The transient oasis: Nutrient-phytoplankton dynamics and particle export in Hawaiian lee cyclones

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A B S T R A C T

Macronutrients, photosynthetic pigments, and particle export were assessed in two eddies during the E-Flux I and III cruises to investigate linkages between biogeochemical properties and export flux in Hawaiian lee cyclonic eddies. Cyclone Noah (E-Flux I), speculated to be in the ‘decay’ stage, exhibited modest increases in macronutrients and photosynthetic pigments at the eddy center compared to ambient waters. Cyclone Opal (E-Flux III) also exhibited modest increases in macronutrient concentrations, but a 2-fold enhancement in total chlorophyll a (TChl a) concentration within the eddy center. As indicated by fucoxanthin concentrations, the phytoplankton community in the deep chlorophyll maximum (DCM) of Opal was comprised mainly of diatoms. During an 8-day time series in the center of Opal, TChl a concentration and fucoxanthin in the DCM decreased by ~50%, which was potentially triggered by silicic acid limitation. Despite the presence of a substantial diatom bloom, Opal did not deliver the expected export of particulate carbon and nitrogen, but rather a large biogenic silica export (~4-fold increase relative to export in surrounding waters). Results suggest that controls on the life cycle of a Hawaiian lee cyclone are likely a combination of physical (eddy dynamics), chemical (nutrient limitation), and biological (growth and grazing imbalance) processes. Comparisons between Noah and Opal and previously studied cyclones in the region point to a relationship between the spin-up duration of a cyclone and the resulting biological response. Nonetheless, Hawaiian lee cyclones, which strongly influence the biogeochemistry of areas 100’s of km in scale in the subtropical North Pacific Ocean, still remain an enigma.

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1. Introduction

Phytoplankton community structure in the Subtropical North Pacific Ocean (SNPO) is primarily influenced by the lack of inorganic macronutrient availability (nitrogen, N; phosphorus, P; and silicon, Si) in the upper euphotic zone. Minute organisms with high surface area-to-volume ratios, such as photosynthetic bacteria (i.e. Prochlorococcus spp.) and picophytoplankton (0.2–2 μm), are efficient at nutrient uptake and light harvesting and comprise the ‘climax community’ in the SNPO (Clements, 1916; Campbell and Vaulot, 1993; Anderson et al., 1996; Karl et al., 2001a). In a two-layer distribution typical of the SNPO, cyanobacteria (i.e. Synechococcus and Prochlorococcus spp.) dominate the mixed layer (~<50 m) and Prochlorococcus and pico- and nanoeukaryotes (i.e. prymnesiophytes and pelagophytes) comprise the deep chlorophyll maximum (DCM, ~90–110 m) (Bidigare et al., 1990, 2008; Ondrusek et al., 1991; Letelier et al., 1993). A standing stock of smaller phytoplankton suggest minimal particulate organic matter flux in the SNPO, since large eukaryotic phytoplankton are often reported to have a critical role in export production (Epplle, 1969; Goldman, 1993; Legendre and Le Fevre, 1995). Additionally, since organic matter production is controlled by the nutrient available in the lowest concentration relative to the needs of phytoplankton growth (Law of the Minimum, Justus von Liebig), lack of organic matter export in the SNPO has been attributed to N or P deficiencies in the euphotic zone (Karl et al., 2001a,b; Karl, 2002) and/or high rates of respiration (Laws et al., 2000). The input of fixed N into the nutrient-limited surface waters of the SNPO via the processes of nitrogen fixation and nitrification plays an important role in the N:P stoichiometry of available nutrient pools in the system. Due to varying supply rates, the SNPO community is reported to alternate between states of N and P limitation via El Niño-Southern Oscillation.
(ENSO) forcing (Karl et al., 2001b; Karl, 2002). Thus, the provenance of nutrient supply in the SNPO has significant implications for productivity, subsequent nutrient limitation, and particulate matter export.

In this region where regenerated production is the status quo, aperiodic displacements of isopycnal surfaces by Rossby waves and mesoscale eddies have been reported to drive an influx of “new” nutrients into the eupholic zone, generating significant variability in plankton biomass and processes in the surface ocean (Eppl ey and Peterson, 197 9; Falkowski et al., 199 1; McGillicuddy and Robinson, 1997; McNeil et al., 1999; Cipollini et al., 2001; Seki et al., 2001; Siegel, 2001; Uz et al., 2001; Bidigare et al., 2003; Vaillancourt et al., 2003; Sakamoto et al., 2004). First baroclinic mode, cold-core, cyclonic eddies are ephemeral yet frequent occurrences during persistent trade wind conditions in the lee of the ‘Alenuihaha Channel between the islands of Maui and Hawai’i (Patzert, 1969; Bienfang et al., 1990; Lumpkin, 1998; Dickey et al., 2008). Intensified northeasterly trade winds and island topography contribute to the formation of these cyclonic eddies to the north of the channel (Lumpkin, 1998; Chavanne et al., 2002; Calli et al., 2008; Dickey et al., 2008). The upward displacement of isopycnal surfaces elicits an ecosystem response by (1) relocating seed populations of nutrient-replete, light-limited phytoplankton to areas of higher light intensity and/or (2) increasing the supply of growth-limiting nutrients to the well-lit zone for light-replete, nutrient-limited phytoplankton. Increased rates of biological processes such as nutrient uptake and carbon fixation often induce substantial phytoplankton blooms in which larger photosynthetic eukaryotes dominate. Therefore, eddies have been hypothesized to enhance rates of carbon export by means of altered food web dynamics namely increased macrozooplankton grazing and subsequent fast-sinking fecal pellets (Falkowski et al., 1991; Goldman, 1993; Legendre and Le Fevre, 1995; Seki et al., 2001; Bidigare et al., 2003).

Variations in eddy dynamics have been attributed to different developmental stages and varying time scales in physical, biological, and biogeochemical responses (Sweeney et al., 2003; Flierl and McGillicuddy, 2002). Sweeney et al. (2003) suggested that the life cycle of a cyclonic eddy is divided into three stages: ‘intensification,’ ‘mature,’ and ‘decay.’ Nutrient injection into the eupholic zone stimulates a biological response during ‘intensification,’ after which a cyclone reaches its ‘mature’ stage as it attains its maximum tangential velocity, production rate, and highest biomass. After some time, the induced biological response is expected to generate increased export. As wind speed diminishes or the eddy migrates from the area of strongest winds in the ‘Alenuihaha Channel, a ‘mature’ cyclone subsides into the ‘decay’ stage as the doming of the isopycnals relaxes and tangential velocity decreases. At this time, the eddy undergoes a significant physical and biological transformation towards ambient conditions, leaving behind a high export signal as the remains of an eddy-induced bloom (Patzert, 1969; Sweeney et al., 2003).

For an eddy-pumping mechanism to contribute significantly to export production in the SNPO, a means to restore isopycnal nutrient concentrations on relatively short time-scales must exist (Garçon et al., 2001; Lewis, 2002; Sakamoto et al., 2004). Essentially, the ‘pumping’ of water from below would only occur once, and nutrients should reach the eupholic zone only as the eddy forms, not as it matures or propagates. Thus, if nutrients on a deeper isopycnal surface are depleted, the biological response of the next eddy would be minimized as less nutrients are injected into the eupholic zone. Therefore, the effectiveness of the eddy mechanism depends on the relative time and vertical length scales of nutrient regeneration and the time period of eddy recurrence in the same general location (Garçon et al., 2001; Lewis, 2002). To date, only a handful of studies have focused on the influence of cyclonic eddies on carbon export (Honjo et al., 1999; Bidigare et al., 2003; Sweeney et al., 2003). The impetus for the E-Flux project was the sizeable potential for cyclonic eddies to increase the transfer of organic carbon to the mesopelagic zone in the oligotrophic North Pacific Ocean. The present study assessed the spatial and temporal variability in macronutrient and phytoplankton distributions and subsequent influences on particulate matter export within Hawaiian lee cyclones. Age-specific variability was examined with respect to the conceptual model described by Sweeney et al. (2003). Ecological predictions of their model were tested using three biological parameters: dissolved macronutrients, phytoplankton community composition, and particulate matter export.

