.K.).
References


Table 1. Oceanographic expeditions to Stn ALOHA between July to mid-September 2012

<table>
<thead>
<tr>
<th>Cruise ID</th>
<th>Project</th>
<th>Dates</th>
</tr>
</thead>
<tbody>
<tr>
<td>KM12-15</td>
<td>C-MORE</td>
<td>Jul 8 - 28</td>
</tr>
<tr>
<td>KM12-16</td>
<td>HOT-244</td>
<td>Jul 30 - Aug 3</td>
</tr>
<tr>
<td>KM12-17</td>
<td>C-MORE</td>
<td>Aug 5 - 14</td>
</tr>
<tr>
<td>KM12-18</td>
<td>HOT-245</td>
<td>Aug 16 - 20</td>
</tr>
<tr>
<td>KM12-19</td>
<td>C-MORE</td>
<td>Aug 22 - Sep 11</td>
</tr>
</tbody>
</table>

Table 2. Summary of productivity measurements conducted at Stn ALOHA during July and September 2012. The values represent MLD-integrated in units of mmol O$_2$ m$^{-2}$ d$^{-1}$ (using a conversion PQ of 1.1 for $^{14}$C-assimilation which are also reported in units of carbon). The mean ± 1 standard deviation are shown for each set of measurements and absence of sample collection or calculation is indicated by not determined (n/d). The dates represent the start and end of each expedition and the number of samples is indicated by (n).

<table>
<thead>
<tr>
<th>Method</th>
<th>8–28 Jul</th>
<th>5–14 Aug</th>
<th>22 Aug to 11 Sept</th>
</tr>
</thead>
<tbody>
<tr>
<td>prior O$_2$/Ar-NCP</td>
<td>6.0 ± 3.2 (n=16)</td>
<td>-7.6 ± 4.2 (n=8)</td>
<td>-0.5 ± 3.1 (n=16)</td>
</tr>
<tr>
<td>real-time O$_2$/Ar-NCP</td>
<td>1.6 ± 2.6</td>
<td>3.9 ± 2.2</td>
<td>n/d</td>
</tr>
<tr>
<td>$^{14}$C-PP (carbon)</td>
<td>36.3 ± 6.5 (n=16)</td>
<td>26.7 ± 5.1 (n=7)</td>
<td>33.1 ± 7.4 (n=16)</td>
</tr>
<tr>
<td>(O$_2$)</td>
<td>39.9 ± 7.2</td>
<td>29.4 ± 5.5</td>
<td>36.4 ± 8.2</td>
</tr>
<tr>
<td>FRRF-PP</td>
<td>52.5 ± 13.2 (n=17)</td>
<td>n/d</td>
<td>52.7 ± 12.9 (n=16)</td>
</tr>
<tr>
<td>$^{17}$ΔO$_2$-GPP</td>
<td>n/d</td>
<td>n/d</td>
<td>90.7 ± 35.3 (n=22)</td>
</tr>
</tbody>
</table>
**Figure 1.** Upper water-column properties at Stn ALOHA during July-September 2012 showing (a-e) temperature, (f-j) salinity, (k-o) oxygen, and (p-t) chla + phaeopigments. CTD profiles were conducted every 3 h during HOT cruises and every 4 h during C-MORE cruises (Table 1) and the white line represents the mixed layer depth.
Figure 2. Upper water-column (0–200 m) profiles of salinity measured between 3 August and 30 October 2012 by a Seaglider. During September 2012, the Seaglider conducted 205 dives along ~370 km of the bowtie dive formation. The dashed lines indicate the time period when shipboard CTD profiles were conducted (shown in Figure 1f).
Figure 3. Figures 3a-c are salinity profiles from three Argo floats in the vicinity of Stn ALOHA between July and November 2012 (Roemmich and Gilson, 2009). The arrows represent surface salinity minimum features thought to correspond with the feature measured at Stn ALOHA in September 2012. Figures 3d-e are 0–100 m averaged salinity for August and September and include the position of the three Argo floats (#5903888 = white; #5903273 = purple, #5902241 = blue) in relation to the Hawaiian Islands and Stn ALOHA (shown by a star).
Figure 4. Depth-averaged (5–25 m) concentrations of (a) phosphate, (b) particulate carbon, and (c) particulate nitrogen during July-September 2012 at Stn ALOHA. The horizontal dashed line and shaded gray area represents the 5–25 m averaged mean concentration and standard deviation during 1989-2011 for the months of July-September.
Figure 5. Depth profiles (0–150 m) of (a-c) Prochlorococcus, (d-f) heterotrophic bacteria, (g-i) Synechococcus, and (j-l) picoeukaryotes during July-September 2012 at Stn ALOHA.
**Figure 6.** Temporal changes in depth averaged (5–25 m) concentrations of diagnostic pigment biomarkers including HOT data: (a) zeaxanthin, (b) divinylchlorophyll $a$, (c) monovinylchlorophyll $a$ (d) 19′-hexanoyloxyfucoxanthin, (e) fucoxanthin, and (f) 19′-butanoyloxyfucoxanthin. The horizontal dashed line represents the mean concentration for each respective pigment averaged for July-September using the 1989–2011 HOT climatological record.
Figure 7. Depth averaged (5–25 m) *nifH* gene copies during July-September 2012 for four major groups of diazotrophs: UCYN-A, *Crocosphaera*, heterocystous cyanobacteria, and *Trichodesmium*.
Figure 8. Productivity and TChlα at Stn ALOHA during July to September 2012: (a) ΔO₂/Ar (%), (b) prior O₂/Ar-NCP, (c) ¹⁴C-PP including HOT data as square symbols, (d) FRRF-PP, and (e) TChlα. The samples were collected at a depth of 25 m and the gray shaded areas indicate months of year.
Figure 9. Comparison of key parameters in March-October 2012 with historical data. Figure 9(a) $^{14}$C-PP productivity (5–25 m depth-averaged) and (b) particulate carbon flux measured at 150 m during March-October 2012 with 1989–2011 climatology. The values measured in 2012 are shown as white circles. The 1989–2011 data are binned by month and are shown as gray bars with the upper and lower boundaries represented by the 5 and 95 percentile and the mean value for each month shown by the horizontal black line. Figure 9(c) Comparison of MODIS-derived chlorophyll $a$ concentrations at Stn ALOHA in March-October 2012 with 2002–2014. The 2012 values are shown by a solid black line and closed circles, the 2002-2014 values are represented by the dashed gray line (mean) and the shaded gray area (minimum and maximum).
Figure 10. Anomaly of chlorophyll $a$ concentration during August 2012 for (a) North Pacific Ocean and Stn ALOHA and the vicinity during (b) July, (c) August, and (d) September 2012. The box drawn around the Hawaiian Islands (Figure 12a) corresponds to the latitude and longitude shown in Figures 12b-d.