ABSTRACT

Two cyclonic eddies were surveyed during the E-Flux I and III cruises to investigate the consequences of spatial and temporal variability in macronutrients and photosynthetic pigments on particle export. Cyclone Noah (E-Flux I) exhibited modest increases in macronutrients and photosynthetic pigments at the eddy center and was hypothesized to be in a ‘decay’ stage. Cyclone Opal (E-Flux III), speculated to be in a ‘mature’ stage, exhibited distinct increases in macronutrient concentrations at the center of the eddy concurrent with a dramatic 2-fold increase in total chlorophyll \( a \) (TChl \( a \)) concentration, comprised mainly of large diatoms, in the deep chlorophyll maximum layer (DCML). During an eight-day time-series in the center of Opal, TChl \( a \) concentration in the DCML decreased by \( \sim 50\% \) with a simultaneous decrease in diatom biomass, potentially triggered by silicic acid limitation. Despite the large diatom bloom, Cyclone Opal did not produce the expected increase in particulate carbon and nitrogen export but rather a \( \sim 4\times \) fold increase in biogenic silica export. This study represents a direct observation of two eddies at different stages in their biological life cycle. 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. Further investigation of recently studied cyclones in comparison with Cyclones Noah and Opal yields speculation of a relationship between the spin-up duration of a cyclone and the resulting biological response. It is clear from this study that variability in Hawaiian lee cyclones, which strongly influence the
biogeochemistry and biology of many areas 100’s of km in scale in the subtropical North Pacific Ocean, still remains an enigma.

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1. INTRODUCTION

1.1. Subtropical North Pacific Ocean phytoplankton community structure

Phytoplankton community structure in the Subtropical North Pacific Ocean (SNPO) is primarily influenced by the lack of inorganic macronutrient (nitrogen, N; phosphorus, P; and silicon, Si) availability in the upper euphotic zone. Minute organisms, such as photosynthetic bacteria (*Prochlorococcus* spp.) and picophytoplankton (0.2-2 µm) that have high surface area-to-volume ratios and are efficient at nutrient uptake and light harvesting, are selected as the ‘climax community’ in the SNPO (Clements, 1916; Campbell and Vaulot, 1993; Anderson et al., 1996; Karl et al., 2001a). In a typical two-layer distribution, cyanobacteria (e.g. *Synechococcus* and *Prochlorococcus* spp.) dominate the mixed layer (ML typically \( \leq 50 \text{ m} \)) while *Prochlorococcus* spp. and photosynthetic pico- and nanoeukaryotes (pyrmenesiophytes and pelagophytes) comprise the deep chlorophyll maximum layer (DCML typically \( \sim 90-110 \text{ m} \)) (Bidigare et al., 1990; Ondrusek et al., 1991; Letelier et al., 1993).

Low standing stocks of phytoplankton in the SNPO imply minimal particulate organic matter flux, contributing little to organic carbon export to the deep ocean floor. Due to the critical role of large, eukaryotic phytoplankton in export production (Eppley, 1969; Goldman, 1993; Legendre and Le Fevre, 1995), and 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, 2001b; Karl, 2002a; Sweeney et al., 2003) and/or high rates of respiration (Laws et al., 2000). The import 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 the available nutrient pools in the system. Due to varying nutrient supply rates, it has been reported that the SNPO community alternates between states of N and P limitation via El Niño-Southern Oscillation (ENSO) forcing (Karl et al., 2001b; Karl, 2002a). Thus, the provenance of the nutrient supply in the SNPO has significant implications for nutrient availability and the succession of subsequent events such as productivity, nutrient limitation, and particulate matter export.
1.2. Mesoscale perturbations and age variability

In this ocean desert 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 euphotic zone, generating significant variability in plankton biomass and processes in the surface ocean (Eppley and Peterson, 1979; Falkowski et al., 1991; 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, occurring 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., 2007). Intensified northeasterly trade winds and island topography contribute to the formation of cyclonic eddies to the north of the channel (Lumpkin, 1998; Chavanne et al., 2002, Calil et al., 2007; Dickey et al., 2007). 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 in the well-lit zone for light-replete, nutrient-limited phytoplankton. Increased rates of biological processes such as carbon fixation and nutrient uptake often induce substantial phytoplankton blooms in which larger photosynthetic eukaryotes dominate the community. Therefore, eddies have been reported to enhance rates of carbon export by means of altered food web dynamics due to increased macrozooplankton grazing and 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 differences in the eddy’s developmental stages and in time scales of physical, biological, and biogeochemical responses (Sweeney et al., 2003; Flierl and McGillicuddy, 2002). As suggested by Sweeney et al. (2003), the life cycle of a cyclonic eddy is divided into three stages: ‘intensification,’ ‘mature,’ and ‘decay.’ A biological response is stimulated during ‘intensification,’ after which a cyclone reaches its ‘mature’ stage as it attains its maximum tangential velocity, production rate, and highest biomass. As wind speed
The transient oasis

diminishes or the eddy migrates from the area of strongest winds in the ‘Alenuihaha Channel, the ‘mature’ stage of a cyclone subsides as the doming of the isopycnals relaxes and tangential velocity decreases. At this time, the eddy recedes into its ‘decay’ stage, undergoing significant changes physically as well as biologically towards ambient conditions (Patzert, 1969; Sweeney et al., 2003). The duration of the ‘mature’ stage is highly variable, making a ‘mature’ eddy a rare feature to encounter during a research cruise.

It has been reported that for an eddy-pumping mechanism to be a significant contributor to export production in the SNPO, then 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 euphotic zone only as the eddy forms, not as it matures or propagates. Thus, if nutrients on a deeper isopycnal surface are depleted without remineralization and the induction of biological processes such as nitrification, biological response during the next eddy event would be minimal due to less bioavailable nutrients being injected into the euphotic 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). However, it is also important for the remineralization process to occur on short enough time scales, yet be spatially uncoupled from the injection of nutrients for efficient export production.

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 in 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

The seasonal intensification of trade winds through the ‘Alenuihaha Channel make the lee region of Hawai‘i an ideal natural laboratory for studying cyclonic eddies during the winter months (Dickey et al., 2007). Sea surface temperature (SST) measurements obtained from Geostationary Operational Environmental Satellites (GOES) radiance sensors (via the EddyWatch section of the NOAA CoastWatch Program, http://oceanwatch.pifsc.noaa.gov/) were used to determine the timing and sampling locations of ship-based observations. E-Flux I (4-22 November 2004) was conducted aboard the University of Hawai‘i’s R/V Ka‘imikai-O-Kanaloa, and Cyclone Noah was identified using GOES and Moderate Resolution Imaging Spectroradiometer (MODIS) SST measurements and along track currents measured with a 153 kHz RDI acoustic Doppler current profiler (ADCP). E-Flux III (10-28 March 2005) was conducted aboard Oregon State University’s R/V Wecoma and Cyclone Opal was identified and sampled using similar methods as aforementioned. Details of eddy tracking during the respective cruises are described in Dickey et al. (2007).