2. Methods

2.1. Eddy tracking

The seasonal intensification of trade winds through the ‘Alenuihaha Channel make the lee of Hawai’i an ideal natural laboratory for studying cyclonic eddies. Cyclone Noah was studied during E-Flux 1 (4–22 November 2004) aboard the University of Hawai’i’s R/V Kōmikai-O-Kanaloa; Cyclone Opal was surveyed during E-Flux III (10–28 March 2005) aboard Oregon State University’s R/V Wecoma. Three main methods were used to determine the locations and track the eddies during ship-based observations. As our first method, satellite-derived measurements of sea-surface temperature (SST) obtained from Geostationary Operational Environmental Satellites (GOES) radiance sensors (via the EddyWatch section of the NOAA CoastWatch Program, http://oceanwatch.pifsc.noaa.gov/) and NASA’s Moderate Resolution Imaging Spectroradiometer (MODIS) were sent electronically to the research vessels and used to determine initial sampling locations. These SST measurements also aided in the placement of drifters in proximal centers as well as in tracking the movements of the eddies during our observations. Secondly, surface currents measured with a 153-kHz RDI acoustic Doppler current profiler (ADCP) were tracked to monitor the locations and to determine the spatial dimensions of the eddies. Thirdly, two drifters were deployed: a surface drifter (OPL drifter) with a 1.5-m cylindrical foam core and a 1-m cross-shaped drogue, which tracked the fluid motion of the eddies and was able to obtain a near real-time, Lagrangian time series of temperature measurements from surface to 150 m at 10-m intervals; and a METOCEAN bio-optical surface drifter that acquired temporal measurements of drifter positions, barometric pressure, air temperature, SST, and fluorescence. A drifting sediment trap array (Section 2.2.2) also proved to be useful as an ad hoc Lagrangian drifter for tracking general patterns of eddy motion. More details on eddy tracking during specific cruises are described in Dickey et al. (2008).

2.2. Sample collection

2.2.1. “Star” transects and process stations

A “star” sampling strategy allowed three-dimensional spatial characterization of eddy variability. This also provided a four-dimensional (x, y, z, t) data set for investigating linkages between nutrient inputs, biological response, and the downward flux of particulate carbon. At least two replicate stations were sampled in the centers of Cyclones Noah and Opal and at control (OUT) stations, which were far-field locations unaffected by eddy dynamics. Hydrographic data (temperature, salinity, pressure, density, fluorescence, and oxygen) and in situ water samples were acquired from a SeaBird SBE 9/11+ CTD system plus
rosette sampler. Photosynthetically available radiation (PAR) \((\mu\text{mol photons m}^{-2}\text{s}^{-1})\) was measured with an attached sensor and the bottom of the euphotic zone was calculated as the depth at which irradiance measurements collected during daylight hours was 1% of the surface light level (LL). Coefficients were derived by correlating daytime 1% LL depths to mean total chlorophyll \(a\) (TChl \(a\)) concentrations between the surface and 1% LL depths, and the relationship was used to determine 1% LL depths for casts collected at night (Morel, 1988). Details concerning sampling strategies and physical and bio-optical measurements for E-Flux I are given in Dickey et al. (2008) and Kuwahara et al. (2008) and for E-Flux III in Dickey et al. (2008) and Nencioli et al. (2008).

For both eddies, a single “star” was sampled which consisted of multiple transects across the eddy with stations \(\sim 18\) km apart. In Noah, samples for macronutrients and photosynthetic pigments were taken at depth intervals from 0 to 500 m during Transect 3 (‘money run,’ casts 27–34, 36, 37), with the ‘center’ of the eddy between casts 31 and 32 according to ADCP current velocities and density profiles (Fig. 1A) (Kuwahara et al., 2008). Samples in Opal were taken at depth intervals from 0 to 350 m during Transect 3 (‘money run,’ casts 13–18, 19A, 22–25) with cast 19A being the ‘center’ of the eddy (Fig. 1B) (Nencioli et al., 2008).

Process stations in Noah were sampled for macronutrients (0–1000 m; IN = 2, OUT = 2) and photosynthetic pigments (0–150 m; IN = 2, OUT = 3). Process stations (IN = 7, OUT = 3) in the center of Opal were sampled daily (16–22 March) for pigments and six of these stations (17–22 March) were sampled for macronutrients. Size-fractionated pigment samples for both Noah (IN = 3, OUT = 3) and Opal (IN = 3, OUT = 2) were taken at the \(-11\%\) (base of mixed layer) and \(-43\%\) (in mixed-layer) light levels. Size-fractionated pigment samples were also collected from the DCM along Transect 6 of Opal (casts 97, 99, 101, 103) extending from the center of the eddy (cast 97) towards the edge (\(\sim 100\) km). A single depth profile to 1000 m was sampled for suspended biogenic silica both inside and outside of Opal.

Water samples for macronutrient concentrations were collected in acid-washed 125-mL HDPE bottles, immediately frozen (-20 °C), and stored upright until analysis. Photosynthetic pigment samples were collected into brown, narrow-mouthed 2-L HDPE bottles, immediately vacuum-filtered onto 25-mm GF/F filters for total pigment biomass or polycarbonate filters (0.2, 2, and 18 \(\mu\)m) for size-fractionated biomass, and stored in liquid nitrogen until analysis. Water for suspended biogenic silica analysis was collected in clear, narrow-mouthed 2-L HDPE bottles, immediately vacuum-filtered onto 25-mm 0.8-μm polycarbonate filters, and kept at \(-20\) °C until analysis.

2.2.2. Sediment trap array

A particle interceptor sediment trap array, or PItS, was suspended at 150 m for a minimum of 3 days in and out of each eddy. The array consisted of 12 cylindrical polycarbonate collector tubes with a 0.0039 m² mouth opening fitted with baffles of 25-mm diameter cells (Knauer et al., 1979; Karl et al., 1996). Tubes were affixed to a PVC cross frame attached to a 12-mm POLYPRO line.

Collector tubes were filled with high-density seawater brine solution to prevent loss of preservative during deployment and loss of sample during recovery. The brine solution was a mixture of 1% formalin and 2.5 kg NaCl dissolved in 50 L of filtered surface seawater. Upon recovery of the array, tubes containing the collected particulate matter were pre-filtered through a 335-μm Nitex mesh to remove accidental zooplankton swimmers. Overlying seawater from each tube was removed with a pipette and the brine solution alone was filtered for specific analyses.

