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## Mesozooplankton biomass and grazing responses to Cyclone *Opal*, a subtropical mesoscale eddy

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### ABSTRACT

As part of E-Flux III cruise studies in March 2005, plankton net collections were made to assess the effects of a cyclonic cold-core eddy (Cyclone *Opal*) on the biomass and grazing of mesozooplankton. Mesozooplankton biomass in the central region of Cyclone *Opal*, an area of uplifted nutricline and a subsurface diatom bloom, averaged  $0.80 \pm 0.24$  and  $1.51 \pm 0.59$  g DW m<sup>-2</sup>, for day and night tows, respectively. These biomass estimates were about 80% higher than control (OUT) stations, with increases more or less proportionately distributed among size classes from 0.2 to >5 mm. Though elevated relative to surrounding waters south of the Hawaiian Islands (Hawai'i lee), total biomass and size distribution in Cyclone *Opal* were almost exactly the same as contemporary measurements made at Stn. ALOHA, 100 km north of the islands, by the HOT (Hawaii Ocean Time-series) Program. Mesozooplankton biomass and community composition at the OUT stations were also similar to ALOHA values from 1994 to 1996, preceding a recent decadal increase. These comparisons may therefore provide insight into production characteristics or biomass gradients associated with decadal changes at Stn. ALOHA. Gut fluorescence estimates were higher in *Opal* than in ambient waters, translating to grazing impacts of  $0.11 \pm 0.02$  d<sup>-1</sup> (IN) versus  $0.03 \pm 0.01$  d<sup>-1</sup> (OUT). Over the depth-integrated euphotic zone, mesozooplankton accounted for 30% of the combined grazing losses of phytoplankton to micro- and meso-herbivores in *Opal*, as compared to 13% at control stations. Estimates of active export flux by migrating zooplankton averaged  $0.81$  mmol C m<sup>-2</sup> d<sup>-1</sup> in Cyclone *Opal* and  $0.37$  mmol C m<sup>-2</sup> d<sup>-1</sup> at OUT stations, 53% and 24%, respectively, of the carbon export measured by passive sediment traps. Migrants also exported  $0.18$  mmol N m<sup>-2</sup> d<sup>-1</sup> (117% of trap N flux) in Cyclone *Opal* compared to  $0.08$  mmol N m<sup>-2</sup> d<sup>-1</sup> (51% of trap flux) at control stations. Overall, the food-web importance of mesozooplankton increased in Cyclone *Opal* both in absolute and relative terms. Diel migrants provided evidence for enhanced export flux in the eddy that was missed by sediment trap and <sup>234</sup>Th techniques, and migrant-mediated flux was the major export term in the observed bloom-perturbation response and N mass balance of the eddy.

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### 1. Introduction

Mesoscale eddies are widespread and dynamic features of ocean circulation that impact water-column biology and biogeochemistry by altering the delivery of new nutrients to the euphotic zone (Falkowski et al., 1991; McGillicuddy et al., 1998, 1999). In oligotrophic waters around the Hawaiian Islands, for example, cyclonic (cold-core) eddies have been shown to enhance nitrate and other nutrients, nitrate assimilation, primary production, photosynthetic efficiency, chlorophyll *a* (Chl *a*), protistan abundance, biomass and growth rates, <sup>234</sup>thorium-derived rates of carbon export, as well as the catches of commercial and

recreational fisheries (Allen et al., 1996; Letelier et al., 2000; Seki et al., 2001, 2002; Bidigare et al., 2003; Vaillancourt et al., 2003; Brown et al., 2008; Landry et al., 2008; Rii et al., 2008). They also have been hypothesized to increase the overall activity of the biological pump in transferring organic C to depth (Bidigare et al., 2003) and to serve as a potential transport and retention mechanism for the recruitment of larvae to and between adjacent reef systems (Lobel and Robinson, 1986, 1988).

The present study was conducted as part of E-Flux investigations of eddies that spin up in the southeastern lee of the Hawaiian Islands (Patzert, 1969; Lumpkin, 1998; Benitez-Nelson et al., 2007). The specific feature of interest was a first-baroclinic mode eddy, Cyclone *Opal*, which appeared in satellite imagery on 18 February 2005 (Dickey et al., 2008). Cyclone *Opal* was a large mature eddy of 4–6 weeks age and 200–220 km diameter at the

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time of our study in March. Isopycnal surfaces and the nutricline were displaced upwards by 80–100 m in its center (Nencioli et al., 2008), and the lower euphotic zone (70–90 m) was dominated by a bloom of large centric diatoms (Brown et al., 2008). Phytoplankton growth rates, as well as biomass and grazing rates of heterotrophic protists, were also elevated above ambient levels in Cyclone *Opal* (Landry et al., 2008). The core region of the eddy therefore represented a strongly up-shifted ecological state relative to the oligotrophic conditions of adjacent waters, and, hence, provided a significant opportunity to assess the biomass and grazing responses of open-ocean mesozooplankton (metazoans of 0.2–5 mm) to contrasting food-web conditions.

As organisms of intermediate trophic status and size, mesozooplankton may play significant roles in transferring enhanced eddy production to higher consumers and in mediating export to depth, as rapidly settling fecal pellets (Fowler and Knauer, 1986; Small et al., 1987) or as increased migratory activity and release of metabolic by-products at depth (e.g. Isla et al., 2004; Goldthwait and Steinberg, 2008). The extent to which these roles are enhanced in eddies depends, however, on whether conditions support the accumulation of biomass or reproductive growth in excess of losses to predators. In the case of the strongly expressed diatom bloom of Cyclone *Opal*, we expected *a priori* that an elevated concentration of large cells would make the coupling between phytoplankton more efficient and therefore translate readily into greater biomass of mesozooplankton and increased herbivorous feeding, as measured by total and weight-specific estimates of gut fluorescence. In retrospect, Cyclone *Opal* exhibited surprisingly low particle export, as measured by  $^{234}\text{Th}$  and particulate carbon (PC) collections in sediment traps (Benitez-Nelson et al., 2007; Maiti et al., 2008; Rii et al., 2008). Thus, mesozooplankton contributions to grazing and active migratory flux were also considered as mechanisms that might help to explain *a posteriori* the fate of phytoplankton production in *Opal*.

## 2. Materials and methods

### 2.1. Net collections

Mesozooplankton samples were collected inside (IN) and outside (OUT) of Cyclone *Opal* with the same net system and protocols used for Hawaii Ocean Time-series (HOT) sampling at Station ALOHA (Landry et al., 2001). The rectangular net frame has a 1-m<sup>2</sup> mouth opening and is used with 0.2-mm Nitex mesh, a General Oceanics flowmeter (GO, Miami, FL) and a Brancker Model XL-200 temperature–pressure recorder (R. Brancker Research, Ottawa, Canada) to measure tow volume and depth, respectively. Net tows were taken obliquely at noon (day) and mid-night (night) from the surface to a mean maximum depth of 166 m (Std.dev. = 24 m). The mean tow duration was about 28 min (at  $\sim 1.5 \text{ km h}^{-1}$ ), and the volume of seawater filtered averaged  $1026 \text{ m}^3 \text{ tow}^{-1}$  (Std.dev. =  $126 \text{ m}^3 \text{ tow}^{-1}$ ), assuming 100% net filtration efficiency.

The collected zooplankton samples were immediately narcotized with carbonated water (Kleppel and Pieper, 1984) and subsampled with a Folsom plankton splitter. Generally, half of the tow was preserved with buffered 4% formalin. One quarter of the total sample was sorted into five size classes by gently wet sieving through nested Nitex screens of 5, 2, 1, 0.5 and 0.2 mm mesh to produce five nominal size classes of 0.2–0.5, 0.5–1, 1–2, 2–5 and >5 mm. Each size fraction of the sorted fresh subsample was concentrated on a pre-weighed 0.2-mm Nitex screen under a low vacuum, rinsed with isotonic ammonium formate solution to remove interstitial sea salt, placed flat in individual plastic Petri dishes and frozen at  $-85 \text{ }^\circ\text{C}$  for later analysis.

### 2.2. Biomass determinations

Dry weight (DW) estimates of the mesozooplankton were made for each size fraction of the net tows after the filters were subsampled for gut fluorescence. In the laboratory, the frozen filters were centered under a plastic template and sectioned into eight pie-shaped fractions with a thin knife blade. Two of the subsamples were removed from the Nitex filter and retained for replicate Chl *a* analyses (see below). The remaining 3/4 of the size fraction (= 3/16 of the original sample) was left on the Nitex and dried for at least 24 h at  $60 \text{ }^\circ\text{C}$ , then cooled to room temperature before weighing to 0.01 mg on an analytical microbalance (Denver Instrument). After subtracting the known weight of the Nitex screen, the DW of each size fraction was obtained by the appropriate multiplication factors for previous subsampling, and total mesozooplankton DW was estimated from the combined biomass values of all size fractions. Areal biomass estimates (i.e.  $\text{mg DW m}^{-2}$ ) were computed from total net sample estimates by multiplying by the factor,  $Z/V$ , which reflects the depth ( $Z$ , m) and water volume ( $V$ ,  $\text{m}^3$ ) sampled.