2.1. Sample collection

2.1.1. “Star” transects and process stations

A “star” sampling strategy allowed 2- and 3-dimensional characterization of eddy variability on both spatial and temporal scales. This also provided a 4-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 stations, presumably far-field areas unaffected by eddy dynamics. Hydrographic data (temperature, salinity, pressure, density, fluorescence, and oxygen) and in situ water samples were derived from a SeaBird SBE 9/11+ CTD system plus rosette sampler. Photosynthetically available radiation (PAR) (µmol photons m⁻² s⁻¹) was measured with an attached sensor and the bottom of the euphotic zone was calculated as the depth at which irradiance was diminished to 1% of the surface light level. Details concerning sampling strategies and physical and bio-optical measurements for E-Flux I are given in Dickey et al. (2007) and
For both eddies, a single “star” was sampled which consisted of multiple transects across the eddy with stations ~18 km apart. In *Noah*, water samples for macronutrients and photosynthetic pigments were taken at depth intervals from 0-500 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 (Figure 1A) (Kuwahara et al., 2007). Samples in Cyclone *Opal* were taken at depth intervals from 0-350 m during Transect 3 (‘money run,’ casts 13-18, 19A, 22-25) with cast 19A being the ‘center’ of the eddy (Figure 1B) (Nencioli et al., 2007).

Process stations in Cyclone *Noah* were sampled for macronutrients (0-1000 m; IN = 2 and OUT = 2) and photosynthetic pigments (0-150 m; IN = 2 and OUT = 3). Process stations (IN = 7 and OUT = 3) in Cyclone *Opal* were also sampled: the center of *Opal* was sampled daily (16-22 March) for pigments and six of these stations (17-22 March) were sampled for macronutrients. Size-fractionated pigment samples were taken from stations in (n = 3) and out (n = 3) of Cyclone *Noah* at the ~11% and ~43% light levels. During Cyclone *Opal*, size-fractionated pigments were sampled from process stations in (n = 3) and out (n = 2) at the same light levels. Size-fractionated pigment samples were also collected from the DCML along Transect 6 of Cyclone *Opal* (casts 97, 99, 101, 103) from the center of the eddy (cast 97) towards the edge (~100 km). A single depth profile to 1000 m was sampled for suspended biogenic silica both in and out of Cyclone *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 µm) for size-fractionated biomass, and stored in liquid nitrogen until analysis. Water for biogenic silica analysis was collected in clear, narrow-mouthed 2-L HDPE bottles and immediately vacuum-filtered onto 25-mm 0.8-µm polycarbonate filters, which were frozen (-20°C) until analysis.
2.1.2. Sediment trap array

A sediment trap array (a.k.a. Particle Interceptor Traps, or PITs) was suspended at 150 m for a minimum of three days inside and outside 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 (Honjo and Doherty, 1988; Karl et al., 1996). Tubes were affixed to a PVC crossframe attached to a 12-mm POLYPRO line (McCave, 1975; Knauer et al., 1979). The location of the array was tracked using a RDF radio, Argos satellite transmitters, and strobe lights.

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 1% formalin solution in a total of 50 g NaCl L⁻¹ 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 pipet and the brine solution alone was filtered for specific analyses.

2.2. Sample Analysis

2.2.1. Inorganic macronutrients

Samples for nitrate + nitrite, 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 IITM and an Alpkem RFA 300™ (Gordon et al., 1994).

2.2.2. Pigments

Chlorophyll and carotenoid pigments were analyzed at the University of Hawai‘i using a Varian 9012 HPLC system and 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 hours. Photosynthetic pigments were separated on a reverse-phase Waters Spherisorb® 5-µm ODS-2 (4.6 x 250 mm) C₁₈ column with a corresponding guard cartridge (7.5 x 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, and relative retention time. Peak identity was determined by comparing retention times with a chlorophyll \( a \) standard and representative culture extracts. Spectra-Physics WOW® software was used to conservatively calculate peak area (Mantoura and Llewellyn, 1983; Wright et al., 1991; Bidigare and Trees, 2000). A dichromatic equation was used to resolve mixtures of monovinyl and divinyl chlorophyll \( a \) spectrally (Bidigare and Trees, 2000). Abbreviations for diagnostic photosynthetic pigments discussed in this study are described in Table 1.

2.2.3. Suspended biogenic silica

Suspended biogenic silica 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 biogenic silica in the samples was determined 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 (Na\(_2\)SiF\(_6\)).

2.2.4. Particulate export

Sediment trap tubes were analyzed for particulate carbon, nitrogen, phosphorus and silica, photosynthetic pigments, and microscopy. Six filters (3 samples, 3 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. Aliquots derived from a controlled reaction mixture were reacted with an ammonium molybdate solution, chemically reduced, incubated, and the absorbance was read at 810 nm (DeMaster, 1981). In addition, trap material was examined by epifluorescence microscopy as per methods described in Scharek et al. (1999b) and Brown et al. (2003).

2.3. Contour plots

Golden Software Surfer® 7.0 software was used to produce contour plots of density, macronutrient, and pigment profiles. Data were gridded and interpolated using the Kriging method with no anisotropy manipulation.

3. RESULTS

3.1. Cyclone Noah

At its first appearance in GOES and MODIS SST imagery between 13-21 August 2004, Cyclone Noah was downwind of the ‘Alenuihaha Channel. Noah intensified and moved southeast into the lee of Hawai‘i over the next two months. The E-Flux group encountered Cyclone Noah (5-17 Nov 2004) within approximately 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., 2007). During three weeks of observations, Noah remained in the same approximate location (~20.1°N, 156.4°W). Cyclone 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 on clear sky days and that subsurface features are often masked by near surface effects (i.e. diurnal heating and cooling, etc.), Cyclone Noah (and presumably other eddies) likely spun up prior to detection of a surface feature; thus, satellite imagery only represents approximate ages (for more details concerning satellite observations, see Dickey et al., 2007).
Physically, *Noah* appeared to be a fully developed cyclonic eddy (Kuwahara et al., 2007). The physical core of *Noah*, with surface tangential velocity up to 80 cm s\(^{-1}\), revealed a shallow (~200 m), semi-elliptical shape by which the major axis measured ~144 km (in the northwest to southeast direction) and the minor axis measured ~90 km. Though semi-elliptical in the upper 100 m, the layer below (100-140 m) was observed to be more circular and symmetric, and it was speculated 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. (2007). The density surface of \(\sigma_{24}\) (\(\sigma_t = 24.0 \text{ kg m}^{-3}\)) was displaced upwards to ~83 m in the center from ~132 m depth in waters unaffected by the eddy. The depth of the euphotic zone, defined as the 1% light level, was 97 m at the center of *Noah* versus 104 m in surrounding waters.