2.3. Sample analysis

2.3.1. Inorganic macronutrients

Samples for nitrate+nitrite (N+N), phosphate, and silicic acid were sent to Oregon State University and were analyzed using a continuous segmented flow system consisting of components of both a Technicon Autoanalyzer II TM and an Alpkem RFA 300 TM (Gordon et al., 1994). Analysis for N+N used the basic method of Armstrong et al. (1967) with modifications to improve the precision and ease of operation. The phosphate method was a modification of the molybdenum blue procedure of Bernhardt and Wilhelms (1967). Silicic acid was measured using the method of Armstrong et al. (1967) as adapted by Atlas et al. (1971). The precision of analyses was a function of the concentration range of each macronutrient: N+N = 0.132 μM/mV, phosphate = 0.132 μM/mV, and silicic acid = 0.482 μM/mV. Detection limits for these specific sample runs were as follows: nitrate = 0.14 μM, nitrite = 0.02 μM, phosphate = 0.0075 μM, and silicic acid = 0.35 μM (J. Jennings, pers. comm.).
2.3.2. Pigments
Chlorophyll and carotenoid pigments were analyzed at the University of Hawai‘i on a Varian 9012 HPLC system using methods described in Bidigare et al. (2005). Filters were extracted in 3 mL of HPLC-grade acetone in culture tubes along with 50 μL of an internal standard (canthaxanthin) at 4 °C for 24 h. Photosynthetic pigments were separated on a reverse-phase Waters Spherisorb® 5-μm ODS-2 (4.6 × 25 mm) C18 column with a corresponding guard cartridge (7.5 × 4.6 mm) and a Timberline column heater (26 °C) (Wright et al., 1991; Bidigare et al., 2005). Separated pigments were detected and the data were transferred to the attached computer system using SpectraSYSTEM Thermo Separation Products UV2000 (dual wavelength UV/VIS) and FL2000 (fluorescence) detectors. Pigment identifications were based on absorbance spectra, co-chromatography with standards, FL2000 (fluorescence) detectors. Pigment identifications were representive culture extracts. Spectra-Physics WOW column heater (26 °C). Monovinyl chlorophyllide Llewellyn, 1983; Wright et al., 1991; Bidigare and Trees, 2000). A was used to conservatively calculate peak area (Mantoura and Brzezinski and Nelson (1995). Samples were digested in 0.2 N spectrophotometer at 810 nm and compared against a standard technique with ammonium molybdate and a reducing agent. The of Hawai‘i according to methods specified in Paasche (1980) and 2.3.3. Suspended biogenic silica
Suspended biogenic silica (BSI) was analyzed at the University of Hawai‘i according to methods specified in Paasche (1980) and Brzezinski and Nelson (1995). Samples were digested in 0.2 N NaOH solution and developed using a time-sensitive dilution technique with ammonium molybdate and a reducing agent. The percent transmittance of the developed sample was read on a spectrophotometer at 810 nm and compared against a standard curve made with a 2.5-mM silicate stock solution (Na2SiF6).

### Table 1

Abbreviations and taxonomic affinities of photosynthetic pigments separated in this study using HPLC

<table>
<thead>
<tr>
<th>Pigment name</th>
<th>Abbreviation</th>
<th>Primary pigment in</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total chlorophyll a*</td>
<td>TChl a</td>
<td>All phytoplankton</td>
</tr>
<tr>
<td>Monovinyl chlorophyll a</td>
<td>MVChl a</td>
<td>All phytoplankton (except Prochlorococcus spp.)</td>
</tr>
<tr>
<td>Divinyl chlorophyll a</td>
<td>DVChl a</td>
<td>Prochlorococcus spp.</td>
</tr>
<tr>
<td>Monovinyl plus divinyl chlorophyll b</td>
<td>MVChl b</td>
<td>Senescence diatoms</td>
</tr>
<tr>
<td>Chlorophyll c-like pigments</td>
<td>TChl c</td>
<td>Chromophytes</td>
</tr>
<tr>
<td>19-Butanoyloxyfucoxanthin</td>
<td>But-fuco</td>
<td>Phaeopigments</td>
</tr>
<tr>
<td>19-Hexanoyloxyfucoxanthin</td>
<td>Hex-fuco</td>
<td>Phaeopigments</td>
</tr>
<tr>
<td>Fucoxanthin</td>
<td>Fuco</td>
<td>Diatoms</td>
</tr>
<tr>
<td>Peridinin</td>
<td>Per</td>
<td>Dinoflagellates</td>
</tr>
<tr>
<td>Prasinoxanthin</td>
<td>Pras</td>
<td>Prasiophytes</td>
</tr>
<tr>
<td>Violaxanthin</td>
<td>Viola</td>
<td>Chlorophytes</td>
</tr>
<tr>
<td>Diadinoxanthin</td>
<td>DiDx</td>
<td>Chromophytes</td>
</tr>
<tr>
<td>Allxanthin</td>
<td>Allox</td>
<td>Cryptophytes</td>
</tr>
<tr>
<td>Diatoxanthin</td>
<td>DTX</td>
<td>Minor pigment in chlorophytes</td>
</tr>
<tr>
<td>Zeaxanthin</td>
<td>Zeax</td>
<td>Cyanobacteria</td>
</tr>
<tr>
<td>α-Carotene</td>
<td>α-Car</td>
<td>Prochlorococcus spp., cryptophytes</td>
</tr>
<tr>
<td>β-Carotene</td>
<td>β-Car</td>
<td>All phytoplankton groups (except Prochlorococcus spp.)</td>
</tr>
</tbody>
</table>

Chromophytes are defined as those microalgae that possess the accessory pigment chlorophyll c.
Pigment descriptions from Jeffrey and Vesk (1997).

2.3.4. Particulate export
Sediment trap tubes were analyzed for particulate carbon, nitrogen, phosphorus and silica, photosynthetic pigments, and microscopy. Six filters (three samples, three blanks) of particulate carbon and nitrogen collected per trap deployment were stored in a shipboard freezer (−20 °C) and analyzed on a Carlo Erba Elemental Analyzer (model NC2500) interfaced with a Finnigan DeltaS ion ratio-monitoring mass spectrometer (Sharp, 1974). Filters for particulate phosphorus were analyzed following the methods of Strickland and Parsons (1972). Filters for photosynthetic pigments of exported material were analyzed using methods described above. During pigment extraction, grinding of the filters was necessary to suspend all sediment and organic material from the filters. Filters for particulate biogenic silica were analyzed as follows using the methods of DeMaster (1981). Time course subsamples were measured colorimetrically to distinguish lithogenic silica from biogenic silica, which dissolves more readily than compounds of mineral origin according to the method described by DeMaster (1981). In addition, trap material was examined by epifluorescence microscopy as described by Scharek et al. (1999b) and Brown et al. (2003).

3. Results

3.1. Cyclone Noah
Cyclone Noah first appeared in GOES and MODIS SST imagery between 13 and 21 August 2004, downwind of the ‘Alenuihaha Channel. Noah intensified and moved southeast into the lee of Hawai‘i over the next 2 months. The E-Flux group encountered Noah (3–17 November 2004) within ~3 months of its appearance, and GOES SST imagery showed that its surface expression was elliptical in shape, possibly indicative of relaxation and decay (Kuwahara et al., 2008). During the 3 weeks of observations, Noah remained in the same approximate location (~20.1°N, 156.4°W). Noah disappeared from GOES imagery on ~21 December 2004, ~4 months after it first appeared. Given that only eddies with surface expressions can be detected via satellite and that subsurface features are often masked by near surface effects (i.e. diurnal heating and cooling, etc.), Noah (and presumably other eddies) likely spun up prior to satellite detection; thus all eddy ages should be viewed as approximate (for more details concerning satellite observations, see Dickey et al., 2008).

Physically, Noah appeared to be a fully developed cyclonic eddy (Kuwahara et al., 2008). Noah had a physical core with maximum tangential velocities (at 40 m depth) up to 80 cm s−1 at 20–40 km from the center and a shallow (~200 m), semi-elliptical shape, which measured ~144 km in the major axis (in the northwest to southeast direction) and ~90 km in the minor axis. Angular velocity varied with distance from the center, indicating that solid body rotation did not occur beyond ~10 km from the estimated geometric center (Kuwahara et al., 2008). Though semi-elliptical in the upper 100 m, the layer below (100–140 m) was observed to be more circular and symmetric, suggesting that the upper layers were beginning to decay while the bottom layer remained as a cohesive body. More detail regarding Noah’s ellipticity and shape is discussed in Kuwahara et al. (2008). The isopycnal density surface of ρ = 24.0 (σ = 24.0 kg m−3) was displaced from 132 ± 8 m (n = 7) in ambient waters upwards to 83 ± 8 m (n = 7) at the eddy center. The depth of the euphotic zone, defined as the depth of 1% surface illumination, was 105 ± 2 m (n = 9) at the center of Noah relative to 111 ± 3 m (n = 9) in surrounding waters.

3.1.1. Macronutrient distributions
Dissolved inorganic macronutrient concentrations increased slightly within the eddy center in the upper 150 m compared to
surrounding waters (Fig. 2, Table 2). Contour plots of N+N, phosphate, and silicic acid followed the doming of isopycnal surfaces. N+N concentrations were just above the limit of detection at ~100 m in the center of Noah compared to ~120 m in surrounding waters, and were negligible in the upper water column above the σt-24.0 isopycnal surface (~85 m in the center). In the center of the eddy, N+N and phosphate concentrations were enhanced slightly in the euphotic zone (as indicated by the yellow line on the contour plots) and silicic acid concentrations were close to the limit of detection in the upper 50 m (Fig. 2).

