Variability in zooplankton distribution at cyclone Enakai in the lee of the Hawaiian Islands

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Non-technical summary

Enakai, a cyclonic eddy, formed in the lee of the Hawaiian Islands and was observed in NAVOCEANO satellite imagery during the week of 30 Oct. 2010. This study examines the physical, chemical and biological processes taking place within Enakai, and attempts to place them within the framework of eddy life histories. Cyclonic eddies are known to distort density surfaces in the ocean, causing deep water nutrients to upwell into the euphotic zone where they can be utilized by phytoplankton. Enhanced primary productivity provides food sources for zooplankton, initiating a cascade of ecosystem productivity. Plankton net tows showed that zooplankton abundances within Enakai were elevated by a factor of 150%-250% relative to surrounding waters at the time of the survey. Peaks of zooplankton productivity were separated from peaks of chlorophyll-a, the primary photosynthetic pigment in phytoplankton, by approximately 35 km. Given flows within eddies, this spatial distance suggests a temporal lag in secondary productivity of 16-17 days and may be the result of transportation and concentration of plankton by eddy-generated radial velocities. Other factors, including reproduction and directional reversals of currents along the eddy's radius, may further concentrate planktonic organisms thereby enhancing the ecological significance of the eddy.

Abstract

Enakai, a cyclonic eddy formed in the lee of the Hawaiian Islands west of the Alenuihaha Channel was first observed in NAVOCEANO satellite imagery during the week of 30 Oct. 2010. This study examines the physical, chemical, and biological

processes taking place within Enakai, and attempts to place them within the framework of eddy life cycles. Macronutrients, photosynthetic pigments, and zooplankton were collected to assess the effects of eddy processes on zooplankton abundance. Nutrient concentration below the euphotic zone increased approaching the center of the eddy, suggesting that nutricline doming occurred. Low nutrient concentration in the euphotic zone at the center of the eddy compared to peaks 80-90 km from the center suggest a donut-shaped pattern of productivity within the euphotic zone. Chlorophyll-a samples followed a similar pattern reaching maxima of $0.11 \mu g \ L^{-1}$ at 88 km from the center of the eddy, and $0.116 \ \mu g \ L^{-1}$ at 104.1 km from the center of the eddy, compared with $0.06 \ \mu g$ L^{-1} 80 km from the center. Average zooplankton abundance was 1.5-2.5 times higher within Enakai, compared to control stations outside the eddy. Zooplankton abundance within Enakai reached a maximum of 166 organisms m^{-3} at only 53 km from the center. This spatial lag of 35 km between peaks of chlorophyll-a concentration and zooplankton abundance implies a temporal lag in processes that influence their distribution. This may be due, in part, to the vertical migration behavior of zooplankton. This behavior may remove them from the influence of radial eddy currents 50% of the time, thereby reducing the speed at which they are advected to the eddy's periphery. In addition, zooplankton generation times may to a temporal lag in secondary productivity. Physical and biological data collected at Enakai may be used in the future to model the influence of eddy processes on the ecology of oligotrophic oceans.

Introduction

Primary productivity in low-nutrient oceanic environments depends on oases of upwelling nutrients generated by physical processes within the ocean (Garçon et al. 2001). It is therefore important to understand the physical mechanisms that concentrate food patches generated by this productivity, and to determine their influences on the ecology of oligotrophic oceans. Upwelling within cyclonic eddies may result in shoaling of the nutricline into the photic zone, enhancing primary productivity by diatoms (Rii et al. 2008). Patterns of high zooplankton biomass are likely to correspond to regions of temporary upwelling at eddies (Eden et al. 2009). I hypothesize that zooplankton are concentrated in and around eddies and fronts by upwelling currents. These same currents generate nutrient flux into the photic zone resulting in phytoplankton blooms. Zooplankton are attracted to the eddy by their behavioral preference for food patches and respond to increased food availability by increasing biomass, setting in motion a trophic cascade that may sustain large nektonic organisms (Tynan et al. 2005).

Eddies have been the subject of extensive study in recent years. Both the E-Flux program in Hawaii and the EDDIES program in the Atlantic Ocean (Benitez-Nelson and McGillicuddy, 2008) focused on interdisciplinary examination of biological, biogeochemical and physical processes at eddies. Nencioli et al. (2008) hypothesized that cyclones have three life stages: an initial 'intensification phase' in which eddy induced upwelling brings nutrients above the 1% light level; a 'mature phase' characterized by phytoplankton maxima; and a 'decay phase' in which the doming of the nutricline relaxes and phytoplankton blooms die down.

Mesoscale eddies are temporary wind-generated phenomena up to 100 km in diameter that can be identified using satellite data of SST, SSH, and ocean color (Calil & Richards, 2010). Eddies in the lee of the Hawaiian Islands have been observed to persist up to 60 days (Yoshida et al. 2010). Cyclonic, cold-core eddies form near the Alenuihaha Channel between Maui and Hawaii (Calil et al. 2008). According to Yoshida et al. (2010) this channel has positive and negative eddy signals caused by wind-stress curl, and eddies are formed at the SW tip of Hawaii as a result of shear between the North Equatorial Current and Hawaiian Lee Countercurrent.