### 3.1.1. Macronutrient distributions

Dissolved inorganic macronutrient concentrations were enhanced within the eddy center in the upper 150 m (Figure 2, Table 2). Contour plots of nitrate + nitrite, phosphate, and silicic acid reflect the doming of isopycnal surfaces. Nitrate + nitrite concentrations were just above the limit of detection (0.14 \(\mu\)M) at ~100 m in the center of *Noah* compared to ~120 m in ambient waters, and were negligible in the upper water column above the isopycnal surface of \(\sigma_{24}\) (~85 m in the center). Silicic acid concentrations were close to the limit of detection (0.35 \(\mu\)M) from 0-50 m in the center of the eddy. Depth-integrated (0-150 m) values in the eddy center were modestly increased compared to surrounding waters by 2.9-, 1.5-, and 1.3-fold for nitrate + nitrite, phosphate, and silicic acid concentrations, respectively (Table 2). Given that the uptake ratio of silicon-to-nitrogen (Si:N) in diatoms is 1 (Leynaert et al., 2001), the Si:N ratio in ambient waters (~4.3) indicated the preferential uptake of N by the phytoplankton community. A decrease in the ratio to 1.7 ± 0.3 (w:w) within Cyclone *Noah* implied enhanced uptake of Si; however, when normalized to respective increases in each inorganic macronutrient, both ratios revealed preferential N uptake by the resident phytoplankton community relative to Si. Based on the Redfield ratio of 106C:16N:1P (Redfield et al., 1963), nitrogen-to-phosphorus (N:P) ratios both inside (~4.8) and outside (~2.2) of Cyclone
Noah indicated N-limitation or excess P in the system, even after normalization to respective increases.

3.1.2. Photosynthetic pigment biomarkers

The water column profiles of TChl \(a\) inside and outside of Cyclone Noah did not show significant differences except for a slight upward displacement of the DCML by ~20 m (Figure 3A). Contour plots of chlorophyll and carotenoid pigment biomarkers depict the DCML shadowing the upward displacement of isopycnal surfaces (Figures 4 and 5). Chlorophyll pigments TChl \(a\), MVChl \(a\), and DVChl \(a\), and carotenoid pigments But-fuco and Fuco were not markedly enhanced in the center of the eddy compared to surrounding waters, indicating that the standing stock of pico- and nanophytoplankton (Prochlorococcus spp. and chromophytes) only modestly increased within Cyclone Noah. Hex-fuco and But-fuco, carotenoid biomarkers for small eukaryotic phytoplankton such as prymnesiophytes and pelagophytes, respectively, increased slightly in the periphery of the center of the eddy (Figure 5A, C). Cyanobacterial pigment Zeax (biomarker for Synechococcus and Prochlorococcus spp.) was concentrated in the mixed layer above the \(\sigma_{24}\) isopycnal surface and remained constant towards the eddy center (not shown). Pigment distributions in the water column indicated that the two-layer distribution (cyanobacteria in the mixed layer and small eukaryotes and Prochlorococcus spp. occupying the DCML) was not disrupted, but displaced upwards by ~20 m.

Photosynthetic pigments were integrated to just below the 1% light level (~0.1% light level) to 110 m inside versus 120 m outside the eddy. Depth-integrated TChl \(a\) concentration was constant inside and outside of Cyclone Noah (Table 3). Most depth-integrated pigment inventories were indistinguishable inside and outside of the eddy when taking into account the high standard deviations. Hex-fuco (biomarker for prymnesiophytes) and Zeax (biomarker for cyanobacteria) dominated the fraction of xanthophyll pigments (accessory pigments that are oxidized derivatives of carotenes, present in green algae) inside Cyclone Noah. The fractions of TChl \(a\) attributed to DVChl \(a\), pigment biomarker exclusive to Prochlorococcus spp., were ~50% both inside and outside of the eddy. Pigments that were rare or below the limit of detection included Allox, DTX, Pras, Viola, and the chlorophyll degradation pigment MVChld \(a\).
3.1.3. Phytoplankton size structure

There was a modest shift in phytoplankton size structure to cells >18 µm at the base of the mixed layer in Cyclone Noah (Table 4). A ~1.3-fold increase in TChl \( a \) concentration was evident within the mixed layer, mainly attributed to flagellates 2-18 µm (e.g. nanoplankton such as pelagophytes and prymnesiophytes). An associated ~3.6-fold increase in phytoplankton >18 µm (microplankton) was most likely due to modest increases in larger eukaryotes, such as pennate diatom species.

3.1.4. Particulate matter export

The sediment trap array remained within Cyclone Noah for the entire duration of the deployment (drifter trajectories for E-Flux I are shown in Dickey et al., 2007). Particulate carbon, nitrogen, and silica exports were not significantly different inside and outside of Cyclone Noah (Table 5). Particulate phosphorus export inside Noah was 60% of that in surrounding waters, a possible indication of preferential N uptake within Cyclone Noah. Exported TChl \( a \) was higher by ~1.2-fold inside Cyclone Noah compared to outside, with concurrent increases in pigment biomarkers DTX and \( \beta \)-Car (not shown). All other exported pigments within the eddy were less than ambient waters by ~30-50%. Negligible difference in exported pigments suggests the importance of remineralization in the Cyclone Noah system.

3.2. Cyclone Opal

Cyclone Opal became visible in GOES and MODIS SST imagery on 18 February 2005, indicating that it likely spun up prior to this date on which it became visible at the surface. Cyclone Opal was approximately a month old at the time of our study (10-22 Mar 2005) and had a distinct center portion of colder temperature evident in satellite imagery. Over the course of our three-week observation, Opal drifted ~165 km (88-89 nmi) southward from its original location (~20.3°N, 156.3°W) while maintaining its physical structure and near surface tangential velocity of ~60 cm s\(^{-1}\). Opal disappeared from satellite imagery on ~25 March 2005, less than two months after it first appeared (Nencioli et al., 2007; Dickey et al., 2007). At 180-200 km in diameter, Cyclone Opal
was a stronger and larger eddy than Cyclone Noah. The dimensions of Cyclone Opal were inferred from hydrographic data, and more detail regarding horizontal and vertical dimensions of the feature is described in Nencioli et al. (2007). Doming of the isopycnals was markedly more intense, as evidenced by the shoaling of the $\sigma_{24}$ density surface (52 m in, 131 m out) and depth of the $\sim$1% light level (89 m in, 132 m out). Like Cyclone Noah, Opal was a relatively shallow feature; the cyclonic circulation was found to be insignificant at depths greater than 200 m (Nencioli et al., 2007).

### 3.2.1. Macronutrient distributions

Similar to Cyclone Noah, macronutrient concentrations reflected the shoaling of isopycnal surfaces but were much more pronounced in Cyclone Opal (Figure 2). During the initial sampling of Cyclone Opal, nitrate + nitrite was present in trace amounts (but still above the limit of detection) above the $\sigma_{24}$ isopycnal, and silicic acid concentration was below its detection limit within a confined area (~20 km) in the center portion of the eddy along the $\sigma_{24}$ isopycnal surface. Depth-integrated (0-150 m) nitrate + nitrite, phosphate, and silicic acid concentrations were higher by 4.1-, 1.8-, and 1.1-fold, respectively, compared to surrounding waters (Table 2). Si:N ratios were ~1.2 inside compared to 4.5 outside, indicating preferential N uptake in surrounding waters and near-equal uptake rates of Si and N inside the eddy. When normalized to respective increases, decreased Si:N ratios inside Opal reflected an artifact of increased N within the eddy. N:P ratios were 7.1 and 3.3, inside and outside, respectively, suggesting N-limitation for both. Individual profiles of N and P suggest the onset of seasonal P-limitation (Karl et al., 1997) due to preferential uptake of P or excess N, possibly due to increased rates of nitrogen fixation.