Macronutrients were first integrated over 0–150 m both in and out of the eddy in order to compare the standing stock of nutrients in a given geometric mass of water. These values revealed 3.3-, 1.6-, and 1.3-fold increases for N+N, phosphate, and silicic acid concentrations, respectively, in Noah compared to surrounding waters (Table 2). Macronutrients were also integrated over the calculated depths of the euphotic zones in (0–110 m) and out (0–115 m) of Noah to assess nutrient availability and utilization by phytoplankton. Increases in these integrated values (3.7-, 1.4-, and 1.2-fold, Table 2) were similar to increases in values integrated over 0–150 m.

3.1.2. Photosynthetic pigment biomarkers

Water-column profiles of TChl a in and out of Noah did not show significant differences except for a slight upward displacement of the DCM by ~20 m (Fig. 3A). Contour plots of chlorophyll and carotenoid pigment biomarkers depict a similar upward displacement of the DCM, shadowing the doming of the isopycnal surfaces and remaining at the base of the euphotic zone.

Fig. 2. Depth contours of N+N (μM, panels A, B), phosphate (PO4^3-, μM, panels C, D), and silicic acid (Si(OH)4, μM, panels E, F) in Cyclones Noah and Opal from Transect 3. Contours of isopycnal surfaces (σt–t, dotted lines), crosses indicating sampling depths, and a yellow line representing the depths of the euphotic zone (1% surface LL) are overlaid on each figure.
Table 2
Depth-integrated inorganic macronutrients during E-Flux I (Cyclone Noah) and E-Flux III (Cyclone Opal)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>E-Flux I</th>
<th>E-Flux III</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cyclone Noah</td>
<td>Cyclone Opal</td>
</tr>
<tr>
<td></td>
<td>IN (n = 2)</td>
<td>OUT (n = 2)</td>
</tr>
<tr>
<td>Nitrate+nitrite (mmol N m⁻²)</td>
<td>136 (18)</td>
<td>41.7 (3.9)</td>
</tr>
<tr>
<td>Phosphate (mmol P m⁻²)</td>
<td>26.5 (1.8)</td>
<td>16.5 (2.3)</td>
</tr>
<tr>
<td>Silicic acid (mmol Si m⁻²)</td>
<td>201 (25)</td>
<td>152 (29)</td>
</tr>
<tr>
<td>Euphotic zone depth-integrated (m)</td>
<td>0–110</td>
<td>0–115</td>
</tr>
<tr>
<td>Nitrate+nitrite (mmol N m⁻²)</td>
<td>45.5 (4.8)</td>
<td>12.4 (5.8)</td>
</tr>
<tr>
<td>Phosphate (mmol P m⁻²)</td>
<td>15.6 (0.1)</td>
<td>10.8 (1.6)</td>
</tr>
<tr>
<td>Silicic acid (mmol Si m⁻²)</td>
<td>129 (9.7)</td>
<td>107 (22)</td>
</tr>
</tbody>
</table>

n Indicates the number of samples averaged and the values in columns indicate mean (range) for Cyclone Noah and mean (± s.d.) for Cyclone Opal. Mean values from E-Flux I: IN = IN Sta. 1–2, OUT = OUT Sta. 1–2; from E-Flux III: IN = IN Sta. 2–7, OUT = OUT Sta. 1–3. Euphotic zone depths were calculated as the depth of 1% LL.

![Water-column profiles of TChl a concentration during E-Flux I (A) and III (B, C). Panel A: IN Sta. (dark triangles) are mean values (error bars = ± s.d.) of IN Sta. 1 and 2 and casts 31 and 32 from Transect 3. OUT Sta. (open circles) are mean values (error bars = ± s.d.) of OUT Sta. 1–3. Panels B (independent parameter is depth) and C (independent parameter is density) show the center station from Transect 3 (cast 19A) and IN Sta. 1–3 (dark triangles), IN Sta. 4–7 (open triangles), and mean values (error bars = ± s.d.) of OUT Sta. 1–3 (open circles).](image-url)
Chlorophyll pigments TChl a, MVChl a, and DVChl a (biomarker for *Prochlorococcus* spp.) were not markedly enhanced in the center of the eddy relative to ambient waters (Fig. 4). Hex-fuco and But-fuco, carotenoid biomarkers for prymnesiophytes and pelagophytes, respectively, increased slightly at the periphery of the center of the eddy (Fig. 5A, C). Cyanobacterial pigment Zeax (biomarker for *Synechococcus*) was concentrated in the mixed layer above the DCM) was not disrupted, but was merely displaced upwards by ~20 m.

Photosynthetic pigments were integrated to the 1% LL (110 m in and 115 m out of the eddy). Depth-integrated TChl a concentrations were relatively constant in and out of Noah, as were most pigment inventories (i.e. TChl b, TChl c, DDX, α-Car, β-Car, Zeax). However, the fraction of TChl a attributed to MVChl a, which is present in all phytoplankton, increased to ~60% in Noah compared to ~50% at OUT stations. In contrast, the fraction of TChl a attributed to DVChl a was ~42% versus ~50% outside of Noah. These fractions indicate that the dominance by *Prochlorococcus* spp. in ambient conditions shifted towards other types of phytoplankton in the eddy, such as diatoms (1.7-fold increase in Fuco), prymnesiophytes (~1.4-fold increase in Hex-fuco), pelagophytes (~1.3-fold increase in But-fuco), and dinoflagellates (~1.7-fold increase in Per). Allox, DTX, Pras, Viola, and the chlorophyll degradation pigment MVChl a were only present in trace amounts both in an out of Noah; hence, all but MVChl a (important in Cyclone Opal, Section 3.2.2) were omitted from Table 3.

### 3.1.3. Phytoplankton size structure

TChl a concentration did not change significantly at the base of the mixed layer in and out of Noah (Table 4). Within that layer, however, a modest shift in phytoplankton size structure to cells >18 µm is apparent (5.4% IN versus 2.8% OUT, Table 4). A ~1.3-fold increase in TChl a concentration was evident within the mixed layer of the center of the eddy, which was comprised mainly of picoplankton 0.7–2 µm (i.e. *Prochlorococcus* sp.) with modest increases in nanoplanckton 2–18 µm such as pelagophytes (15.0% IN compared to 11.3% OUT) and microplankton >18 µm such as diatoms (7.6% IN compared to 3.0% OUT).

![Fig. 4. Depth contours of chlorophyll pigment biomarkers from Transect 3: TChl a = MVChl a+DVChl a+MVChl b (mg m$^{-3}$, panels A, B), MVChl a (mg m$^{-3}$, panels C, D), and DVChl a (mg m$^{-3}$, panels E, F) in Cyclones Noah and Opal, with overlays of isopycnal surface contours and a yellow line representing the depths of the euphotic zone (1% surface LL). Crosses indicate sampling locations.](image-url)
3.1.4. Particulate matter export
The sediment trap array remained within Noah for the entire duration of the deployment (drifter trajectories for E-Flux I are shown in Dickey et al., 2008). Particulate carbon, nitrogen, and silica exports were not significantly different in and out of Noah (Table 5). Exported TChl $a$ was higher by $\sim$1.2-fold in the eddy compared to out, with concurrent increases in exported pigments DTX and $\beta$-Car (data not shown). All other exported pigments within the eddy were $\sim$30-50% less than those in surrounding waters.

3.2. Cyclone Opal
Cyclone Opal became visible in GOES and MODIS SST imagery on 18 February 2005, but likely formed below the surface prior to this date. Opal was approximately a month old at the time of our study (10-22 March 2005) with colder surface water evident in satellite imagery. Over our 3-week observation, Opal drifted $\sim$165 km (88-89 nmi) southward from its original location ($\sim$20.3 N, 156.3 W) while maintaining its physical structure. Opal remained visible in satellite imagery until April 2005, $\sim$2 months after it first appeared (Nencioli et al., 2008; Dickey et al., 2008).