To assess the magnitude of phytoplankton contamination affects on the zooplankton biomass measurements, we used Chl *a* estimates from the replicate 1/8 subsamples and multiplied those times 200 to crudely account for conversions of pigment to carbon and carbon to DW. The cruise-averaged C:Chl *a* estimate from microscopy was about 70, and C:Chl *a* values more typically ranged from 30 to 60 in the depth range of highest abundance of large diatom cells (70–90 m) (S. Brown, personal communication). The multiplicative factor of 200, implying a DW:C of 2.8–4.5, therefore makes a reasonable allowance for phytoplankton mass, including some detritus and silica. Contamination estimates from these calculations were trivial, averaging 1.3% ( $\pm 0.2\%$ ) of zooplankton biomass for samples collected in the eddy and 0.5% ( $\pm 0.4\%$ ) for samples collected at control sites. Contamination estimates for the smallest size fraction (0.2–0.5 mm) were a little higher but also small, consistently less than double the estimates for the total sample. We therefore view the size-fractionation process as being relatively effective, though not perfect, in minimizing phytoplankton contamination of zooplankton biomass estimates. We report uncorrected biomass estimates here to be consistent with previous analyses of HOT zooplankton samples (e.g. Landry et al., 2001; Al-Mutairi and Landry, 2001; Sheridan and Landry, 2004).

### 2.3. Community composition

Subsamples (typically 1%) of the preserved net tows were examined microscopically in order to compare community compositions between IN and OUT stations and to previous analyses from HOT sampling at Stn. ALOHA (Landry et al., 2001). Only a few dominant taxa were identified to species. Most were grouped at the family level so that counts of 10s to 100 individuals per category were made in each sample analyzed.

### 2.4. Gut pigment estimates

Replicate ( $1/32 = 1/8 \times 1/4$ ) subsamples from the size-fractionated zooplankton tows were ground in 90% acetone with a tissue homogenizer to extract pigments. Particulate matter was removed by centrifugation, and the extract was analyzed with a Turner model TD-700 fluorometer for Chl *a* and phaeopigment (Phaeo) concentrations (Strickland and Parsons, 1972). After the fact, it was noted that a significant number of the computed Phaeo estimates were negative. In subsequent tests of the identical samples on both the new TD-700 fluorometer against a reliable

Turner 10-AU, the TD-700 performed erratically in distinguishing Chl *a* and Phaeo, even though comparable values for total pigment (Chl *a*+Phaeo) were achieved. Since it was not possible to resolve the disparate P100 Phaeo values with a simple recalibration correction, we took the total pigment estimates from these analyses as an “upper” bound to the amount of phytoplankton chlorophyll potentially in the guts of the collected animals. This overestimates true gut pigment content to the extent that at least some of the Chl *a* was present in the form of net-collected phytoplankton.

For “lower” bound estimates of gut pigment content, we conducted additional analyses on subsamples of the formalin-preserved plankton tows which had been kept in dark boxes since collection. This approach is comparable to pigment analyses from sediment traps (Head et al., 1994), which have been shown to be similar for material collected with and without preservatives in short-term trap deployments and for material preserved with formalin or mercury in both short- and long-term deployments (Landry et al., 1992). For our analyses, triplicate subsamples (approximately 1% of the total) were taken volumetrically from each well-mixed preserved sample with a calibrated large-bore pipette. Each subsample was rinsed and scanned carefully with magnifying glass to remove any residual detritus and phytoplankton. The subsamples were then filtered, homogenized and extracted in 90% acetone and analyzed on the 10-AU fluorometer. For these analyses, we used the measured Phaeo concentrations as lower bound estimates of gut pigment content, some pigment likely having been lost during preservation (e.g. regurgitation) and storage. To be strictly comparable to the total Chl+Phaeo analyses for frozen samples (above), we also did not correct the preserved Phaeo estimates for digestive degradation of Chl *a* to non-fluorescent molecules, as is generally the case in gut pigment studies (Båmstedt et al., 2000). As noted further below, pigment estimates from the fresh-frozen versus preserved sample analyses generally agreed within a factor of 2–3.

### 2.5. Grazing rates and phytoplankton impacts

Mesozooplankton grazing rates ( $G$ , mg pigment  $m^{-2} d^{-1}$ ) were estimated as  $G = GPC \times K \times 1440$ , where  $GPC$  (mg pigment  $m^{-2}$ ) is the gut pigment content integrated over the euphotic zone,  $K$  ( $min^{-1}$ ) is the gut evacuation rate constant, and 1440 extrapolates per minute to per day rates. Gut evacuation rates ( $min^{-1}$ ) were computed from the temperature-dependent relationship ( $T$ , °C) of Dam and Peterson (1988),  $K = 0.0117 + 0.001794T$ , where  $T$  is depth-averaged temperature for the euphotic zone (means = 22.4 and 24.6 °C, respectively, for IN and OUT of the eddy).

Biomass-specific rates of mesozooplankton grazing on phytoplankton (mg pigment  $mg DW^{-2} d^{-1}$ ) were calculated for the community as a whole and for individual size classes as  $G \times B^{-1}$ , where  $B$  is biomass ( $mg DW m^{-2}$ ). Lastly, we computed the daily instantaneous rate of mortality ( $d^{-1}$ ) of phytoplankton due to mesozooplankton grazing as  $G \times Chl_z^{-1}$ , where  $Chl_z$  is the depth-integrated concentration of Chl *a* in the euphotic zone ( $mg Chl a m^{-2}$ ).

As a basis of comparison to the mesozooplankton grazing estimates of phytoplankton mortality, net growth rates of the ambient phytoplankton community were determined from experimental incubations of natural seawater samples spanning the depth of the euphotic zone. As described in more detail by Landry et al. (2008), we conducted five depth profile experiments in the center region of Cyclone *Opal* (IN stations) from 16 to 21 March 2005 and three additional experiments at OUT stations from 24 to 26 March. For each experiment, water was collected from seven depths from 10 to 90–140 m, the deepest sample at the depth

corresponding to a mean of 0.5% of surface illumination. Polycarbonate bottles (2.7 or 2.2 L) were gently filled directly from the Niskin bottles using a length of silicone tubing. Each bottle was placed in a net bag and incubated *in situ* for 24 h at the depth of collection attached to a weighted line hanging from a free-drifting surface float. All experiments were started in the early morning prior to sunrise. Each bottle was sampled for Chl *a* at the beginning and end of the experiments. Net daily rates of Chl *a* growth ( $d^{-1}$ ) were computed at each depth as  $LN(Chl_{24}/Chl_0)$ , where the subscripts indicate Chl *a* concentrations at  $t = 0$  and at 24 h. Daily rates of Chl *a* change for the euphotic zone were computed similarly from depth-integrated (trapezoidal method) ratios of the final ( $t = 24$  h) to initial values of Chl *a* in the bottle incubations.

## 3. Results

### 3.1. Biomass and size structure

Mesozooplankton biomass in Cyclone *Opal* averaged about 80% higher than collections made at the control site (Fig. 1). Mid-day and mid-night averages ( $\pm$ Std.dev.) were  $0.80 \pm 0.24$  and  $1.51 \pm 0.59$  g DW  $m^{-2}$ , respectively, at IN stations and  $0.47 \pm 0.10$  and  $0.78 \pm 0.03$  g DW  $m^{-2}$  at the OUT stations. Higher variability was evident in the *Opal* tows, especially those on 20 March, which produced the lowest daytime and the highest nighttime biomass estimates in the eddy. For day and night collections considered separately, the number of tows conducted was insufficient for nonparametric testing of the statistical significance of IN–OUT station differences. However, combined day and nighttime biomass estimates in *Opal* were significantly higher than those at the OUT stations ( $p < 0.05$ , Mann–Whitney “U”-test).

IN–OUT station differences for individual size categories of the mesozooplankton were typically 1.5–2-fold higher in Cyclone *Opal* than at OUT stations, essentially following the pattern for total biomass (Fig. 2). As a consequence, combined day and night tow estimates for all size classes  $< 2$  mm were similarly different

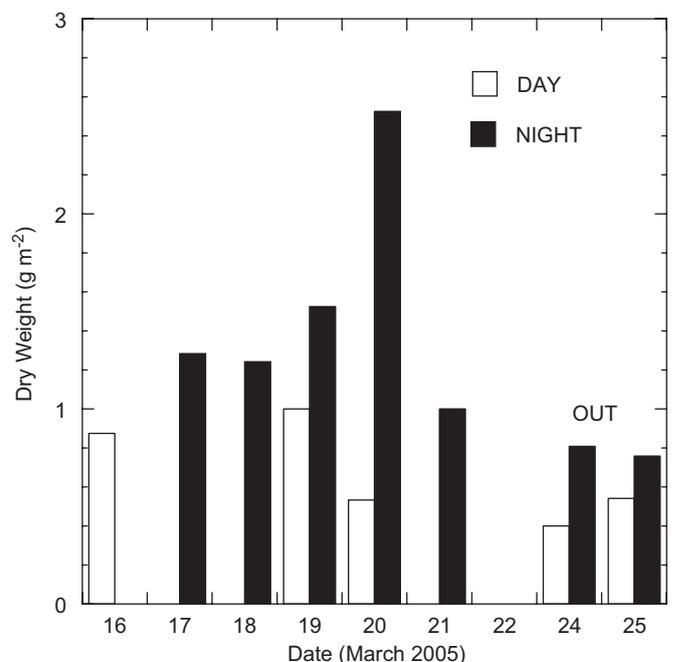


Fig. 1. Depth-integrated estimates of total mesozooplankton biomass ( $g DW m^{-2}$ ) from daytime and nighttime net tows IN (16–21 March 2005) and OUT (24–25 March) of Cyclone *Opal*.