### 3.2.2. Photosynthetic pigment biomarkers

Depth profiles of TChl $a$ in the center portion and outside of Cyclone Opal showed a sharp and dramatic increase in TChl $a$ concentration within Opal, as indicated by a $\sim$50 m upward displacement and a marked $>2$-fold increase in the concentration at the DCML (Figure 3B). The depth of the DCML at IN stations varied dramatically during our study; however, the DCML was confined within a narrow band of isopycnal
The transient oasis surfaces $\sigma_{24.2} (\sigma_i = 24.2 \text{ kg m}^{-3})$ and $\sigma_{24.4} (\sigma_i = 24.4 \text{ kg m}^{-3})$ (Figure 3C). The DCML inside Cyclone Opal also occupied a denser isopycnal surface ($\sigma_{24.3}$) than the DCML in surrounding waters ($\sigma_{23.8}$; Figure 3C). Contour plots of chlorophyll pigments (Figure 4) mirror the doming of isopycnal surfaces, with the core TChl $a$ biomass being contained within the isopycnal surfaces $\sigma_{24.2}$ and $\sigma_{24.3}$ (Figure 4B). The TChl $a$ bloom was comprised mostly of phytoplankton containing MVChl $a$ (Figure 4D) and xanthophyll pigments Hex-fuco (prymnesiophyte biomarker), But-fuco (pelagophytes biomarker), and Fuco (diatom biomarker) (Figure 5B, D, F). Most notably, diatom pigment biomarker Fuco exhibited a $\sim$60-fold increase in the DCML in the center of Opal compared to the concentration in ambient waters. Prochlorococcus spp. (as represented by pigment DVChl $a$) did not appear to contribute to the bloom, as the highest DVChl $a$ concentrations were observed at the periphery of the TChl $a$ bloom at the Opal center (Figure 4F). Similar to Cyclone Noah, cyanobacterial pigment Zeax (biomarker for Synechococcus and Prochlorococcus spp.) was present primarily in the mixed layer above the $\sigma_{24}$ isopycnal surface (not shown). Zeax concentration did not change across the eddy, again suggesting that eddy processes do not disrupt the two-layer distribution but displace populations upwards by $\sim$50 m.

Euphotic zone depth-integrated TChl $a$ concentrations (0-110 m in and 0-150 m out; 0.1% light level) were constant in and out of Cyclone Opal (Table 3). However, MVChl $a$ comprised 66% of the TChl $a$ concentration inside the eddy as compared to 52% outside. The DVChl $a$ fraction of TChl $a$ decreased 2-fold within Opal, comprising only 27% of TChl $a$ inside the eddy compared to 47% outside. The remaining fraction (7%) of TChl $a$ was made up of the chlorophyll degradation pigment MVChld $a$, typically due to the presence of senescent diatom cells or zooplankton fecal pellets. In comparison, only 0.08% of TChl $a$ outside of Opal was comprised of MVChld $a$. This marked increase in MVChld $a$ proportion within the eddy center was due to a 9.4-fold increase in depth-integrated MVChld $a$ concentration, likely related to a 4.3-fold increase in the diatom biomarker Fuco. No associated increase was noted in Hex-fuco (prymnesiophyte biomarker), which signified that the enhancement in Fuco pigment inside Cyclone Opal was primarily attributed to the presence of large diatoms. Concurrent with the increase in Fuco was a 50% decrease in cyanobacterial pigments
Zeax, \(\alpha\)-Car, and DVChl \(a\), indicating an altered phytoplankton species dynamic in the center of the eddy.

### 3.2.3. Phytoplankton size structure

A \(\sim\)1.5-fold increase in TChl \(a\) concentration and an associated \(\sim\)1.3-fold increase in picoplankton was evident at the base of the mixed layer inside Cyclone \textit{Opal} (Table 4). Within that mixed layer community, there was a shift towards phytoplankton >2 \(\mu\)m in cell size: \(\sim\)3-fold increase in nanoplankton and a \(\sim\)7-fold increase in microplankton. Greater than 50% of the diatom community in the DCML inside \textit{Opal} was due to diatoms >18 \(\mu\)m, as represented by size-fractionated Fuco concentration. The concentration of microplankton size-fractioned pigments decreased dramatically from the center towards the edge of the eddy in Transect 6 (not shown). In contrast, DVChl \(a\), unique pigment biomarker for \textit{Prochlorococcus} spp., displayed a modest increase towards the edge of the eddy.

### 3.2.4. Time-series in Opal center

The phytoplankton community in the center of Cyclone \textit{Opal} evolved substantially over the course of 8 days (Figure 6A-D). The center station (cast 19A) during transect 3 was included in this time-series as \(t_0\) (\(t = 0\) h), and therefore the gap between \(t_0\) and IN Station 1 (\(t_1 = 58\) h) is due to lack of data, not lack of pigment. From \(t_0\) to \(t_1\), the DCML deepened in the water column from \(\sim\)50-70 m to 70-90 m, and then varied considerably during consecutive days. This variability in DCML depth can be attributed to eddy dynamics, internal tides, or inertial variability, which has a \(\sim\)31 hour periodicity (Karl et al., 2002b). The variability could have also been caused by our insufficiency in tracking the center of the fast-moving Cyclone \textit{Opal}, and hence poor positioning on the part of the ship. However, the DCML remained confined within the narrow band between isopycnal surfaces \(\sigma_{24.2}\) and \(\sigma_{24.4}\) (as indicated by dotted lines, Figure 6). Within this layer, TChl \(a\) concentration decreased dramatically after four days to half its original concentration (\(\sim\)1.1 to 0.5 mg m\(^{-3}\), Figure 6A). The decline of this phytoplankton bloom was largely due to the decrease in diatom concentration, as represented by the biomarker pigment Fuco (Figure 6B). Pelagophyte and
prymnesiophyte biomarkers But-fuco and Hex-fuco maintained the same elevated concentration throughout the eight days at the center station, representing a continuing small eukaryote-dominated bloom (Figure 6C). DVChl \(a\) concentration remained constant over time, representing the population of *Prochlorococcus* spp. over which the diatom bloom was imprinted (Figure 6D).

### 3.2.5. Suspended biogenic silica profiles

A single profile of suspended biogenic silica (BSi) was obtained both inside and outside of Cyclone Opal (Figure 7). The BSi maximum was displaced upwards from ~120 m in the surrounding waters to ~45 m within the eddy center with a ~20-fold increase compared to ambient BSi concentration.

### 3.2.6. Particulate matter export

The sediment trap array remained within Cyclone Opal throughout its deployment, staying with the eddy as it traveled southward during the study (drifter tracks are shown in Dickey et al., 2007). Particulate carbon and nitrogen exports were similar inside and outside of Cyclone Opal (Table 5). However, particulate silica export was ~4-fold higher inside Cyclone Opal. Microscopic examination of trap solution from outside Cyclone Opal showed little material whereas samples collected within Opal contained nearly empty frustules of large diatoms (Figure 8). Increased silica export within the eddy was most likely due to the export of these frustules, containing little visible chlorophyll or cellular protein.