At 160-180 km in diameter and with a maximum eddy uplift of 80–100 m, Opal was a stronger and larger eddy than Noah at the time of sampling. Near-surface tangential velocities of $\sim$60 cm s$^{-1}$ increased almost linearly from the center up to a radial distance of $\sim$25 km. The angular velocity of $\sim$2.4 x $10^{-5}$ rad s$^{-1}$ (orbital period is $\sim$3 days) remained nearly constant within the radial distance. This area of constant angular velocity indicates that this portion of the eddy was in near-solid-body rotation, relatively isolated from surrounding waters (Nencioli et al., 2008). The dimensions of Opal were inferred from hydrographic data; more detail regarding horizontal and vertical dimensions of the feature is described in Nencioli et al. (2008). Doming of isopycnals was markedly more intense in Opal than Noah, as evidenced by shoaling of the $\sigma$-1400 density surface (52 $\pm$ 8 m IN, 131 $\pm$ 15 m OUT) and depth of the 1% LL (91 $\pm$11 m IN, $n$ = 45; 112 $\pm$4 m OUT, $n$ = 21). Opal was a relatively shallow feature as the cyclonic circulation was insignificant at depths greater than 200 m (Nencioli et al., 2008).

3.2.1. Macronutrient distributions
Similar to Noah, macronutrient concentrations reflected shoaling of isopycnal surfaces but were much more pronounced in Opal (Fig. 2). During the initial sampling of Opal, N+N was present in...
Particulate carbon (Particulate phosphorus (Size-fractionated TChl a 

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>% Light level</th>
<th>Location in mixed layer</th>
<th>Location in eddy</th>
<th>Size-fractionated [TChl a] (mg m⁻³)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.7–2 µm (% total)</td>
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### E-Flux I Cyclone Noah

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<tr>
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<tbody>
<tr>
<td>Cyclone</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Noah</td>
<td>16</td>
<td>43</td>
<td>In ML</td>
<td>IN</td>
</tr>
<tr>
<td>Opal</td>
<td>20</td>
<td>43</td>
<td>In ML</td>
<td>OUT</td>
</tr>
<tr>
<td></td>
<td>39</td>
<td>11</td>
<td>Base of ML</td>
<td>IN</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>11</td>
<td>Base of ML</td>
<td>OUT</td>
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### E-Flux III Cyclone Opal

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<td></td>
</tr>
<tr>
<td>Noah</td>
<td>15</td>
<td>43</td>
<td>In ML</td>
<td>IN</td>
</tr>
<tr>
<td>Opal</td>
<td>20</td>
<td>43</td>
<td>In ML</td>
<td>OUT</td>
</tr>
<tr>
<td></td>
<td>35</td>
<td>11</td>
<td>Base of ML</td>
<td>IN</td>
</tr>
<tr>
<td></td>
<td>55</td>
<td>11</td>
<td>Base of ML</td>
<td>OUT</td>
</tr>
</tbody>
</table>

Size-fractionated TChl a is presented as a percentage of the total TChl a. Values in columns indicate mean (± s.d. or range) taken from IN Sta. 1–3 (n = 3) and OUT Sta. 1–2 (n = 3) for Cyclone Noah, and from IN Sta. 1, 3, 4 (n = 3) and OUT Sta. 1–2 (n = 2) for Cyclone Opal.

### Table 5

Particulate export fluxes (± s.d.) obtained using a sediment trap array deployed in (n = 3) and out (n = 3) of Cyclones Noah and Opal

<table>
<thead>
<tr>
<th>Parameter</th>
<th>IN</th>
<th>OUT</th>
<th>ANOVA*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Particulate biogenic silica (mmol Si m⁻² d⁻¹)</td>
<td>0.12 (0.04)</td>
<td>0.10 (0.0)</td>
<td>p = 0.5 NO 1.2</td>
</tr>
<tr>
<td>Noah</td>
<td>0.43 (0.03)</td>
<td>0.11 (0.06)</td>
<td>p = 0.002 YES 3.9</td>
</tr>
<tr>
<td>Opal</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Particulate carbon (mmol C m⁻² d⁻¹)</td>
<td>2.20 (0.2)</td>
<td>2.31 (0.3)</td>
<td>p = 0.6 NO 1.0</td>
</tr>
<tr>
<td>Noah</td>
<td>1.54 (0.1)</td>
<td>1.52 (0.2)</td>
<td>p = 0.9 NO 1.0</td>
</tr>
<tr>
<td>Opal</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Particulate nitrogen (mmol N m⁻² d⁻¹)</td>
<td>0.24 (0.03)</td>
<td>0.27 (0.03)</td>
<td>p = 0.5 NO 0.9</td>
</tr>
<tr>
<td>Noah</td>
<td>0.15 (0.01)</td>
<td>0.16 (0.02)</td>
<td>p = 0.3 NO 0.9</td>
</tr>
<tr>
<td>Opal</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Particulate phosphorus (µmol P m⁻² d⁻¹)</td>
<td>2.57 (0.3)</td>
<td>4.28 (0.7)</td>
<td>p = 0.02 YES 0.6</td>
</tr>
<tr>
<td>Noah</td>
<td>2.69 (1.0)</td>
<td>2.07 (1.1)</td>
<td>p = 0.5 NO 1.3</td>
</tr>
</tbody>
</table>

*Single-factor analysis of variance tested whether the means are significantly different from one another with 95% confidence.

All pigments were depth-integrated to the depth of the euphotic zone (1% LL): Noah (110 m IN, 115 m OUT), Opal (100 m IN, 115 m OUT). Values in columns indicate mean (± s.d. or range). Mean values from E-Flux I: IN = IN Sta. 1–2, OUT = OUT Sta. 1–3; from E-Flux III: IN = Cast 19A and IN Sta. 1–7, OUT = OUT Sta. 1–3. Pigments that were detected but present in trace amounts (<0.2 mg m⁻³, Allox, DTX, Pras, Viola) were omitted from the table.

3.2.2. Photosynthetic pigment biomarkers

Depth profiles of TChl a in the center showed a sharp and dramatic increase within Opal, as indicated by a ~50 m upward
displacement and a marked >2-fold increase at the DCM (Fig. 3B). The depth of the DCM at IN stations varied dramatically during our study though the DCM was confined within a narrow band of isopycnal surfaces \( \sigma -t_{24.2} \) (\( \sigma_{1} = 24.2 \text{ kg m}^{-3} \)) and \( \sigma -t_{24.4} \) (\( \sigma_{1} = 24.4 \text{ kg m}^{-3} \)) (Fig. 3C). The DCM in the eddy occupied a denser isopycnal surface (\( \sigma -t_{24.3} \)) as compared to the DCM in surrounding waters (\( \sigma -t_{23.8} = 23.8 \text{ kg m}^{-3} \); Fig. 3C). The TChl \( \alpha \) bloom was comprised mostly of phytoplankton containing MVChl \( \alpha \) (Fig. 4D) and pigments Hex-fuco, But-fuco, and Fuco (Fig. 5). Most notably, Fuco exhibited a 3–6-fold increase in the DCM in the center of Opal relative to ambient waters. Prochlorococcus spp. dominance to eukaryotic phytoplankton in Opal at the base of the mixed layer in community at the base of the mixed layer in DVChl \( \alpha \) (Fig. 4D) and pigments Hex-fuco, But-fuco, and Fuco (Fig. 5).