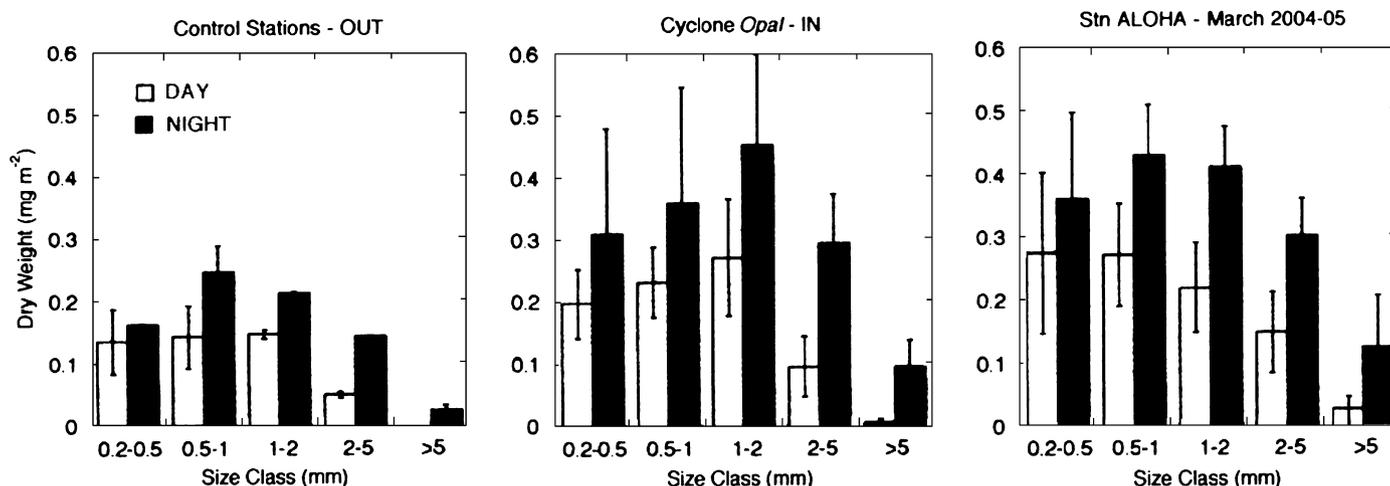


Fig. 2. Comparison of size-fractionated DW estimates from mesozooplankton collections IN Cyclone *Opal* (16–21 March 2005), at OUT controls stations adjacent to Cyclone *Opal* (24–25 March 2005) and at Stn. ALOHA during HOT monthly cruises in March 2004 and 2005 (three days and three night tows each year). All collections were made with the same net system and sample processing protocols. Error bars are standard deviations.

between IN and OUT stations ( $p < 0.05$ ). Relative to total biomass, the larger zooplankton size classes tended to be disproportionately higher in *Opal* (e.g.  $>5$  mm biomass was 3 times higher than control estimates during the day, and 4 times higher at night). Nonetheless, their combined day and night tows were not significantly different between IN and OUT stations because of the greater diel variability of the larger organisms due to vertical migrations (i.e. as evident in the biomass difference between day and night tows).

Despite the clear biomass difference between Cyclone *Opal* and adjacent control stations, there were no statistically significant differences in zooplankton biomass estimates for *Opal* versus recent March (2004 and 2005) collections at Stn. ALOHA (Fig. 2). In fact, *Opal* and Stn. ALOHA collections were quite similar in terms of mean total biomass (ALOHA day =  $0.93 \pm 0.17$  g DW  $m^{-2}$ ; night =  $1.62 \pm 0.17$  g DW  $m^{-2}$ ) as well as in the distribution of size-structured biomass. Additionally, like *Opal*, combined day–night DW estimates from Stn. ALOHA were significantly higher than those from E-Flux OUT stations with respect to total biomass ( $p < 0.01$ ) and biomass in the smaller size categories (0.2–0.5 and 0.5–1 mm; both at  $p < 0.05$ ).

### 3.2. Community composition

Despite the biomass differences between IN and OUT stations, microscopical analyses revealed similar zooplankton assemblages in most respects (Table 1). OUT stations were typical of the subtropical Pacific at Stn. ALOHA in the numerical dominance of small species of the genera *Oncaea*, *Oithona*, *Corycaeus*, *Clausocalanus*, *Lucicutia* and *Mecynocera*. In most categories, copepod abundance estimates for the OUT stations were well within a factor of 2 of mean springtime estimates at ALOHA, the main exception being the higher abundance of the carnivorous species, *Euchaeta rimana*. Abundance of the vertically migrating genus *Pleuromamma* was also higher than the mean at Stn. ALOHA, but within the range of natural variability.

Zooplankton abundances at both IN and OUT stations were strongly dominated by copepods ( $89 \pm 2\%$  versus  $87 \pm 3\%$  of the total community, respectively). Consistent with biomass differences noted above, total copepod and zooplankton abundances were higher IN Cyclone *Opal* than at the OUT stations, although the differences were negligible for some groups (e.g. *Oithona*, appendicularians) and slightly higher in OUT samples for others

Table 1

Mean ( $\pm$ Standard deviation) estimates of zooplankton community abundances from night-time net tows at stations IN ( $n = 5$ ) and OUT ( $n = 2$ ) of Cyclone *Opal*

Taxon	Abundance (individuals $m^{-2}$ )		
	IN stations	OUT stations	ALOHA
Poecilostomatoida: <i>Oncaea</i> , <i>Corycaeus</i> , <i>Copilia</i>	13000 $\pm$ 3100	7400 $\pm$ 2400	10100
Cyclopoida: <i>Oithona</i>	7800 $\pm$ 1,900	7500 $\pm$ 200	7400
Clausocalanidae: <i>Clausocalanus</i> , <i>Ctenocalanus</i>	7100 $\pm$ 1900	5100 $\pm$ 1600	5500
Lucicutiidae: <i>Lucicutia flavicornis</i>	2100 $\pm$ 870	950 $\pm$ 310	860
Mecynoceridae: <i>Mecynocera clausii</i>	1700 $\pm$ 630	900 $\pm$ 900	890
Eucalanidae: <i>Eucalanus</i> , <i>Subeucalanus</i>	1500 $\pm$ 770	100 $\pm$ 20	50
Calanidae: <i>Mesocalanus</i> , <i>Neocalanus</i> , <i>Nanocalanus</i>	880 $\pm$ 300	1000 $\pm$ 210	900
Metridiidae: <i>Pleuromamma</i>	870 $\pm$ 540	640 $\pm$ 250	320
Euchaetidae: <i>Euchaeta</i> , <i>Paraeuchaeta</i>	560 $\pm$ 230	860 $\pm$ 100	94
Total copepods (adult, copepodid)	69000 $\pm$ 18000	48000 $\pm$ 12000	
Appendicularians	3600 $\pm$ 1500	3400 $\pm$ 690	
Ostracods	2100 $\pm$ 540	1600 $\pm$ 120	
Chaetognaths	1200 $\pm$ 600	760 $\pm$ 300	
Pteropods	860 $\pm$ 840	710 $\pm$ 490	
Higher crustacea (euphausiids, decapods)	600 $\pm$ 110	490 $\pm$ 200	

Italics give the major genera or species contributing to the category. Estimates of copepod abundances from Stn. ALOHA are geometric means ( $n = 6$ ) of spring-collected samples from 1994 to 1996 (from Table 7; Landry et al., 2001).

(e.g. Calanidae, Euchaetidae). Euphausiids in the eddy were notably larger than at OUT stations, and more subtle differences in organism sizes for other taxa may have contributed, in addition to abundance, to the greater biomass at IN stations.

Since most taxa were at least somewhat more abundant in Cyclone *Opal* compared to OUT stations, the general impression is one of a broad zooplankton community increase, which is consistent with the observed biomass differences across all size classes (Fig. 2). The microscopical comparison does, however, reveal that large suspension feeders of the family Eucalanidae were found at much higher densities in *Opal* than in OUT samples or in previous collections at Stn. ALOHA (Table 1). Most of these enumerated animals were subadults and could not be assigned to species. About half of the adults were large animals of the *Eucalanus hyalinus* group, most likely *E. spinifera* according to the recent taxonomic revision and biogeographic analysis of Goetze (2005). A smaller species, likely *Subeucalanus subtenuis*,

co-dominated at the IN stations, and at least two more species were also present, one closely resembling *S. subcrassus*. It is not known whether these animals grew to high abundance (i.e. were selected for) as a response to the eddy-stimulated phytoplankton bloom, or if they were simply present in unusually high numbers (i.e. disproportionate seeding) when the eddy formed. These alternative mechanisms could also be linked if eddy-stimulated bloom activity is an important dimension of the trophic ecology of this copepod group, leading to their high abundances as a normal condition in the Hawaii lee region.