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

4.1. Possible Si limitation

The presence of large, chain-forming diatoms in Cyclone Opal at our initial encounter was unexpected given previous findings (Olaizola et al., 1993; Seki et al., 2001; Bidigare et al., 2003; Vaillancourt et al., 2003). Furthermore, the sudden decline of diatom populations after our fourth day inside the eddy emphasizes the importance of timing in the sampling of mesoscale eddy features in the open ocean. Assuming that the diatom bloom began prior to our arrival at Cyclone Opal, it is difficult to assess the duration of the bloom. Regardless of how long the bloom lasted, we attribute physiological stress due to nutrient limitation as a possible cause of the demise of the diatom bloom.

Since silicic acid is taken up by diatoms and is essential for the formation of their cell frustules (Guillard, 1975; Brzezinski and Nelson, 1996), trace amounts of silicic acid (below the limit of detection) observed at the center of Opal in Transect 3 indicate that low silicic acid concentrations may have limited growth by diatoms. Studies have reported that ambient silicic acid concentrations of ≤1-2 µM 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 measured to be <2 µM in the euphotic zone (above 1% light level) within Cyclone Opal (Figure 9B), further suggesting that low levels of this macronutrient limited uptake by diatoms and hence growth and production. In contrast, silicic acid concentrations in Cyclone Noah (0-3 µM) did not limit uptake by phytoplankton in the euphotic zone because these populations (e.g. dominated by non-diatoms) did not require Si for growth (Figure 9A). Although low concentrations do not necessarily prove nutrient limitation, there appears to be other evidence for diatom physiological stress. Relative to outside the eddy, high levels of the chlorophyll degradation pigment MVChld \textit{a}, present in senescent phytoplankton and fecal pellets, were measured in the DCML concurrent with a 60-fold increase in Fuco pigment. Reports regarding decreased growth rate in the 50-60 m intermediate zone of physiologically unhealthy diatoms (Landry et al., 2007), distinct depths strata of senescent versus healthy cells (Brown et al., 2007), and lack of phytoplankton response to
N, P, or Fe additions (Bibby et al., 2007) within Cyclone Opal all point to Si limitation as the primary cause of the decline in diatom biomass. It is likely that the high levels of suspended particulate biogenic silica at ~50 m inside Cyclone Opal (Figure 7) was comprised of senescent, large, spiny diatoms with slow sinking rates, such as Chaetoceros spp. (Brown et al., 2007).

If silicic acid limitation accounts for the decline of the diatom populations, depletion of Si would lead to the use of a “next” limiting nutrient, for only one essential nutrient can limit growth rate at a specific time (Tilman, 1980). Nutrient addition experiments showed that phytoplankton in Cyclone Opal did not respond to N addition, whereas those in Cyclone Noah increased their photosynthetic efficiency (Bibby et al., 2007). Consequently, populations in Cyclone Noah were assumed to be N-limited while populations in Cyclone Opal were not. After the demise of the diatom bloom, sustained background population of smaller eukaryotes and cyanobacteria continued to be maintained by sufficient N and P remaining within Cyclone Opal. Therefore, the “apparent” succession from a diatom-dominated community to pico- and nanophytoplankton (Prochlorococcus spp., pelagophytes, and prymnesiophytes), as observed during the time-series at the Opal center, was likely a result of limited Si availability.

After a ‘bloom and bust’ scenario of phytoplankton with high maximum nutrient uptake rates ($V_{max}$) such as diatoms, phytoplankton with lower nutrient uptake rates (i.e. prymnesiophytes and pelagophytes) may outcompete unhealthy diatoms to dominate the phytoplankton community. 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 Si depletion (Henson et al., 2006).

Even though diatoms require Si to form frustules, several species such as Hemiaulus and Mastogloia spp. produce thinner frustules (Brzezinski and Nelson, 1996; Scharek et al., 1999a) under substrate limitation. These lightly silicified species were observed at the end of the time-series inside Cyclone Opal (Benitez-Nelson et al., 2007; Brown et al., 2007).

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 maintained by recycling. Once N reaches a minimum annual 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. Suspended particulate N was enhanced within Cyclone Opal (Mahaffey et al., 2007), markedly in the DCML, 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 (Mahaffey et al., 2007). However, increases in inorganic N (nitrate, nitrite) or N export flux was not observed, indicating a shift towards recycled production (via NH₄⁺ assimilation) and/or new production via nitrogen fixation as the primary means of N supply (Mahaffey et al., 2007).

4.2. Subtropical eddies: A silica pump?

Enhanced biological activity and a shift in size structure of the phytoplankton community to large diatoms 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 the export fluxes in Cyclone Noah did not display significant differences between inside and outside of the eddy. Despite variability in phytoplankton populations in Cyclone Opal, the presence of large, centric diatoms was an unexpected occurrence in the SNPO and enhanced rates of carbon export was expected. Several biases have been reported to be associated with sediment trap use, such as hydrodynamic flow above the trap mouth and the 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, a modest 1.3-fold increase in ²³⁴Th-derived carbon flux (Benitez-Nelson et al., 2007; Maiti et al., 2007) corresponded to trap-derived export estimates in the center of Opal. Though it can be argued that we may have missed the timely carbon export event of Cyclone Opal, we believe that the major export event had already occurred and consisted of biogenic silica. It was determined that 86% of net community production was
accumulated as total organic carbon (comprised mostly of dissolved organic carbon), leaving only ~14% to be exported (Benitez-Nelson et al., 2007), consistent with the minimal carbon export evidenced in the traps and in $^{234}$Th-derived measurements. Hence, most of the carbon generated within Cyclone Opal was remineralized and not exported.

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 it is in the SNPO (Laws et al., 2000; Benitez-Nelson et al., 2007). The absence of a major carbon flux event is likely due to strong microbial community coupling of production, microzooplankton grazing (Landry et al., 2007), and thus remineralization processes. In the case of Cyclone Opal, the minimal carbon flux was replaced by a large biogenic Si flux. Subtropical cyclonic eddies must now be re-evaluated as potential silica pumps, which would suggest that phytoplankton in the SNPO will be limited by Si following a major eddy event (Benitez-Nelson et al., 2007). The role of subtropical cyclonic eddies as Si export-producing mechanisms must be investigated in future studies.