A 1.4-fold increase in TChl \( \alpha \) concentration was evident at the DCM (Fig. 3B). No substantial changes in DVChl \( \alpha \) concentrations indicated a 1.5-fold increase in Opal compared to out (Table 3). MVChl \( \alpha \) comprised 66% of the TChl \( \alpha \) concentration in the center during our time series. Near real-time ADP velocites, combined with underway \textit{in situ} temperature, proved to be the most useful tool in tracking the center and permitted real-time modifications of the original sampling pattern. Data was then treated as quasi-synoptic when plotted and interpreted with respect to the moving center of the eddy in a quasi-Lagrangian reference frame. Trajectories of the OPL drifter, the METOCEAN bio-optical drifter, and the sediment trap array were analyzed post-cruise to locate the geometric centers of the trajectories for comparison with the sampled ‘centers’ of the eddy. Further information concerning the center of Opal was inferred from the analyses of the distributions of the differential anomalies of temperature and density. All of the above methods indicate that we were able to sample the ‘center’ of Opal. Nencioli et al. (2008) detail the post-cruise analyses on the physical aspects of Opal and the quasi-Lagrangian framework of sampling, validating a time series in the ‘center’ of Opal.

The phytoplankton community in the center of Opal evolved substantially over the 8-day time series (Fig. 6). The center station (cast 19A) during transect 3 was included in this time series as \( t_{0} \) (\( t = 0 \text{ h} \)) such that the gap between \( t_{0} \) and IN Station 1 (\( t_{1} = 58 \text{ h} \)) represents lack of data, not lack of pigment. From \( t_{0} \) to \( t_{1} \), the DCM deepened in the water column from ~50–70 m to 70–90 m, and then varied considerably during consecutive days. The variability in DCM depth may be attributed to ship positioning, eddy dynamics, internal tides, or inertial variability, which has
a ~31-h periodicity (Karl et al., 2002). Despite the variability, the DCM remained narrowly confined within isopycnal surfaces \( \sigma - t_{2,4.2} \) and \( \sigma - t_{2,4.4} \) (as indicated by dotted lines, Fig. 6), implying that sampling occurred in the same water mass. Within this layer, TChl \( a \) concentration decreased dramatically after 4 days to half its original concentration (from \( \approx 1 \) to 0.5 mg m\(^{-3}\), Fig. 6A). The decline of the bloom was largely due to the decrease in diatoms, as indicated by Fuco (Fig. 6B). But-fuco and Hex-fuco maintained the same elevated concentration throughout the 8 days in the center of Opal, representing a persistent bloom dominated by pelagophytes and prymnesiophytes (Fig. 6C). DVChl \( a \) also remained constant over time, representing the ambient population of Prochlorococcus spp. (Fig. 6D).

3.2.5. Suspended biogenic silica profiles

A single profile of suspended BSI was obtained both in (IN Sta. 2) and out (OUT Sta. 3) of Opal (Fig. 7). The BSI maximum was displaced upwards from \( \approx 120 \) m in the surrounding waters to \( \approx 45 \) m within the eddy center with a \( \approx 20 \)-fold increase compared to ambient BSI concentrations.

3.2.6. Particulate matter export

The sediment trap array remained within Opal as it traveled southward during the study (drifter tracks are shown in Dickey et al., 2008). Particulate carbon and nitrogen export was similar in and out of the eddy, but particulate silica export was \( \approx 4 \)-fold higher at the eddy center (Table 5). Microscopic examination of trap solution from out of Cyclone Opal showed little material whereas samples collected within Opal contained nearly empty frustules of large diatoms. Increased silica export within the eddy was likely due to the export of such frustules, which contained little visible chlorophyll or cellular organic material.

Exported TChl \( a \) was \( \approx 1.3 \)-fold higher in Opal compared to out (data not shown). An associated increase in exported MVChl \( a \) from inside Opal was concurrent with a \( \approx 1.5 \)-fold increase in exported Fuco, with noticeable increases in Pras, DTX, and DDX relative to out of Opal. Exported Zeax was greater out of the eddy by \( \approx 1.5 \)-fold. Surprisingly, exported But-fuco, Hex-fuco, and Per were also higher (~2-fold) out of the eddy, indicating greater export of smaller pelagophytes, prymnesiophytes, and dinoflagellates from the water column out of Opal.

4. Discussion

4.1. The transient oasis

The uniqueness of Cyclone Opal is highlighted by the presence of large, chain-forming diatoms, which was unexpected given previous findings (Olaizola et al., 1993; Seki et al., 2001; Bidigare et al., 2003; Vaillancourt et al., 2003). In addition to significant increases in diatom biomass (indicated by Fuco concentration), Brown et al. (2008) observed a 100-fold increase in >20 \( \mu \)m diatom biomass as measured using microscopy at 70–90 m in the center of Opal. The sudden decline of the diatom bloom after our fourth day in the center of Opal emphasizes the importance of timing in the sampling of mesoscale eddy features in the open ocean. It is difficult to estimate the duration of the bloom, for it likely began prior to our arrival. The decay of the diatom bloom may have been the result of several biological processes, including grazing pressure, interspecies competition, as well as viral infection. After close examination of our data, we attribute physiological stress due to Si limitation as a probable cause of the demise of the diatom bloom.

Si is essential for the formation of diatom frustules (Guillard, 1975; Brzezinski and Nelson, 1996). The strongest evidence for Si limitation, given that direct uptake experiments were not performed in this study, was silicic acid depletion (<limit of detection) at \( \approx 40–60 \) m in the center of Opal in Transect 3. These depths contained the DCM and a 60-fold increase in Fuco. It has been reported that ambient silicic acid concentrations of \( <1–2 \mu \text{M} \) limit uptake by diatoms in surface waters of most mid-ocean gyres (Egge and Aksnes, 1992; Brzezinski and Nelson, 1995, 1996; Brzezinski et al., 1998, 2001; Henson et al., 2006). Silicic acid levels during E-Flux III were correlated with density surfaces and were found to be \( <2 \mu \text{M} \) in the euphotic zone in Opal (Fig. 8B); these levels likely limited silicic acid uptake by diatoms. In contrast, silicic acid concentrations in Noah ranged from 0 to 3 \( \mu \text{M} \) (Fig. 8A) and did not seem to limit uptake by phytoplankton, as the phytoplankton community within Noah was dominated by non-diatom phytoplankton that do not require Si for growth.

Although low concentrations do not prove nutrient limitation, diatoms in Opal did show signs of physiological stress. High levels of MVChl \( a \), indicative of senescent phytoplankton and fecal pellets, were measured in the DCM concurrent with a 60-fold increase in Fuco pigment. Landry et al. (2008) reported depressed growth rates and a higher biomass of physiologically unhealthy diatoms in the 50–60 m depth zone, while healthy diatoms were observed immediately below at the base of the euphotic zone (70–90 m). Brown et al. (2008) observed a similar phenomenon in which a distinct layer of senescent diatoms were present in these upper depths while healthier diatoms were present directly below. All of the above, plus the lack of phytoplankton response to N, P, and Fe additions in the eddy, point to Si limitation as the primary cause of the decline in diatom biomass (Benitez-Nelson et al., 2008).

If Si limitation indeed accounts for the decline of the diatom population, depletion of Si would then lead to utilization of the “next” limiting nutrient, for only one essential nutrient can limit growth rate at a specific time (Tilman, 1980). After the demise of the diatom bloom, the sustained background population of smaller eukaryotes and cyanobacteria was maintained by sufficient N and P remaining within Cyclone Opal. This would suggest that the “apparent” succession of large Si-dependent diatoms by...
pico- and nano-phytoplankton (Prochlorococcus spp., pelagophytes, prymnesiophytes, and other lightly silicified diatoms), as observed during the time series in the Opal center was primarily caused by nutrient limitation. It is likely that phytoplankton with high maximum nutrient uptake rates ($V_{\text{max}}$) (i.e. diatoms), in their unhealthy state, may be outcompeted by those with lower $V_{\text{max}}$ (i.e. prymnesiophytes and pelagophytes), ultimately altering phytoplankton community dynamics. Similar changes in phytoplankton community structure have been observed during a North Atlantic spring bloom event, when diatoms were outcompeted by non-siliceous phytoplankton upon silicic acid depletion (Henson et al., 2006). Even though diatoms require Si to form frustules, several species such as Hemialus and Mastogloia spp. produce thinner frustules (Brezinski and Nelson, 1996; Scharek et al., 1999a) under substrate limitation. These lightly silicified species were observed at the end of the time series in Cyclone Opal (Benitez-Nelson et al., 2008; Brown et al., 2008).