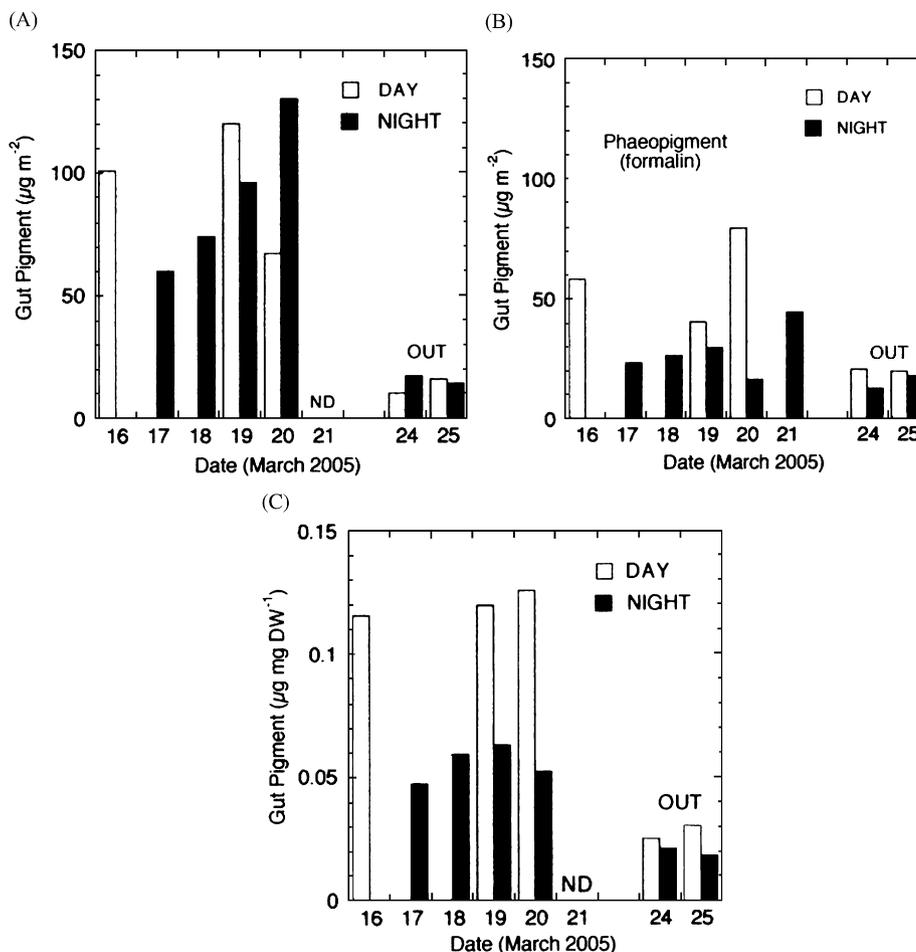
Eucalanidae were present in comparable numbers in day and night samples examined, as were small copepods, *Euchaeta* spp., appendicularians and chaetognaths. Strong migratory taxa, defined as those that are virtually absent from the euphotic zone in daytime tows, were similar to those described by Al-Mutairi and Landry (2001). *Pleuromamma* spp. were numerical dominants among a suite of migrant copepods and ostracods in the <2-mm size fractions. Euphausiids, shrimp and an occasional mesopelagic fish comprised the larger-size fractions.

### 3.3. Gut fluorescence

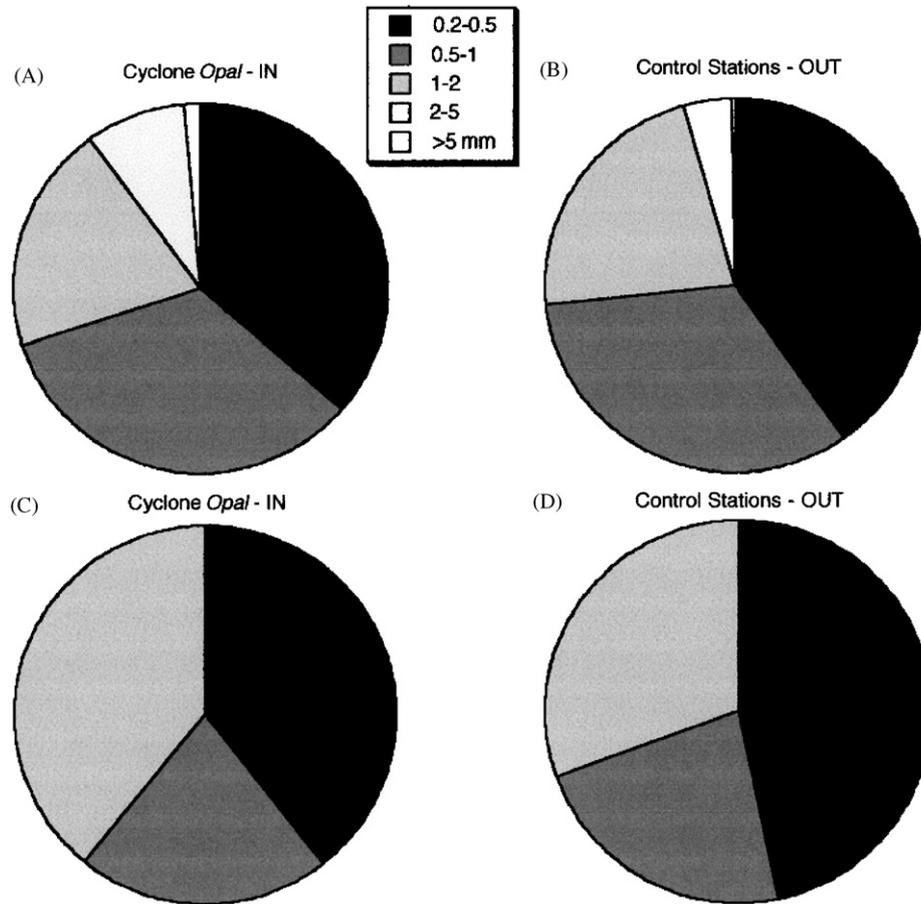
Estimates of mesozooplankton gut fluorescence averaged 4–7 times higher in Cyclone *Opal* than at control stations (Fig. 3). The

higher IN:OUT ratios came from analyses of total of Chl *a* plus Phaeo on freshly collected, frozen samples (day:  $96 \pm 27$  versus  $13 \pm 4 \mu\text{g pigment m}^{-2}$  for IN and OUT tows, respectively; night:  $90 \pm 31$  versus  $15 \pm 2 \mu\text{g pigment m}^{-2}$ ). The lower ratios came from analyses of Phaeo from formalin-preserved subsamples (day:  $44 \pm 16$  versus  $9 \pm 1 \mu\text{g pigment m}^{-2}$  for IN and OUT tows; night:  $38 \pm 10$  versus  $11 \pm 5 \mu\text{g pigment m}^{-2}$ ). Combined day–night estimates were significantly higher for *Opal* compared to control stations for both fresh ( $p < 0.01$ ) and preserved analyses ( $p < 0.05$ , Mann–Whitney “U”-test). Analyses of fresh and preserved subsamples did not give statistically significant differences for zooplankton collected at the control stations, but for Cyclone *Opal* collections, the 2-fold higher estimate for fresh analyses was significant at  $p = 0.01$  (paired *t*-test). In addition, weight-specific estimates of gut fluorescence were significantly elevated in *Opal* relative to controls ( $p < 0.01$  for fresh analyses, Fig. 3;  $p < 0.05$  for preserved, not shown; Mann–Whitney “U”-test).

Irrespective of the type of gut pigment analysis, each zooplankton size fraction had significantly higher gut pigment contents at IN versus OUT stations ( $p < 0.01$  for the three size classes <2 mm;  $p < 0.05$  for the two fractions >2 mm). Gut pigments were highest among the smaller size classes of mesozooplankton, with the 0.2–0.5 and 0.5–1 mm size fractions accounting for about 70% of the measured fluorescence in fresh



**Fig. 3.** Gut pigment estimates for mesozooplankton collected during daytime and nighttime net tows IN and OUT of Cyclone *Opal*. Left upper panel gives depth-integrated estimates ( $\mu\text{g pigment m}^{-2}$ ) based on total pigments (Chl *a*+phaeopigments) analyzed from freshly collected, flash-frozen samples. Right upper panel gives depth-integrated estimates of gut phaeopigment from formalin-preserved samples. Lower panel presents total gut pigment (Chl *a*+phaeopigments, frozen samples) as  $\mu\text{g Chl mg}^{-1}$  DW mesozooplankton.



**Fig. 4.** Size-distribution of gut pigment estimates for mesozooplankton collected IN and OUT of Cyclone *Opal*. Upper panels are size distributions for total pigments (Chl *a*+phaeopigments) analyzed from freshly collected, flash-frozen samples. Lower panels are gut phaeopigment distributions from formalin-preserved samples (0.2–2 mm size fractions only). Day and night samples are averaged in this figure to represent mean estimates over a 24-h day.

**Table 2**

Biomass, gut fluorescence and grazing estimates from mesozooplankton net collections in Cyclone *Opal* and at control (OUT) stations during March 2005

Date/time	D/N	Chl <i>a</i> (mg m <sup>-2</sup> )	Biomass (g DW m <sup>-2</sup> )	Gut pigment (μg Chl <i>a</i> g DW <sup>-2</sup> )		Grazing impact (d <sup>-1</sup> )		
				Fresh	Preserv	Fresh	Preserv	
IN Cyclone <i>Opal</i>								
16 March	1220	D	31.0	0.87	116	58	0.28	0.13
17 March	0000	N	34.5	1.28	47	23	0.14	0.07
18 March	2200	N	27.5	1.24	59	26	0.22	0.09
19 March	1220	D	28.9	1.00	120	40	0.37	0.11
20 March	0000	N	30.2	1.52	63	29	0.27	0.12
20 March	1200	D	26.4	0.53	126	79	0.21	0.13
20 March	2200	N	24.0	2.52	52	16	0.52	0.13
21 March	2200	N	25.0	1.00	ND	44	ND	0.14
OUT stations								
24 March	1220	D	26.0	0.40	25	20	0.03	0.03
25 March	0000	N	27.0	0.81	21	12	0.05	0.03
25 March	1200	D	26.3	0.55	30	19	0.05	0.03
26 March	0000	N	25.6	0.76	18	17	0.04	0.04

D/N = day or night tow. Pigment and grazing estimates are for analyses based on total Chl *a* and Phaeo from fresh frozen subsamples (fresh) and for Phaeo only from zooplankton subsamples preserved in formalin (preserv).

sample analyses (Fig. 4). Larger zooplankton (>2 mm) accounted for <5% of gut pigments at the control stations but increased disproportionately to about 9% in Cyclone *Opal*. Among the three size categories that can be compared between fresh and preserved analyses, gut fluorescence in the 1–2-mm fraction increased from

21% (fresh) to 35% (preserved) of the total, while the 0.5–1-mm fraction decreased from 33% to 22%. These shifts may reflect differences in sieve retention efficiencies for formalin-hardened animals and/or better removal of pigment containing phytoplankton debris from the smaller fractions.