4.3. Noah vs. Opal: The age hypothesis

Cyclones Noah and Opal are hypothesized to represent two out of three stages in a cyclonic eddy’s biological life cycle. This study depicts Cyclones Noah and Opal as two different eddies physically as well as biologically, although only about 6 weeks apart in “age.” Physical data (Kuwahara et al., 2007) as well as nutrient inventories and photosynthetic pigment distributions suggest that Cyclone Noah was indeed in the ‘decay’ stage. Cyclone Opal was a ‘mature’ eddy that began to ‘decay’ biologically after exhibiting a short-lived diatom bloom, though physically it remained a ‘mature’ eddy (Nencioli et al., 2007). Neither eddy produced enhanced carbon export, which was hypothesized to characterize the ‘decay’ stage according to the age model by Sweeney et al. (2003). Did Cyclone Noah contain a large diatom bloom like Cyclone Opal? Do all eddies develop into a fully ‘mature’ eddy with large, chain-forming diatoms? Does the
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age model, with the definition of a ‘mature’ eddy as having diatoms and a ‘decaying’ eddy as having export, apply to all eddies that spin up in the lee of Hawai‘i? Nencioli et al. (2007) hypothesized that Cyclone Opal was a completely 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 peripheral portion, along the isopycnal surfaces of \( \sigma_{23.6} \) and \( \sigma_{24.4} \). This ‘open-bottom/horizontally leaky’ eddy hypothesis accounted for additional injections of nutrients along the path of propagation, leaving a wake of increased TChl \( a \) biomass behind. Thus, they reported that the eddy’s translation speed and velocity field may significantly affect the eddy system in terms of it being closed or partially open, and in turn, its productivity. However, given that the upper water column (~70 ± 10 m) of Cyclone Opal was reported to be a closed system (Mahaffey et al., 2007) and additionally in solid body rotation (Nencioli et al., 2007), the above hypothesis still does not explain the unique phytoplankton community cultivated within Cyclone Opal and not in previously studied eddies. A closer look at recently studied cyclones Mikalele, Loretta, and Haulani (Seki et al., 2001; Bidigare et al., 2003) provided us with the following insights.

Cyclones Mikalele and Loretta (Seki et al., 2001) were ~1 month and 6 months old, respectively. Loretta first spun up at the mouth of the ‘Alenuihaha Channel and soon drifted northwestward. A few months later, Mikalele spun up in the same approximate location. During their period of observations, Loretta had been a cohesive eddy for ~6 months but still displayed significant ~2-fold increases in Fuco, But-fuco, and Hex-fuco, with outcroppings of isopycnal surfaces resembling that in Cyclone Opal (Seki et al., 2001). Loretta was ~100 km in diameter and, according to satellite imagery, it was speculated that its mature stage occurred three months prior to the observations, indicating that it was in its ‘decay’ stage at the time of encounter. Loretta was able to maintain a bloom of prymnesiophytes and pelagophytes even after 6 months as a cyclonic eddy. Cyclone 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. How was Loretta able to maintain a bloom for so long when Opal
illustrated a classic ‘bloom and bust’ situation? Why did Mikalele and Opal, both 1 month old, support such different communities of phytoplankton? Adding to the inconsistencies is Cyclone Haulani, a more recent study, which exhibited a ~25-fold increase in prymnesiophytes (mostly coccolithophores) but without large, centric diatoms (Vaillancourt et al., 2003). At 2 months old (like Cyclone Noah), Haulani’s shape alternated between circular to elliptical and back to circular within the first month, possibly due to variability in wind strength. Despite the variability, Haulani was the only cyclone studied to date that exhibited a ~2.6-fold increase in carbon export (Bidigare et al., 2003). Moreover, Haulani remained visible in satellite imagery for 3 more months after the observational period, implying that Haulani may not have been in a ‘decay’ phase. Why, then, was there carbon export in Haulani if it was not in the ‘decay’ phase? Assessment of previously studied cyclones drives us to question whether discrepancies in the biological responses of these cyclones are indeed due to age variability. No seemingly common thread runs between any of these eddies, making the attribution of these differences to age variability troublesome.

4.4. Noah vs. Opal: The ‘spin-up rate’ hypothesis

There are various factors to consider in explaining cyclone variability besides developmental stages: sampling resolution, validity of OUT stations, coastal water entrainment, trace metal effects, grazing dynamics, and the possibility of each cyclone being different water masses. The average lifespan of Hawaiian lee cyclones has been reported to be between roughly 3 and 8 months, significantly shorter than that of anticyclones, which propagate farther, generally spin more slowly than cyclones, and often last for longer than a year before it merges with surrounding waters (Patzert, 1969; Lumpkin, 1998). From this information, it can be hypothesized that anticyclones last longer than cyclones either due to slower spinning speed or because they are generally weaker in strength. Patzert (1969) reported that the distinguishing characteristic between ‘strong’ and ‘weak’ eddies was spin-up duration: a ‘weak’ eddy takes 1-2 weeks to spin up, while a ‘strong’ eddy is developed after a spin-up duration of 30 days or more. If this is the case, then ‘strong’ eddies may be “different” from ‘weak’ eddies in terms of
biological response. Hence, we speculate that spin-up duration may directly influence the type of bloom in a Hawaiian lee cyclone and consequently the type of export.

For this hypothesis to be considered, ‘spin-up duration’ must be properly defined. Spin-up duration can be defined in numerous ways - i.e., 1) the duration of upward flux of nutrients in the ‘intensification’ stage, and 2) the duration before which the potential energy of an eddy is directly proportional to the doming of the density structure (Patzert, 1969). However, for this study, the definition of ‘spin-up duration’ will simply be referred to as the time period in which isopycnal surfaces are upwardly displaced into the euphotic zone, introducing nutrients into a well-lit zone. Therefore, spin-up rate, or the rate of nutrient input into the euphotic zone, is related to wind velocity, direction, eddy shear dynamics, and circulation dynamics within the cyclone.

If spin-up rate does indeed influence the type of phytoplankton bloom and consequently export within a subtropical cyclonic eddy, then the dynamic between phytoplankton community structure and the rate of nutrient input must be closely evaluated. Regarding the paradoxical nature of closely competing phytoplankton species co-existing in a uniform body of water (Hutchinson, 1961), reports have shown that this co-existence occurs 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, and P may limit other phytoplankton. In this case, a single varying nutrient concentration could lead to a shift in phytoplankton dominance (Eppley, 1969) and thus, differences in nutrient supply could lead to the dominance of specific types of phytoplankton (Turpin and Harrison, 1979). In the case of Rossby waves, which similarly uplift isopycnals into a well-lit zone but continuously in their line of propagation, haptophytes and pelagophytes flourish because their seed populations are abundant in ambient conditions and they are smaller organisms that grow rapidly and can exploit excess (but less amounts of) N. Since the time-scale for the residence of a constantly propagating Rossby wave is relatively short, phytoplankton that are efficient at nutrient-harvesting and have a faster generation time will flourish. In nonlinear features such as cyclonic eddies, faster input of nutrients or a single large addition into the surface waters of a cyclone due to stronger, concentrated winds would provide an advantage to phytoplankton with high $V_{\text{max}}$ (diatoms) over those with lower $V_{\text{max}}$ (prymnesiophytes
and pelagophytes) (also see Brown et al., 2007). 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 (Figure 10A). Without a substantial increase in grazing by large zooplankton, remineralization processes dominate and the resultant export is opal-based 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 (coccolithophores), and as a result of altered food web dynamics due to an increase in macrozooplankton biomass, there would be an increase in organic carbon exported into the mesopelagic zone (Figure 10B).