Presumably, once Si becomes limiting to diatom growth, production by non-siliceous phytoplankton would continue until all remaining N or P has been consumed. However, Henson et al. (2006) showed that although Si may limit a bloom and by extension export production, subsequent utilization of N or P serves to ultimately restore conditions towards production by recycling nutrients. Once N reaches a minimum value, all further production must rely on recycled forms of N (Henson et al., 2006), suggesting that phytoplankton in the ‘decay’ stage of a cyclonic eddy would ideally return to regenerated production. Mahaffey et al. (2008) reported that suspended particulate N was markedly enhanced in the DCM within Opal, possibly due to small fecal pellets and/or organic matter that had yet to be exported. Mixed-layer depth-integrated values of particulate N decreased significantly during the time series at the Opal center, indicating either remineralization or export of N. However, increases in inorganic N (nitrate, nitrite) or N export flux was not observed, indicating a shift towards recycled production (via NH$_4$ assimilation) and/or new production via nitrogen fixation as the primary means of N supply.

4.2. Subtropical eddies: a silica pump?

Enhanced biological activity and a shift up in size structure of the phytoplankton community are thought to stimulate rates of carbon export (McCave, 1975; Eppley and Peterson, 1979; Knauer et al., 1979; Goldman, 1988, 1993). Given modest increases in photosynthetic pigment biomass, it is not surprising that export fluxes in Noah did not exhibit significant differences from ambient waters. Despite variability in phytoplankton populations in Opal, the presence of large diatoms had foreshadowed enhanced rates of carbon export. Several biases are associated with sediment trap use, such as hydrodynamic flow above the trap mouth and over- or underestimation of organic carbon attached to swimmers accidentally caught in trap tubes (Butman et al., 1986; Buesseler, 1991; Buesseler et al., 2000). However, only a modest 1.3-fold increase in $^{234}$Th-derived carbon flux (Benitez-Nelson et al., 2008; Maiti et al., 2008) was observed, corresponding to the trap-derived export estimates in the center of Opal. It can be argued that we may have missed the timely carbon export event of Opal, but this is unlikely. Mass balance estimates suggest that >85% of net community production accumulated as total organic carbon (comprised mostly of dissolved organic carbon) within the system (Benitez-Nelson et al., 2008), consistent with the minimal carbon export evidenced in traps and in $^{234}$Th- and $^{210}$Po-derived measurements. Hence, most of the carbon generated within Opal was remineralized rather than exported (Maiti et al., 2008; Verdeny et al., 2008). We suspect that the major export event consisted primarily of BSI, as observed in the form of empty diatom frustules in the sediment trap array. In addition, high levels of suspended BSI were observed at ~50 m (Fig. 7), likely due to large and spiny senescent diatoms with slow sinking rates, such as Chaetoceros spp. (Brown et al., 2008). Furthermore, these results suggest that cyclonic eddies formed in subtropical waters may not necessarily be an efficient mechanism for exporting particulate carbon to the mesopelagic zone. This finding is consistent with a recent temperature-dependent food web model that predicts low carbon export efficiencies in waters with surface temperatures exceeding 25 °C, as is the SNPO (Laws et al., 2000; Benitez-Nelson et al., 2008). The absence of a major carbon flux event is likely due to strong microbial community coupling of production, microzooplankton grazing (Landry et al., 2008), and thus remineralization processes. In the case of Opal, minimal

![Fig. 8. Scatterplots of silicic acid against density from all samples (Transect 3 and process stations) from E-Flux I (Cyclone Noah, panel A) and E-Flux III (Cyclone Opal, panel B): silicic acid concentrations in the euphotic zone (above 1% LL, closed diamonds) and below the euphotic zone (below 1% LL, open diamonds) are specified.](image-url)
carbon flux was replaced by a large BSi flux (~4-fold higher than out of the eddy). Subtropical cyclonic eddies must now be re-evaluated as potential silica pumps, suggesting that phytoplankton in the SNPW will be limited by Si following a major eddy event (Benitez-Nelson et al., 2008).

4.3. Noah vs. Opal

Based on the age model of Sweeney et al. (2003), Cyclones Noah and Opal represent two out of three stages in a cyclonic eddy’s biological life cycle. Physical data (Kuwahara et al., 2008) as well as nutrient inventories and photosynthetic pigment distributions suggest that Noah, ~3 months old, was in the ‘decay’ stage. Opal, a month old at the time of encounter, appeared to be ‘mature’ but began to ‘decay’ biologically while it remained physically ‘mature’ (Nencioli et al., 2008). If we follow the biological life cycle model, it is feasible to presume that Noah had contained a diatom bloom in its ‘mature’ stage like in Opal, and would then exhibit signals of enhanced export in its ‘decay’ stage. However, enhanced carbon export was not observed in either eddy in our study. Nencioli et al. (2008) hypothesized that Opal was a unique case in which its fast southward translation during our observational period resulted in radial movements of water between the center and outer portions along the upper density surfaces. They inferred an exchange between waters at 70–90 m in the center portion and waters at 130–150 m in the density surfaces. They inferred an exchange between waters at 100–130 m of Opal was reported to be in solid body rotation (Nencioli et al., 2008), the above hypothesis explains neither the unique phytoplankton community in Opal nor previously studied eddies. A closer look at recently studied cyclones Mikalele, Loretta, and Haulani (Seki et al., 2001; Bidigare et al., 2003) provides several insights.

Cyclones Mikalele and Loretta (Seki et al., 2001) were ~1 and 6 months old, respectively. During observation, Mikalele, a small eddy (~100 km) that was speculated to be ‘intensifying,’ expressed strong surface thermal gradients and a ~1.5-fold increase in Fuco and Hex-fuco. Loretta, also ~100 km in diameter, appeared to be in its ‘decay’ stage at the time of observation and had been a cohesive eddy for ~6 months, yet still displayed significant ~2-fold increases in Fuco, But-fuco, and Hex-fuco, with outcappings of isopycnal surfaces resembling that of Opal (Seki et al., 2001). Loretta maintained a bloom of prymnesiophytes and pelagophytes even after 6 months. How was Loretta able to maintain a bloom for so long when Opal illustrated a classic ‘bloom and bust’ scenario? Why did Mikalele and Opal, both 1 month old, support such different communities of phytoplankton?

Further confounding interpretations, Cyclone Haulani exhibited a ~25-fold increase in prymnesiophytes (mostly coccolithophores) and an increase in small, pennate diatoms (Vaillancourt et al., 2003). At 2 months old (like Noah), Haulani’s shape alternated between circular and elliptical within the first month, possibly due to variability in wind strength. Haulani was the only cyclone studied to date that exhibited a ~2.6-fold increase in carbon export, albeit the absolute magnitude was still low (Bidigare et al., 2003). Moreover, Haulani remained visible in satellite imagery for 3 months after observation, implying that Haulani may not have been in a ‘decay’ phase at the time of enhanced carbon export. These inconsistencies raise the question of whether discrepancies in the biological responses of these cyclones are indeed due to age variability.

There are various other factors to consider in explaining cyclonic variability, such as sampling resolution, validity of OUT or control stations, coastal water entrainment, trace metal effects, grazing dynamics, and the possibility of cyclones born from different water masses (see Brown et al., 2008; Landry et al., 2008; Nencioli et al., 2008; Noble et al., 2008). The average lifespan of Hawaiian lee cyclones is between 3 and 8 months, significantly shorter than that of anticyclones, which propagate farther, generally spin more slowly and often last for over a year (Patzert, 1969; Lumpkin, 1998), or of eddies in the northwest Atlantic Ocean, which spin up as a result of baroclinic instability with a lifespan of at least 6 months (i.e. McGillicuddy and Robinson, 1997; Garçon et al., 2001; Flierl and McGillicuddy, 2002; Sweeney et al., 2003; McGillicuddy et al., 2007). Thus it can be hypothesized that anticyclones (and Sargasso Sea eddies) outlive cyclones due to slower spinning speed or because they are generally weaker in strength. Patzert (1969) distinguished between ‘strong’ and ‘weak’ eddies based on spin-up duration: a ‘weak’ eddy takes 1–2 weeks to spin up, while a ‘strong’ eddy requires 30 days or more. If so, ‘strong’ eddies may differ from ‘weak’ eddies in terms of biological response. Hence, spin-up duration may directly influence the type of bloom in a cyclone and consequently, the export flux.