**Table 3**

Depth range, initial chlorophyll and depth-integrated net rates of chlorophyll change for 24-h *in situ* bottle incubations conducted on drift arrays in Cyclone *Opal* and at adjacent control (OUT) stations

Date	Integration depth (m)	Initial Chl <i>a</i> (mg m <sup>-2</sup> )	Net growth rate (d <sup>-1</sup> )
IN Cyclone <i>Opal</i>			
16 March	90	25.6	0.15
17 March	120	32.1	0.09
18 March	110	23.0	0.32
20 March	110	28.0	0.27
21 March	90	20.9	0.06
OUT stations			
24 March	140	24.2	0.14
25 March	140	25.1	0.13
26 March	130	25.6	0.14

### 3.4. Grazing impact

Grazing impact estimates from the gut pigment analyses in Cyclone *Opal* averaged  $0.29 \pm 0.12$  d<sup>-1</sup> for fresh and  $0.11 \pm 0.02$  d<sup>-1</sup> for preserved samples (Table 2). Comparable estimates for the control stations were  $0.04 \pm 0.008$  and  $0.03 \pm 0.007$  d<sup>-1</sup>. Based on 24-h experimental incubations on *in situ* drift arrays, net growth rates of Chl *a* for the depth-integrated euphotic zone averaged  $0.18 \pm 0.11$  d<sup>-1</sup> in *Opal* and  $0.14 \pm 0.008$  d<sup>-1</sup> at OUT stations (Table 3). Lower (preserved) and upper (fresh) estimates of mesozooplankton grazing can therefore account for the utilization of 62–160% of net phytoplankton growth in Cyclone *Opal*, but only 22–29% at control stations.

## 4. Discussion

### 4.1. Mesozooplankton biomass response

Relative to adjacent control stations, mesozooplankton biomass was significantly elevated in the central region of Cyclone *Opal* by a mean factor of 1.8 (1.7 in day samples; 1.9 at night), and the effect was more or less evenly distributed across size categories. Zooplankton enrichment effects of comparable magnitudes have been reported for previous studies of mesoscale eddies (e.g. Fossheim et al., 2005; Riandey et al., 2005; Goldthwait and Steinberg, 2008), but the mechanisms can be quite different and difficult to compare. For example, anticyclonic eddies with enhanced zooplankton in the Bay of Biscay (Isla et al., 2004) appear to originate as advective rings shed from poleward currents on the Spanish slope (Fernandez et al., 2004). Advective processes involving coastal filaments also strongly contribute to biomass patterns associated with well-studied eddies off the Canary Islands, where anticyclones entrain and concentrate zooplankton from chlorophyll-rich island waters while divergent flows in downstream cyclonic eddies lead to reduced zooplankton biomass (e.g. Hernandez-Leon et al., 2001; Almeida et al., 2002). Previous studies have further shown that shear zones on the outer periphery of mesoscale eddies can be regions of increased biological activity and zooplankton concentration (Riandey et al., 2005; Goldthwait and Steinberg, 2008). We did not, however, look for such effects as part of this study.

The elevated concentration of zooplankton in the center of *Opal*, an area of about 30-km diameter with high diatom biomass (Brown et al., 2008), could reasonably have occurred due to growth over the course of days to weeks prior to our sampling. Phytoplankton biomass and production in this central region were

both higher than control sites by a factor of 2 (Benitez-Nelson et al., 2007), and small zooplankton with adequate food are capable of growth rates of half to one doubling of biomass per day at subtropical temperatures (Huntley and Lopez, 1992; Hirst and Sheader, 1997). Nonetheless, according to the “open-bottom, horizontally leaky” hypothesis of Nencioli et al. (2008), lateral flow may have occurred along isopycnal surfaces as Cyclone *Opal* moved southward over the course of our study (mean translational speed  $\sim 8$  km d<sup>-1</sup>; Dickey et al., 2008). While we regard passive accumulation as an unlikely explanation for the bulk of the increased biomass in Cyclone *Opal*, it is possible that some zooplankton were attracted to the high food concentration in the eddy center and aggregated there as result of advective or random-encounter processes.

The similarity between mesozooplankton biomass in Cyclone *Opal* and the monthly mean at HOT Stn. ALOHA is an intriguing result that emphasizes both the difficulty of defining appropriate reference controls for eddy comparisons as well as potentially subtle effects of water-column production processes on zooplankton responses. With regard to the first point, Goldthwait and Steinberg (2008) observed that eddy effects on zooplankton biomass in the subtropical Atlantic were clearer in comparison to the long-term summer mean at the BATS sampling station and more difficult to distinguish from contemporaneous collections at adjacent “control” stations. They attributed this result to the complexities of eddy-eddy interactions and edge effects in their study region and took the BATS sampling mean as their most appropriate reference for comparative purposes. In the present study, all of our stations were located to the south and on the eastern edge of the Hawaiian Island archipelago while Stn. ALOHA is located 100 km north of the central island. We thus interpret the biomass differences between Stn. ALOHA and OUT controls as reflecting different conditions north and south of the islands or perhaps a more gradual north-south gradient in zooplankton stocks (e.g. Hayward and McGowan, 1985). Either way, we view OUT controls south of the islands as the appropriate basis of comparison for eddy effects in our study region.

Of relevance to all of the data comparisons, there has been a gradual secular increase in mesozooplankton biomass at Stn. ALOHA since net collections began in 1994. Recent daytime estimates are approximately double what they were a decade ago (Sheridan and Landry, 2004). The earlier estimates (e.g. Landry et al., 2001) are in fact comparable both in total biomass and size distribution to contemporary OUT controls of the present study, even as recent ALOHA estimates resemble the enriched zooplankton stocks in Cyclone *Opal*. The ALOHA doubling has occurred without the dramatic contrast of IN-OUT station differences in production and diatom standing stocks of our present study, but with an apparently more subtle but effective stimulation of lower trophic level production processes by enhanced summertime diazotrophy (Karl et al., 1997; Fennel et al., 2002), decreased stratification and winter-spring nutrient mixing, or perhaps a combination of both. Enhanced production at Stn. ALOHA is evident in small ( $\sim 20\%$ ) but significant increases in <sup>14</sup>C-labelled uptake and particulate nitrogen export flux to sediment traps (Corno et al., 2007), but the effect is apparently amplified for zooplankton by as yet poorly resolved food-web processes.

### 4.2. Grazing inferences from gut fluorescence

Despite relatively high concentrations of Chl *a* (up to 1 mg m<sup>-3</sup>) in the diatom-dominated lower euphotic zone (70–90 m) of Cyclone *Opal*, the much deeper photic zones of control stations contained almost as much depth-integrated Chl *a* as the eddy

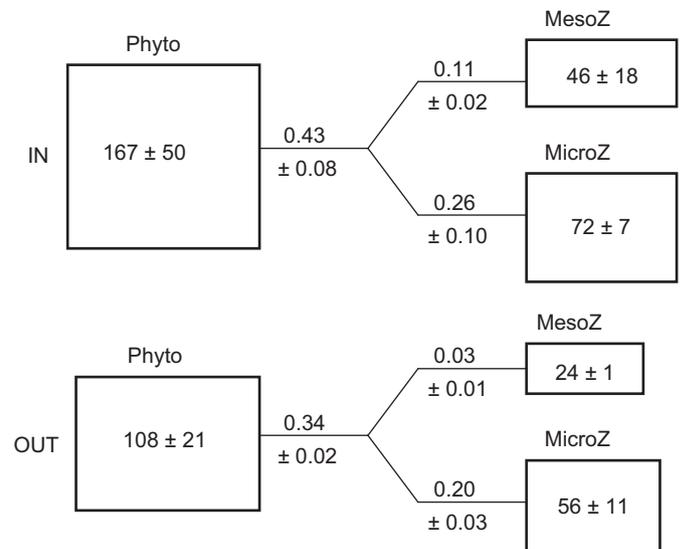
(Tables 1 and 2; Rii et al., 2008). As a consequence, the observed differences in gut pigment content of mesozooplankton IN and OUT of the eddy are mostly attributable to increases in total biomass of zooplankton and in weight-specific Chl *a* consumption, rather than an increase in total Chl *a*. The zooplankton biomass response to elevated food concentration in *Opal* accounts for a factor of 1.8 increase in gut fluorescence  $m^{-2}$ , assuming a proportional increase in suspension feeders. The weight-specific effect accounts for a factor of 2.3 (preserved) to 3.5 (fresh) increase in gut fluorescence. This latter effect is presumably due to a larger fraction of the total Chl *a* residing in large cells that are more accessible to meso-sized grazers. For example, approximately 56% of the depth-integrated phytoplankton carbon in Cyclone *Opal* was attributable to diatoms, compared to only 3% at control stations (Landry et al., 2008). The present estimates of eddy enhancement of zooplankton gut fluorescence are consistent with previous reports of 2- to several-fold effects for individual grazers (e.g. Yebra et al., 2004; Goldthwait and Steinberg, 2008), but they are on the higher end of the range for the zooplankton community as a whole due to the magnitude of *Opal*'s effect on phytoplankton size structure.