The two scenarios illustrated above can be evidenced in cyclones we have studied to date. The fast ‘spin-up rate’ scenario was seen in Cyclone Opal, with large, rarely seen diatoms and significant opal export in place of organic carbon. Furthermore, Landry et al. (2007) reported a biologically stratified water column, in which the upper mixed zone (defined as 0-40 m) within Cyclone Opal exhibited little biomass response but significant increases in growth, grazing, and production rates of the Prochlorococcus spp.-dominated ambient community, while the lower euphotic zone (defined as 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. Another slow ‘spin-up rate’ scenario may have been seen in Cyclone Haulani, with its enhanced carbon export due to inorganic carbon (CaCO3) contained within coccolithophores, a type of prymnesiophyte commonly found in the subtropical North Pacific. In fact, coccolithophores dominated the increased prymnesiophyte biomass (25-fold) within Cyclone Haulani (Vaillancourt et al., 2003). It is also important to note that Cyclone Loretta moved northwestward quickly after formation (Seki et al., 2001). Though its translation speed and eddy velocity field is not known, we can speculate that Cyclone Loretta may have also been an ‘open-bottom/horizontally leaky’ eddy (Nencioli et al., 2007), 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
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‘spin-up rate’ hypothesis attempts to explain 1) Cyclone Opal’s large centric diatom ‘bloom and bust’ occurrence and an increased silica export, 2) the enhanced rate of carbon flux associated with increased coccolithophores in Cyclone Haulani, and 3) Cyclone Loretta’s 6-month-long sustained bloom.

In the case of Cyclone Opal as an ‘open-bottom/horizontally leaky’ eddy (Nencioli et al., 2007), 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 inside Opal can be attributed to continuous nutrient input into the center and peripheral portions of Opal due to the ‘open-bottom.’ Nevertheless, these hypotheses emphasize the uniqueness of Cyclone Opal: its size, its movement, its biological community structure, and its lack of expected carbon export. With future collaboration, qualitative measurements of ‘spin-up rate’ and numerical models of production type determined by ‘spin-up rate’ could provide further insight into investigating the various hypotheses presented in this study.

5. SUMMARY AND CONCLUSIONS

The two cyclones observed during this study, Noah and Opal, were very different eddies in terms of physical and biogeochemical attributes. Both eddies supported very different plankton communities in response to similar enhancements in euphotic-zone integrated macronutrients. While Cyclone Noah exhibited only modest increases in the ambient phytoplankton community (dominated by Prochlorococcus spp. and small eukaryotes), Opal displayed a phytoplankton bloom dominated primarily by large diatoms in the DCML. The diatom-dominated bloom in Cyclone Opal declined dramatically (as represented by a 50% decrease in Fuco) on the fourth day of our study period, which was possibly caused by silicic acid limitation. Despite the presence of a large phytoplankton bloom, enhanced rates of carbon or nitrogen export were not observed in Cyclone Opal (or in Cyclone 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.

Differences between cyclones have previously been attributed to developmental stages of cyclonic eddies; however, the characteristics of each eddy and its associated “age” are not in accordance. The characterization of Noah as being in the ‘decay’ stage and Opal in the ‘mature’ stage implies that Noah once contained large diatoms similar to that observed in Opal. In addition, only one eddy in the past, Cyclone Haulani, showed an enhancement in carbon export consistent with the hypothesis that Hawaiian lee cyclonic eddies are efficient mechanisms for transferring organic carbon to the mesopelagic zone. Thus, we hypothesize that Hawaiian lee eddies may follow different paths of development, depending on factors that affect the ‘intensification’ stage. These factors include physical processes such as wind strength, intensity of upwelling, the dynamics of surface divergence, and as hypothesized by Nencioli et al. (2007), eddy translation speeds, ambient conditions prior to eddy passage (did a warm- or cold-core feature recently pass through the path of the eddy?), and tangential velocity, all of which ultimately dictate the rate of nutrient input into the euphotic zone, and in turn, the biological response. By better determining the controls on the physical and biogeochemical life stages of cyclonic eddies, we can further 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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REFERENCES


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* TChl *a* = MVChl *a* + DVChl *a* + MVChld *a*  

Pigment description from Jeffrey and Vesk (1997)

**Table 1.** Abbreviations and taxonomic affinities of photosynthetic pigments separated in this study using HPLC. Chromophytes are defined as those microalgae that possess the accessory pigment chlorophyll *c*.  

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<table>
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<th>Cyclone <em>Opal</em></th>
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</tr>
<tr>
<td>Silicic acid (mmol Si m(^{-2}))</td>
<td>199 ± 15</td>
<td>152 ± 29</td>
</tr>
<tr>
<td>Si:N (w:w)</td>
<td>1.7 ± 0.3</td>
<td>4.3 ± 0.5</td>
</tr>
<tr>
<td>N:P (w:w)</td>
<td>4.8 ± 0.8</td>
<td>2.2 ± 0.1</td>
</tr>
</tbody>
</table>

**Table 2.** Depth (0-150 m) integrated inorganic macronutrients during E-Flux I (Cyclone *Noah*) and E-Flux III (Cyclone *Opal*). N is the number of samples averaged, and the values in columns indicate the mean ± s.d. Mean values from E-Flux I: IN samples are from IN Sta. 1-2 and the two center stations from Transect 3, OUT samples are from OUT Sta. 1-2. Mean values from E-Flux III: IN samples are from IN Sta. 2-7, OUT samples are from OUT Sta. 1-3.
## Table 3.

Depth-integrated photosynthetic pigments (mg m⁻³) during E-Flux I and E-Flux III. All pigments were depth-integrated to 0.1% light level: Cyclone Noah (110 m INSIDE, 120 m OUTSIDE), Cyclone Opal (110 m INSIDE, 150 m OUTSIDE). Numbers indicate mean (s.d.). Mean values from E-Flux I: IN samples are from IN Sta. 1-2 and the two center stations from Transect 3, OUT samples are from OUT Sta. 1-3. Averaged values from E-Flux III: IN samples are from the center station from Transect 3 and IN Sta. 1-7, OUT samples are from OUT Sta. 1-3.
Table 4. Size-fractionated TChl $a$ in and out of Cyclones *Noah* and *Opal* within and at the base of the mixed layer. %LL refers to % of irradiance assuming a 100% at the sea surface.