‘Spin-up duration’ first must be properly defined. It can be characterized as: (1) the duration of upward flux of nutrients in the ‘intensification’ stage, or (2) the duration before which the potential energy of an eddy is directly proportional to the dome of the density structure (Patzert, 1969). In this study, the definition of ‘spin-up duration’ is simply the time period over which isopycnal surfaces are upwardly displaced into the euphotic zone, introducing nutrients into well-lit waters. Therefore, spin-up rate, or the rate of nutrient input into the euphotic zone, is dependent on wind velocity, direction, eddy shear dynamics, and circulation dynamics.

If spin-up rate does influence the type of phytoplankton bloom and subsequent export within a Hawaiian lee cyclonic eddy, then the dynamic between phytoplankton community structure and the rate of nutrient input is relevant. In reference to the paradoxical nature of closely competing phytoplankton species co-existing in a uniform body of water (Hutchinson, 1961), this co-existence is thought to occur primarily via limitation by different essential nutrients (Petersen, 1975): e.g., as Si limits diatom growth, N may limit growth of some diatoms as well as other phytoplankton, etc. In this case, a single varying nutrient concentration could lead to a shift in phytoplankton dominance (Eppley, 1969), and differences in nutrient supply could also lead to the dominance of specific phytoplankton (Turpin and Harrison, 1979).

Linear features such as Rossby waves uplift isopycnals into a well-lit zone continuously in their line of propagation. Though the time-scale for the residence of a constantly propagating Rossby wave is relatively short, the nutrient input in a given passage area is relatively slow and constant. Thus, haptophytes and pelagophytes flourish because seed populations are abundant and smaller organisms are able to exploit excess (but less amounts of) N (Siegel, 2001; Uz et al., 2001; Sakamoto et al., 2004). In nonlinear features such as cyclonic eddies, faster input of nutrients or a single large addition into surface waters of a cyclone due to strong winds would provide an advantage to phytoplankton with high Vmax (diatoms) over those with lower Vmax (prymnesiophytes and pelagophytes) (also see Brown et al., 2008). An intense diatom bloom would be quickly limited by Si limitation and result in a ‘bloom and bust’ scenario, followed by a shift in phytoplankton community structure (Fig. 9A). Without a substantial increase in grazing by large zooplankton, remineralization would lead to opal-based export rather than carbon. However, slower input of nutrients due to weaker but longer
duration of winds would favor a sustained bloom of carbon-rich phytoplankton such as prymnesiophytes (coccochlorophytes), altered food web dynamics, and an increase in macrozooplankton grazing. As a result, there would be an increase in organic carbon exported as fecal pellets into the mesopelagic zone (Fig. 9B).

The two scenarios are illustrated by the Hawaiian lee cyclones studied to date. The fast 'spin-up rate' scenario describes Cyclone Opal, with an abundance of large diatoms and significant opal export. Furthermore, Landry et al. (2008) reported a biologically stratified water column, in which the upper mixed zone (0–40 m) within Opal exhibited little biomass response, but significant increases in growth, grazing, and production of the ambient community, while the lower euphotic zone (70–90 m) was dominated by low growth rates but high biomass of large diatoms. The stratification may have been the result of slow nutrient input (in the upper mixed zone) and faster nutrient input (in the lower euphotic zone), indicating that spin-up rate could further dictate the depth structure of the plankton community within a cyclone.

The slow 'spin-up rate' scenario describes Haulani, with enhanced carbon export due to inorganic carbon (CaCO$_3$) contained within cocolithophores, a commonly found prymnesiophyte in the subtropical North Pacific. In fact, cocolithophores dominated the 25-fold increase in prymnesiophyte biomass within Haulani (Vaillancourt et al., 2003). It is also important to note that Loretta moved northwest quickly after formation (Seki et al., 2001). Though its translation speed and eddy velocity field is not known, we can speculate that Loretta may have also been an 'open-bottom/horizontally leaky' eddy (Nencioli et al., 2008), indicating that its 6-month long bloom was sustained by a continuous injection of nutrients. According to the 'spin-up rate' hypothesis, a continuous nutrient input over a period of 6 months would indeed sustain a bloom of smaller eukaryotes. Therefore, this 'spin-up rate' hypothesis attempts to explain (1) Opal's large centric diatom 'bloom and bust' occurrence and increased silica export, (2) the enhanced rate of carbon flux associated with increased cocolithophores in Haulani, and (3) Loretta's 6-month-long sustained bloom.

In the case of Opal as an 'open-bottom/horizontally leaky' eddy (Nencioli et al., 2008), the 'spin-up rate' hypothesis still holds in the upper euphotic zone where phytoplankton with high $V_{\text{max}}$ (diatoms) would have outcompeted those with lower $V_{\text{max}}$ (prymnesiophytes and pelagophytes) after a single large nutrient addition. Perhaps the succession of phytoplankton from diatoms to smaller eukaryotes observed at the end of the time series in Opal can be attributed to continuous nutrient input into the center and peripheral portions of Opal due to the 'open-bottom,' similar to a Rossby wave. Nevertheless, these hypotheses emphasize the uniqueness of Opal: size, movement, community structure, and lack of expected carbon export.

Sweeney et al. (2003) briefly discussed the relevance of their conceptual model in terms of an eddy's age, intensity, and nutrient injection (i.e. single, multiple, consecutive). For eddies in the northwest Atlantic, which are significantly influenced by seasonal cycles, the 'spin-up' hypothesis becomes more complex in that the 'spin-up rate' of a Sargasso Sea eddy may be directly related to factors other than those in the SNPO. Correlations with 'spin-up rate' and the biological responses previously studied eddies in the Sargasso Sea would allow further development and a broader application of this hypothesis. Quantitative measurements of 'spin-up rate' as well as numerical models of production determined by 'spin-up rate' would provide further insight into investigating the various hypotheses presented here.

5. Summary and conclusions

The two cyclones observed during this study, Noah and Opal, differed in terms of physical and biogeochemical attributes. Both eddies supported very different plankton communities in response to similar enhancements in standing stocks of macronutrients. While Noah exhibited only modest enhancements of the ambient phytoplankton community (dominated by Prochlorococcus spp. and small eukaryotes), Opal displayed a phytoplankton bloom dominated primarily by large diatoms in the DCM. The diatom-dominated bloom in Opal declined dramatically (as represented by a 50% decrease in Fuco) on the fourth day of our study period, likely due to Si limitation. Despite the presence of a large phytoplankton bloom, enhanced export of carbon or nitrogen was not observed in Opal (or in Noah); instead, a 4-fold increase in silica export (attributed to empty diatom frustules) was observed in Opal. Therefore, it is likely that remineralization remained the key process within both eddy systems, despite enhancements in photosynthetic pigment biomass.

Previously, differences between cyclones have been attributed to the developmental stages of cyclonic eddies; however, characteristics of each eddy and its associated ‘age’ are not in accordance. The characterization of Noah in the ‘decay’ stage and Opal as ‘mature’ implies that Noah once contained large diatoms similar to that observed in Opal. In addition, only one eddy in the past, Haulani, showed an enhancement in carbon export and the absolute magnitude was still low. Thus, we hypothesize that Hawaiian lee cyclones may follow different paths of development.
stemming from differences in the ‘intensification’ stage. These differences may include wind strength, intensity of upwelling, eddy translation speeds, prior eddy activity in the area, and tangential velocity, all of which govern the rate of nutrient input into the euphotic zone, and in turn, the biological response. By further exploring the controls on the physical and biogeochemical life stages of cyclonic eddies, we can better characterize the impacts of a cyclone on nutrient cycling, plankton physiology and variability, and both the silica and carbon budgets of the world’s oceans.

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