Cyclone *Opal*'s effect on mesozooplankton grazing should roughly scale with gut fluorescence. The data therefore suggest an eddy enhancement of relative grazing impact on phytoplankton of 6–7-fold for analyses based on fresh samples and 3.5–5-fold for analyses of preserved samples. The former likely contain some Chl *a* contamination of the sized-fractionated net collections from large phytoplankton, and therefore might exaggerate relative grazing in the eddy. The latter were more scrupulously scanned to remove contaminants, but the zooplankton may have lost some gut content to regurgitation, egestion or pigment degradation in the fixation process. Given the vagaries of these methods, it is reassuring that they produce values that generally agree within a factor of 2–3, and even better for control stations.

In applying gut fluorescence estimates to grazing rate assessments, we made no correction for digestive degradation of chlorophyll to non-fluorescent by-products. Literature estimates for pigment loss range from 0% to 100% of ingested chlorophyll (Conover et al., 1986; Lopez et al., 1988; Penry and Frost, 1991; Head and Harris, 1992; Mayzaud and Razouls, 1992), and field studies typically use a multiplication factor of 1.5 to correct gut fluorescence measurements for an assumed mean pigment recovery efficiency of  $\sim 70\%$  (Båmstedt et al., 2000). Gut fluorescence measurements could also be low if capture stress reduced feeding or increased the rate of defecation. While the net effect of these factors (preservation, digestive degradation and capture stress) is to make our estimates of gut fluorescence likely conservative measures of the standing stocks of recently consumed phytoplankton, this is partly offset by the use of a relatively high estimate of gut turnover rate, which translates to mean hourly rates of 3.1 and 3.3  $h^{-1}$  for IN and OUT stations, respectively. These rates are about 50% higher than experimentally measured estimates in the Equatorial Pacific (2.1–2.3  $h^{-1}$ ; Zhang et al., 1995; Rollwagen Bollens and Landry, 2000). Thus, the same grazing impact estimates would be achieved if we corrected 50% for pigment degradation and used the lower gut turnover estimates.

#### 4.3. Mesozooplankton grazing and the fate of phytoplankton production

The experimental incubations conducted on drift arrays included diluted as well as natural seawater treatments and therefore lend themselves not only to assessments of the daily net changes of phytoplankton stocks (Table 2), but to instantaneous



**Fig. 5.** Summary of biomass, phytoplankton growth and grazing processes in Cyclone *Opal* (IN) and at control sites (OUT). Box size is scaled to biomass estimates, which are given inside (mean  $\pm$  Std.dev.) in units of  $mmol C m^{-2}$ . Rate estimates ( $d^{-1}$ ) between boxes are phytoplankton community growth rate ( $\mu$ ) and grazing mortality impacts ( $g_{micro}$  and  $g_{meso}$ ) of micro- and mesozooplankton feeding on phytoplankton. Phytoplankton and microzooplankton biomass and microzooplankton grazing rates are from Landry et al. (2008). All estimates are depth-integrated values for the euphotic zone.

rate estimates of phytoplankton growth and microzooplankton grazing by the dilution method (Landry et al., 2008). Since these experiments were designed to span the depth range of the euphotic zone to about 0.5% incident surface light, the rate results can all be expressed in terms of depth-integrated Chl *a* and compared directly to mesozooplankton grazing estimates from our integrated net tows.

The summary of these results in Fig. 5 indicates that microzooplankton grazing dominated as the main source of phytoplankton mortality IN and OUT of Cyclone *Opal*. However, the micro- and mesozooplankton components of grazing were more equal in the eddy than in the ambient waters, as might be expected by the shifted size structure of the phytoplankton community. Within measurement errors, grazing losses to combined micro- and meso-herbivory are in balance with phytoplankton growth in Cyclone *Opal*. The difference of  $0.06 d^{-1}$  would also be eliminated if we used fresh estimates of gut fluorescence as the basis for grazing rate estimates, rather than the more conservative preserved estimates. In contrast, a grazing balance cannot be argued for the OUT stations, where the measurement errors and the difference between fresh and preserved gut analyses are both substantially smaller.

Despite the reasonably closed growth-grazing budget for Cyclone *Opal* based on bottle incubations and net collections (Fig. 5), grazing processes per se do not account for a 2-fold decrease in phytoplankton biomass observed in the eddy center over the course of our study (Brown et al., 2008; Landry et al., 2008) or for the lack of a response in particulate carbon export as measured by sediment traps or  $^{234}Th$  (Benitez-Nelson et al., 2007). The former represents an unexplained imbalance of loss over production of about  $0.1 d^{-1}$  averaged over the euphotic zone and the course of a week. The latter should have scaled with increasing mesozooplankton biomass or grazing if their fecal pellets made a major contribution to export.

Physiological death, observed as a layer of senescent and decaying diatoms at 50–60 m in microscopical analyses (Brown et al., 2008), may have played a role in the decline of the

phytoplankton stock, with much of the reduced particulate biomass accumulating in the dissolved organic pool (Benitez-Nelson et al., 2007). Since most of the mesozooplankton grazing occurred in smaller size classes, it is also reasonable to assume that much of their egested material sank slowly enough to degrade and recycle within the euphotic zone (e.g. Paffenhöfer and Knowles, 1979; Hofmann et al. 1981). Still, we can take these arguments only so far in explaining the export paradox of Cyclone *Opal* as it would seem quite unusual for biomass and activity increases in all components of the food web from phytoplankton to mesozooplankton to occur without at least a *proportional* increase in carbon export.

In this regard, Nencioli et al. (2008) have advanced the hypothesis that some of the export may have occurred in horizontal (leaky) flow along isopycnal surfaces in the lower euphotic zone (70–90 m) as the eddy moved. Such a mechanism would produce a broad and dilute trail of export in the eddy's wake that would have been difficult to sample by sediment traps captured in the eddy's moving frame of reference. Nonetheless, the exported material would presumably have left a measurable signal in  $^{234}\text{Th}$ : $^{238}\text{U}$  deficiency in the overlying waters, and that was not observed (Maiti et al., 2008).

#### 4.4. Vertical migration and active export

Previous studies have shown an elevated intensity of diel vertical migrations associated with eddy features, suggesting that the release of metabolic products by migratory animals at depth could be a major contributor to enhanced biological pump activity in such systems (Isia et al., 2004; Almeida et al., 2005; Goldthwait and Steinberg, 2008). Given the lack of a demonstrable eddy effect on sediment trap and  $^{234}\text{Th}$ -based estimates of passive export flux in Cyclone *Opal* (Benitez-Nelson et al., 2007), active migrant flux is therefore an alternate route by which eddy-enhanced production could have made its way out of the euphotic zone.

To assess the magnitude of this contribution to total export in *Opal*, we estimated active export using the approach of Al-Mutairi and Landry (2001). Migratory biomass was defined as the difference between day and nighttime estimates of biomass in each size fraction (Fig. 1). Average DW values for animals within each specific size class were determined from previous size-fractionated samples collected at Stn. ALOHA ( $n = 144$  samples per size class from monthly samples over 3 years; Landry et al., 2001). Metabolic rate estimates were based on equations for oxygen respiration and nitrogen excretion as a function of animal DW and temperature from Ikeda (1985), where temperature was taken as the depth-integrated average from 300 to 500 m and oxygen respiration was converted to carbon equivalents assuming a respiratory quotient of 0.8 (largely protein diet). The latter assumption is consistent with the observation that gut pigment estimates per unit biomass were substantially higher during the daytime than when migrants entered surface waters at night (Fig. 3); hence, herbivorous feeding appears mostly attributable to non-migrants. To be consistent with published estimates of migrant flux, we further assumed that 24% of the carbon (DOC excreted+ $\text{CO}_2$  respired) released at depth was in the form of organic excretion, and 53% of the nitrogen was released as organics (Eppley et al., 1973; Le Borgne and Rodier, 1997; Steinberg et al., 2000, 2002; Al-Mutairi and Landry, 2001).

Migrant fluxes calculated in this manner averaged  $0.81 \pm 0.74 \text{ mmol C m}^{-2} \text{ d}^{-1}$  in Cyclone *Opal* and  $0.37 \pm 0.05 \text{ mmol C m}^{-2} \text{ d}^{-1}$  at OUT stations (Table 4). These values represent 53% of the passive C flux in *Opal* and 24% at OUT stations as measured by sediment traps (Benitez-Nelson et al., 2007; Rii et al., 2008). Because of the similarity of day–night mean biomass estimates

**Table 4**

Comparison of active and passive estimates of export flux from Cyclone *Opal* IN and OUT stations and Stn. ALOHA (March 2004–2005)

Parameter	IN stations	OUT stations	Stn. ALOHA
Migrant biomass ( $\text{mg DW m}^{-2}$ )	711 ± 594	309 ± 32	692 ± 190
Carbon export ( $\text{mmol C m}^{-2} \text{ d}^{-1}$ )			
Active (migrants)	0.81 ± 0.74	0.37 ± 0.05	0.80 ± 0.24
Passive (traps)	1.54 ± 0.11	1.52 ± 0.20	2.72 ± 0.04
Nitrogen export ( $\text{mmol N m}^{-2} \text{ d}^{-1}$ )			
Active (migrants)	0.18 ± 0.17	0.08 ± 0.01	0.17 ± 0.05
Passive (traps)	0.15 ± 0.01	0.16 ± 0.02	0.34 ± 0.17
N mass balance	0.42 ± 0.13	0.21 ± 0.07	

Active export fluxes are computed from size-fractionated estimates of migrant biomass (night tows–mean daytime) according to Al-Mutairi and Landry (2001). For IN–OUT stations, estimates of passive particulate export to sediment traps and N mass balance are from Benitez-Nelson et al. (2007). Passive trap fluxes at Stn. ALOHA are from the HOT Program data site ([http://hahana.soest.hawaii.edu/hot/hot\\_jgofs.html](http://hahana.soest.hawaii.edu/hot/hot_jgofs.html)).

and size structure for *Opal* and Stn. ALOHA collections, contemporaneous estimates of migrant flux at ALOHA ( $0.80 \pm 0.24 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ) were virtually identical to those in the eddy. They differ, however, in terms of the relative contributions of active to passive fluxes because trap fluxes at Stn. ALOHA are approximately double those measured in *Opal*. In relative terms, the OUT controls and Stn. ALOHA are similar, the OUT stations having approximately half the mesozooplankton biomass, half the migrant flux and half the passive sediment trap flux as ALOHA. Consequently, the percentage of active to passive C flux at the OUT stations is similar to the 20% average estimate for Stn. ALOHA (Al-Mutairi and Landry, 2001). In comparison, the much higher percentage in Cyclone *Opal* appears to indicate a non-equilibrium condition where passive flux remained similar to that in the parent water (i.e. OUT controls) while active flux increased in response to the eddy enhancement of plankton biomass.