<table>
<thead>
<tr>
<th>Depth</th>
<th>[TChl $a$]</th>
<th>% LL</th>
<th>Total</th>
<th>0.7-2µm</th>
<th>2-18µm</th>
<th>&gt;18µm</th>
</tr>
</thead>
<tbody>
<tr>
<td>16 m</td>
<td><em>Noah IN</em></td>
<td>43%</td>
<td>90.6</td>
<td>69.5</td>
<td>13.5</td>
<td>7.5</td>
</tr>
<tr>
<td>39 m</td>
<td>11%</td>
<td>117.2</td>
<td>99.6</td>
<td>11.3</td>
<td>6.4</td>
<td></td>
</tr>
<tr>
<td>20 m</td>
<td><em>Noah OUT</em></td>
<td>43%</td>
<td>69.9</td>
<td>60.1</td>
<td>7.8</td>
<td>2.1</td>
</tr>
<tr>
<td>50 m</td>
<td>11%</td>
<td>117.5</td>
<td>102.7</td>
<td>11.6</td>
<td>3.2</td>
<td></td>
</tr>
<tr>
<td>15 m</td>
<td><em>Opal IN</em></td>
<td>43%</td>
<td>120.9</td>
<td>98.6</td>
<td>16.1</td>
<td>6.2</td>
</tr>
<tr>
<td>35 m</td>
<td>11%</td>
<td>175.3</td>
<td>120.1</td>
<td>39.5</td>
<td>15.7</td>
<td></td>
</tr>
<tr>
<td>20 m</td>
<td><em>Opal OUT</em></td>
<td>43%</td>
<td>88.5</td>
<td>75.3</td>
<td>10.2</td>
<td>3.0</td>
</tr>
<tr>
<td>55 m</td>
<td>11%</td>
<td>129.7</td>
<td>115.3</td>
<td>11.8</td>
<td>2.7</td>
<td></td>
</tr>
</tbody>
</table>
Table 5. Particulate export fluxes (± standard deviation) obtained using a sediment trap array deployed in and out of Cyclones *Noah* and *Opal*. N = sample quantity.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>IN</th>
<th>OUT</th>
<th>ANOVA*</th>
<th>N</th>
<th>IN/OUT</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Particulate Silica (mmol Si m⁻² d⁻¹)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyclone <em>Noah</em></td>
<td>0.12 (0.04)</td>
<td>0.10 (0.0)</td>
<td>p = 0.5 NO</td>
<td>3</td>
<td>1.2</td>
</tr>
<tr>
<td>Cyclone <em>Opal</em></td>
<td>0.43 (0.03)</td>
<td>0.11 (0.06)</td>
<td>p = 0.002 YES</td>
<td>3</td>
<td>3.9</td>
</tr>
<tr>
<td><strong>Particulate Carbon (mmol C m⁻² d⁻¹)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyclone <em>Noah</em></td>
<td>2.20 (0.2)</td>
<td>2.31 (0.3)</td>
<td>p = 0.6 NO</td>
<td>3</td>
<td>1.0</td>
</tr>
<tr>
<td>Cyclone <em>Opal</em></td>
<td>1.54 (0.1)</td>
<td>1.52 (0.2)</td>
<td>p = 0.9 NO</td>
<td>3</td>
<td>1.0</td>
</tr>
<tr>
<td><strong>Particulate Nitrogen (mmol N m⁻² d⁻¹)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyclone <em>Noah</em></td>
<td>0.24 (0.03)</td>
<td>0.27 (0.03)</td>
<td>p = 0.5 NO</td>
<td>3</td>
<td>0.9</td>
</tr>
<tr>
<td>Cyclone <em>Opal</em></td>
<td>0.15 (0.01)</td>
<td>0.16 (0.02)</td>
<td>p = 0.3 NO</td>
<td>3</td>
<td>0.9</td>
</tr>
<tr>
<td><strong>Particulate Phosphorus (µmol P m⁻² d⁻¹)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyclone <em>Noah</em></td>
<td>2.57 (0.3)</td>
<td>4.28 (0.7)</td>
<td>p = 0.02 YES</td>
<td>3</td>
<td>0.6</td>
</tr>
<tr>
<td>Cyclone <em>Opal</em></td>
<td>2.69 (1.0)</td>
<td>2.07 (1.1)</td>
<td>p = 0.5 NO</td>
<td>3</td>
<td>1.3</td>
</tr>
</tbody>
</table>

*Single factor analysis of variance tested whether the means are significantly different from one another with 95% confidence.
Figure 1. “Star” sampling scheme (triangles) and process stations (circles) for E-flux I (A) and III (B). Closed triangles indicate Transect 3 on which all biogeochemical samples were taken. IN (closed circles) and OUT (open circles) process stations and Transect 6 (closed squares) are denoted.
Figure 2. Depth contours of nitrate + nitrite (µM, A-B), phosphate (µM, C-D), and silicic acid (µM, E-F) in Cyclones *Noah* and *Opal* from Transect 3. Contours of isopycnal surfaces ($\sigma_t$) and crosses indicating sampling depths are overlaid on each figure.
Figure 3. Water column profiles of TChl $a$ concentration during E-Flux I (A) and III (B-C). Panel A: IN Sta. (dark triangles) are averages of IN Sta. 1 and 2, and casts 31 and 32 from Transect 3. OUT Sta. (open circles) are averages of OUT Sta. 1-3. Panels B and C show the center station from Transect 3 and first 3 IN Sta. (dark triangles), last 4 IN Sta. (open triangles), and averaged OUT Sta. ($n = 3$, open circles).
Figure 4. Depth contours of chlorophyll pigment biomarkers from Transect 3: TChl $a = \text{MVChl } a + \text{DVChl } a + \text{MVChld } a$ (mg m$^{-3}$, A-B), MVChl $a$ (mg m$^{-3}$, C-D), and DVChl $a$ (mg m$^{-3}$, E-F) in Cyclones Noah and Opal, with overlays of isopycnal surface contours. Crosses indicate the depth of sampling at each station.
Figure 5. Depth contours of carotenoid pigment biomarkers from Transect 3: Hex-fuco (mg m$^{-3}$, A-B), But-fuco (mg m$^{-3}$, C-D), and Fuco (mg m$^{-3}$, E-F) in Cyclones Noah and Opal, with overlays of isopycnal surface contours. Crosses indicate the depth of sampling at each station.
Figure 6. 8-Day time-series of photosynthetic pigments at the Cyclone Opal center (casts 19A, IN stations 1-7): TChl $a$ (mg m$^{-3}$, A), Fuco (mg m$^{-3}$, B), Hex-fuco + But-fuco (mg m$^{-3}$, C), and DVChl $a$ (mg m$^{-3}$, D). Crosses indicate depths of sampling at each station. Dotted lines indicate the location of isopycnal surfaces $\sigma_{24.2}$ and $\sigma_{24.4}$ and the gray box indicates the time lacking sampled data.
Figure 7. Depth profile of suspended biogenic silica from 0-140 m at the control station (open circles) and inside Cyclone Opal (closed triangles).
Figure 8. Microscopic images of sediment trap samples at 150 m inside and outside of Cyclone Opal. Panels A and B show nearly empty diatom frustules of an unknown species and Rhizosolenia spp., respectively, from inside Opal. Panel C shows a typical slide of waters at control stations. Images courtesy of Dr. Susan Brown.
Figure 9. Scatterplots of silicic acid and density from all samples (transect 3 and process stations) during E-Flux I (Cyclone Noah, A) and E-Flux III (Cyclone Opal, B): silicic acid concentrations in the euphotic zone (above 1% light level, closed diamonds) and below the euphotic zone (below 1% light level, open diamonds) are specified.
Figure 10. Cartoon schematics of various types of controls on the biological life cycle of a cyclonic eddy in response to faster input of nutrients (panel A) and slower nutrient input (panel B).