As in previous observations at Stn. ALOHA (Al-Mutairi and Landry, 2001), migrant export of nitrogen in the present study was higher than carbon in relation to their respective elemental fluxes by passive sinking (Table 4). For IN stations, migrants exported  $0.18 \pm 0.17 \text{ mmol N m}^{-2} \text{ d}^{-1}$ , which is equivalent to 117% of the measured trap flux ( $0.15 \pm 0.01 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ). For the OUT stations, active export by migrants was  $0.08 \pm 0.01 \text{ mmol N m}^{-2} \text{ d}^{-1}$ , or 51% of trap flux ( $0.16 \pm 0.02 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ). According to these estimates, migrating zooplankton accounted for 43% of the total export of N ( $0.42 \pm 0.13 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ) from Cyclone *Opal* based on  $^{15}\text{N}$  mass balance calculations (Benitez-Nelson et al., 2007; Mahaffey et al., 2008), and 38% of total N export ( $0.21 \pm 0.07 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ) at the OUT stations. Measurement uncertainties for the flux estimates are substantial, and they may not fully account for spatial variability within the eddy or the differing times scales of the processes involved. Nonetheless, it is notable that the sums of active and passive export processes (IN =  $0.33 \pm 0.18 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ; OUT =  $0.24 \pm 0.03 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ) agree reasonably, ( $\pm$  measurement errors) with the inferences from N mass balances. Thus, at least at the time of our study, the flux response to the nutrient infusion and phytoplankton bloom in Cyclone *Opal* was mainly evident as an increase in zooplankton biomass and active migration, rather than the passive sinking export of particles. Since larger zooplankton and migrating mesopelagics were no doubt undersampled by our small, slowly towed net, a full accounting of the active migrants could likely come closer to resolving the export balance of Cyclone *Opal*.

## 5. Conclusion

Previous studies have shown positive, but variable, effects of eddy-stimulated production on mesozooplankton biomass and gut fluorescence. It is not surprising, therefore, that significant and substantial responses were found for both parameters in the well-developed phytoplankton bloom of Cyclone *Opal*. Within the broader context of experimental studies of phytoplankton growth, microzooplankton grazing and export, the roles and importance of mesozooplankton in trophic interactions were enhanced in Cyclone *Opal* both in absolute and relative terms compared to control sites. The mesozooplankton contribution to combined meso- and micro-herbivory increased from 13% in the ambient environment to 30% in *Opal*. The increased abundance and biomass of diel migratory zooplankton also provide evidence of enhanced export flux in the eddy that was not accounted for by sediment trap and  $^{234}\text{Th}$  techniques. Estimates of migrant-mediated export of N in Cyclone *Opal* exceed those from passive trap collections, making active flux a dominant export term in the N mass balance of the eddy, as well as the major observed export response to the *Opal* bloom perturbation on the time scale of our study.

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## References

- Allen, C.B., Kanda, J., Laws, E.A., 1996. New production and photosynthetic rates within and outside a cyclonic mesoscale eddy in the North Pacific Subtropical Gyre. *Deep-Sea Research I* 43, 917–936.
- Almeida, C., Aristegui, J., Gomez, M., Hernandez-Leon, S., Portillo-Hahnefeld, A., Rodriguez, J.M., 2002. Zooplankton biomass and indices of feeding and metabolism in relation to an upwelling filament off Northwest Africa. *Journal of Marine Research* 60, 327–346.
- Almeida, C., Hernandez-Leon, S., Yebra, L., 2005. Vertical distribution of zooplankton and active flux across an anticyclonic eddy in the Canary Island waters. *Deep-Sea Research I* 52, 69–83.
- Al-Mutairi, H., Landry, M.R., 2001. Active export of carbon and nitrogen at Station ALOHA by diel migrant zooplankton. *Deep-Sea Research II* 48, 2083–2104.
- Båmstedt, U., Gifford, D.J., Irigoien, X., Atkinson, A., Roman, M., 2000. Feeding. In: Harris, R.P., Wiebe, P.H., Lenz, J., Skjoldal, H.R., Huntley, M. (Eds.), *ICES Zooplankton Methodology Manual*. Academic Press, London, pp. 297–399.
- Benitez-Nelson, C., Bidigare, R.R., Dickey, T.D., Landry, M.R., Leonard, C.L., Brown, S.L., Nencioli, F., Rii, Y.M., Maiti, K., Becker, J.W., Bibby, T.S., Black, W., Cai, W.J., Carlson, C., Chen, F.Z., Kuwahara, V.S., Mahaffey, C., McAndrew, P.M., Quay, P.D., Rappé, M., Selph, K.E., Simmons, M.P., Yang, E.J., 2007. Mesoscale eddies drive increased silica export in the subtropical Pacific Ocean. *Science* 316, 1017–1021.
- Bidigare, R.R., Benitez-Nelson, C., Leonard, C.L., Quay, P.D., Parsons, M.L., Foley, D.G., Seki, M.P., 2003. Influence of a cyclonic eddy on microheterotroph biomass and carbon export in the lee of Hawaii. *Geophysical Research Letters* 30, 51–54.
- Brown, S.L., Landry, M.R., Selph, K.E., Yang, E.J., Rii, Y.M., Bidigare, R.R., 2008. Diatoms in the desert: Plankton community response to a subtropical mesoscale eddy in the subtropical North Pacific. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2008.02.012].
- Conover, R.J., Durvasula, S.R., Wang, R., 1986. Probable loss of chlorophyll-derived pigments during passage through the gut of zooplankton, and some of the consequences. *Limnology and Oceanography* 31, 878–887.
- Corno, G., Karl, D.M., Church, M.J., Letellier, R.M., Lukas, R., Bidigare, R.R., Abbott, M.R., 2007. Impact of climate forcing on ecosystem processes in the North Pacific Subtropical Gyre. *Journal of Geophysical Research*, Oceans 112, C04021, doi:10.1029/2006JC003730.
- Dam, H.G., Peterson, W.T., 1988. The effect of temperature on the gut clearance rate constant of planktonic copepods. *Journal of Experimental Marine Biology and Ecology* 123, 1–14.
- Dickey, T., Nencioli, F., Kuwahara, V., Leonard, C., Black, W., Bidigare, R., Rii, Y., Zhang, Q., 2008. Physical and bio-optical observations of oceanic cyclones west of the island of Hawai'i. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2008.01.006].
- Eppley, R.W., Renger, E.H., Venrick, E.L., Mullin, M.M., 1973. A study of plankton dynamics and nutrient cycling in the central gyre of the North Pacific Ocean. *Limnology and Oceanography* 18, 534–551.
- Falkowski, P.G., Ziemann, D., Kolber, Z., Bienfang, P.K., 1991. Role of eddy pumping in enhancing primary production in the ocean. *Nature* 352, 55–58.
- Fennel, K., Spitz, Y.H., Letellier, R.M., Abbott, M.R., Karl, D.M., 2002. A deterministic model for  $\text{N}_2$  fixation at stn. ALOHA in the subtropical North Pacific Ocean. *Deep-Sea Research II* 49, 149–174.
- Fernandez, E., Alvarez, F., Anadon, R., Barquero, S., Bode, A., Garcia, A., Garcia-Soto, C., Gil, J., Gonzalez, N., Iriarte, A., Mourino, B., Rodriguez, F., Sanchez, R., Teira, E., Torres, S., Valdes, L., Varela, M., Varela, R., Zapata, M., 2004. The spatial distribution of plankton communities in a Slope Water anticyclonic Oceanic eddy (SWODDY) in the southern Bay of Biscay. *Journal of the Marine Biological Association of the United Kingdom* 84, 501–517.
- Fossheim, M., Zhou, M., Tande, K.S., Pedersen, O.P., Zhu, Y., Edvardsen, A., 2005. Interactions between biological and environmental structures along the coast of northern Norway. *Marine Ecology Progress Series* 300, 147–158.
- Fowler, S.W., Knauer, G.A., 1986. Role of large particles in the transport of elements and organic compounds through the oceanic water column. *Progress in Oceanography* 16, 147–194.
- Goetze, E., 2005. Global population genetic structure and biogeography of the oceanic copepods *Eucalanus hyalinus* and *E. spinifer*. *Evolution* 59, 2378–2398.
- Goldthwait, S.A., Steinberg, D.K., 2008. Elevated biomass of mesozooplankton and enhanced fecal pellet flux in cyclonic and mode-water eddies in the Sargasso Sea. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2008.01.003].
- Hayward, T.L., McGowan, J.A., 1985. Spatial patterns of chlorophyll, primary production, macrozooplankton biomass, and physical structure in the central North Pacific Ocean. *Journal of Plankton Research* 7, 147–167.
- Head, E.J.H., Harris, L.R., 1992. Chlorophyll and carotenoid transformation and destruction by *Calanus* spp. grazing on diatoms. *Marine Ecology Progress Series* 86, 229–238.
- Head, E.J.H., Hargrave, B.T., Subba Rao, D.V., 1994. Accumulation of a phaeophorbide *a*-like pigment in sediment traps during late stages of a spring bloom: a product of dying algae? *Limnology and Oceanography* 39, 176–181.
- Hernandez-Leon, S., Almeida, C., Gomez, M., Torres, S., Montero, I., Portillo-Hahnefeld, A., 2001. Zooplankton biomass and indices of feeding and metabolism in island-generated eddies around Gran Canaria. *Journal of Marine Systems* 30, 51–66.
- Hofmann, E.E., Klinck, J.M., Paffenhöfer, G.A., 1981. Concentrations and vertical fluxes of zooplankton fecal pellets on a continental shelf. *Marine Biology* 61, 327–335.
- Hirst, A.G., Shearer, M., 1997. Are *in situ* weight-specific growth rates body-size independent in marine planktonic copepods? A re-analysis of the global syntheses and a new empirical model. *Marine Ecology Progress Series* 154, 155–165.
- Huntley, M.E., Lopez, M.D.G., 1992. Temperature-dependent production of marine copepods: a global synthesis. *American Naturalist* 140, 201–242.
- Ikeda, T., 1985. Metabolic rates of epipelagic marine zooplankton as a function of body size and temperature. *Marine Biology* 85, 1–11.
- Isla, J.A., Ceballos, S., Huskin, I., Anadon, R., Alvarez-Marques, F., 2004. Mesozooplankton distribution, metabolism and grazing in an anticyclonic Slope Water Oceanic eddy (SWODDY) in the Bay of Biscay. *Marine Biology* 145, 1201–1212.
- Karl, D., Letellier, R., Tupas, L., Dore, J., Christian, J., Hebel, D., 1997. The role of nitrogen fixation in biogeochemical cycling in the subtropical North Pacific Ocean. *Nature* 388, 533–538.
- Kleppel, G.S., Pieper, R.E., 1984. Phytoplankton pigments in the gut contents of planktonic copepods from coastal waters off Southern California. *Marine Biology* 78, 193–198.
- Landry, M.R., Peterson, W.K., Andrews, C.C., 1992. Particulate flux in the water column overlying Santa Monica Basin. *Progress in Oceanography* 30, 167–195.
- Landry, M.R., Al-Mutairi, H., Selph, K.E., Christensen, S., Nunnery, S., 2001. Seasonal patterns of mesozooplankton abundance and biomass at Station ALOHA. *Deep-Sea Research II* 48, 2037–2062.
- Landry, M.R., Brown, S.L., Rii, Y.M., Selph, K.E., Bidigare, R., Yang, E.J., Simmons, M.P., 2008. Depth-stratified phytoplankton dynamics in Cyclone *Opal*, a subtropical mesoscale eddy. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2008.02.001].
- Le Borgne, R., Rodier, M., 1997. Net zooplankton and the biological pump: a comparison between the oligotrophic and mesotrophic Equatorial Pacific. *Deep-Sea Research II* 44, 2003–2023.
- Letellier, R.M., Karl, D.M., Abbott, M.R., Flament, P., Freilich, M., Lukas, R., Strub, T., 2000. Role of late winter mesoscale events in the biogeochemical variability of the upper water column of the North Pacific Subtropical Gyre. *Journal of Geophysical Research*, Oceans 105, 28,723–28,739.
- Lobel, P.S., Robinson, A.R., 1986. Transport and entrapment of fish larvae by ocean mesoscale eddies and current in Hawaiian waters. *Deep-Sea Research* 33, 483–500.
- Lobel, P.S., Robinson, A.R., 1988. Larval fishes and zooplankton in a cyclonic eddy in Hawaiian waters. *Journal of Plankton Research* 10, 1209–1223.
- Lopez, M.D.G., Huntley, M.E., Sykes, P.F., 1988. Pigment destruction by *Calanus pacificus*: impact on the estimation of water column fluxes. *Journal of Plankton Research* 10, 715–734.

- Lumpkin, C.F., 1998. Eddies and currents in the Hawaiian Islands. Ph.D. Dissertation, University of Hawaii, 281pp.
- Mahaffey, C., Benitez-Nelson, C.R., Bidigare, R.R., Rii, Y., Karl, D.M., 2008. Nitrogen dynamics within a wind-driven eddy. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2008.02.004].
- Maiti, K., Benitez-Nelson, C.R., Rii, Y., Bidigare, R., 2008. The influence of a mature cyclonic eddy on particle export in the lee of Hawaii. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2008.02.008].
- Mayzaud, P., Razouls, S., 1992. Degradation of gut pigment during feeding by a subantarctic copepod: importance of feeding history and digestive acclimation. *Limnology and Oceanography* 37, 393–404.
- McGillicuddy Jr., D.J., Robinson, A.R., Siegel, D.A., Jannasch, H.W., Johnson, R., Dickey, T.D., McNeil, J., Michaels, A.F., Knap, A.H., 1998. Influence of mesoscale eddies on new production in the Sargasso Sea. *Nature* 394, 263–266.
- McGillicuddy Jr., D.J., Johnson, R., Siegel, D.A., Michaels, A.F., Bates, N.R., Knap, A.H., 1999. Mesoscale variations of biogeochemical properties in the Sargasso Sea. *Journal of Geophysical Research* 104, 13381–13394.
- Nencioli, F., Dickey, T.D., Kuwahara, V.S., Black, W., Rii, Y.M., Bidigare, R.R., 2008. Physical dynamics and biological implications of a mesoscale cyclonic eddy in the lee of Hawaii: Cyclone *Opal* observations during E-Flux III. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2008.02.003].
- Paffenhöfer, G.-A., Knowles, S., 1979. Ecological implications of fecal pellet size, production and consumption by copepods. *Journal of Marine Research* 37, 35–49.
- Patzert, W.C., 1969. Eddies in Hawaiian Islands. Report no. HIG-69-8, Hawaii Institute of Geophysics, University of Hawaii at Manoa.
- Penry, D.L., Frost, B.W., 1991. Chlorophyll *a* degradation by *Calanus pacificus*: dependence on ingestion rate and digestive acclimation to food resources. *Limnology and Oceanography* 36, 147–159.
- Riandey, V., Champalbert, G., Carlotti, F., Taupier-Letage, I., Thibault-Botha, D., 2005. Zooplankton distribution related to the hydrodynamic features in the Algerian Basin (western Mediterranean Sea) in summer 1997. *Deep-Sea Research I* 52, 2029–2048.
- Rii, Y.M., Brown, S.L., Nencioli, F., Kuwahara, V., Dickey, T., Karl, D.M., Bidigare, R.R., 2008. The transient oasis: nutrient-phytoplankton dynamics and particle export in Hawaiian Lee Cyclones. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2008.01.013].
- Rollwagen Bollens, G.C., Landry, M.R., 2000. Biological response to iron fertilization in the eastern Equatorial Pacific (IronEx II). II. Mesozooplankton abundance, biomass, depth distribution and grazing. *Marine Ecology Progress Series* 201, 43–56.
- Seki, M.P., Polovina, J.J., Brainard, R.E., Bidigare, R.R., Leonard, C.L., Foley, D.G., 2001. Biological enhancement at cyclonic eddies tracked with GOES thermal imagery in Hawaiian waters. *Geophysical Research Letters* 28, 1583–1586.
- Seki, M.P., Lumpkin, R., Flament, P., 2002. Hawaii cyclonic eddies and blue marlin catches: the case study of the 1995 Hawaiian International Billfish Tournament. *Journal of Oceanography* 58, 739–745.
- Sheridan, C.C., Landry, M.R., 2004. A nine-year increasing trend in mesozooplankton biomass at the Hawaii Ocean Time-series Station ALOHA. *International Council for the Exploration of the Seas. Journal of Marine Science* 61, 457–463.
- Small, L.F., Knauer, G.A., Tuel, M.D., 1987. The role of sinking fecal pellets in stratified euphotic zones. *Deep-Sea Research* 34, 1705–1712.
- Steinberg, D.K., Carlson, C.A., Bates, N.R., Goldthwait, S.A., Madin, L.P., Michaels, A.F., 2000. Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea. *Deep-Sea Research I* 47, 137–158.
- Steinberg, D.K., Goldthwait, S.A., Hansell, D.A., 2002. Zooplankton vertical migration and the active transport of dissolved organic and inorganic nitrogen in the Sargasso Sea. *Deep-Sea Research I* 49, 1445–1461.
- Strickland, J.D.H., Parsons, T.R., 1972. *A Practical Handbook of Seawater Analysis*, second ed. Fisheries Research Board of Canada, Ottawa.
- Vaillancourt, R.D., Marra, J., Seki, M.P., Parsons, M.L., Bidigare, R.R., 2003. Impact of a cyclonic eddy on phytoplankton community structure and photosynthetic competency in the subtropical North Pacific Ocean. *Deep-Sea Research I* 50, 829–847.
- Yebra, L., Hernandez-Leon, S., Almeida, C., Becognee, P., Rodriguez, J.M., 2004. The effect of upwelling filaments and island-induced eddies on indices of feeding, respiration and growth in copepods. *Progress in Oceanography* 62, 151–169.
- Zhang, X., Dam, H.G., White, J.R., Roman, M.R., 1995. Latitudinal variations in mesozooplankton grazing and metabolism in the central tropical Pacific during the US JGOFS EqPac study. *Deep-Sea Research II* 42, 695–714.