Both warm and cold core eddies have been shown to generate surface fronts where elevated concentrations of chlorophyll-a are correlated with changes in SST and SSH (Calil and Richards, 2010). Cold core cyclonic eddies bring nutrients into the euphotic zone, where they stimulate phytoplankton growth at the center of the eddy (Kuwahara et al. 2008; Bidigare et al, 2003). Phytoplankton community structure varies within the cold core of the eddy as a function of spin-up rate, nutrient availability and eddy maturity (Rii et al. 2008). Large or rapid influxes of nutrients into the euphotic zone stimulate diatom blooms favored by grazing mesozooplankton, while slower nutrient influx may favor smaller types of phytoplankton.

Landry et al (2008) found mesozooplankton biomass inside the eddy Cyclone Opal to be nearly double that outside the eddy. Eden et al (2009) found a doubling of euphausiid abundance at the center and a five-fold increase in abundance at the periphery of an eddy in the Sargasso Sea compared to abundance outside the eddy. These observations provide evidence supporting the hypothesis that zooplankton patchiness

may be enhanced at eddies, by stimulating primary productivity and concentrating food sources.

 Euphausia pacifica are known to spawn at the peak of diatom blooms (Gutierrez et al. 2007), suggesting that large zooplankton would spawn during the mature phase of a cyclone. This phase of a productive eddy would therefore be characterized by large concentrations of adult organisms and eggs. As the eddy matures or enters its 'decay phase', both diatoms and non-swimming larval organisms are advected toward the periphery where they are concentrated by radial currents at a front between the warm external water mass and cold internal water mass. A highly productive decaying eddy may be characterized by reduced concentrations of diatoms and increased abundance of zooplankton in varied life stages near the periphery.

 Here, I examine the variability of zooplankton abundance at cyclone Enakai in the lee of the Hawaiian Islands to test the hypothesis that eddy processes enhance zooplankton productivity by concentrating food patches. I suggest that the spatial distance between peaks of macronutrients, chlorophyll-a, and zooplankton abundance along the eddy's radius are caused by advection by eddy currents, as well as enhanced primary productivity initiated by eddy generated upwelling of macronutrients. I use radial velocities from cyclone Opal (Nencioli et al. 2008) and estimates of copepod biomass from Roman et al. (2002) and generation times (Zhang et al. 2002) to examine the temporal lag in productivity implied by the spatial distance between peaks of zooplankton abundance and chlorophyll-a concentration.

Methods

Eddy tracking

In the weeks prior to the cruise, Enakai, a cyclonic eddy in the lee of Hawaii was tracked using sea surface temperature (SST), sea surface height (SSH) anomalies and currents shown on the Navy's NAVOCEANO 1/32° Global NLOM Model (http://www7320.nrlssc.navy.mil/global_nlom32/haw.html). Enakai became visible during the week of 30 Oct. 2010 and was tracked weekly from 60 days before the cruise (TN260) until the *R/V Tommy G. Thompson's* departure from Oahu on 27 Dec. 2010. SST models from the same site were consulted, but the large size and diffuse character of the cyclone made current observations a more effective tracking method. Eddy stations were chosen in a cross pattern (not shown) based on the location of Enakai at the start of the cruise on 27 Dec. 2010. Between 1 Jan. 2011 and 3 Jan. 2011 the eastern edge of the cyclone translated approximately 9.3 km eastward and the estimated center of the eddy translated approximately 16.6 km eastward. Stations 0, 1, 2 and 12 were chosen based on the eddy location at the start of the cruise on 27 Dec. 2010. Stations 13.5, 17, 19, and 20 were chosen based on the new location of eddy on January 2, 2011 (Fig. 1).

While underway, data from a 75 KHz RDI Ocean Surveyor acoustic Doppler current profiler (ADCP) was used to track eddy currents in near real time. The nominal center of the eddy was defined as the location at which current vectors approached 0 m s^{-1} and reversed direction (Fig. 2), this became the location of Station 13.5. Underway SST was tracked using shipboard sensors and used to confirm the eddy perimeter and position of fronts associated with the eddy.

Satellite SST data from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) satellite was used to map sampling locations across Enakai after the cruise. MODIS Aqua night time 4 km resolution 3-day averaged SST data from Jan. 1-3, 2011 was imported into ArcGIS and mapped with station locations. Stations 0 and 19 were designated OUT stations, based on their respective distances of 123 km and 129.6 km from the center of the eddy on 2 Jan. 2011. Samples from Stations 1, 2, 12, 13.5, 17 and 20 were designated IN stations.

Fig. 1 Eddy stations and SST reflectance determined by Modis Aqua satellite data averaged from 1-3 Jan. 2011 and SST measured along the cruise track by the ship's sensors.
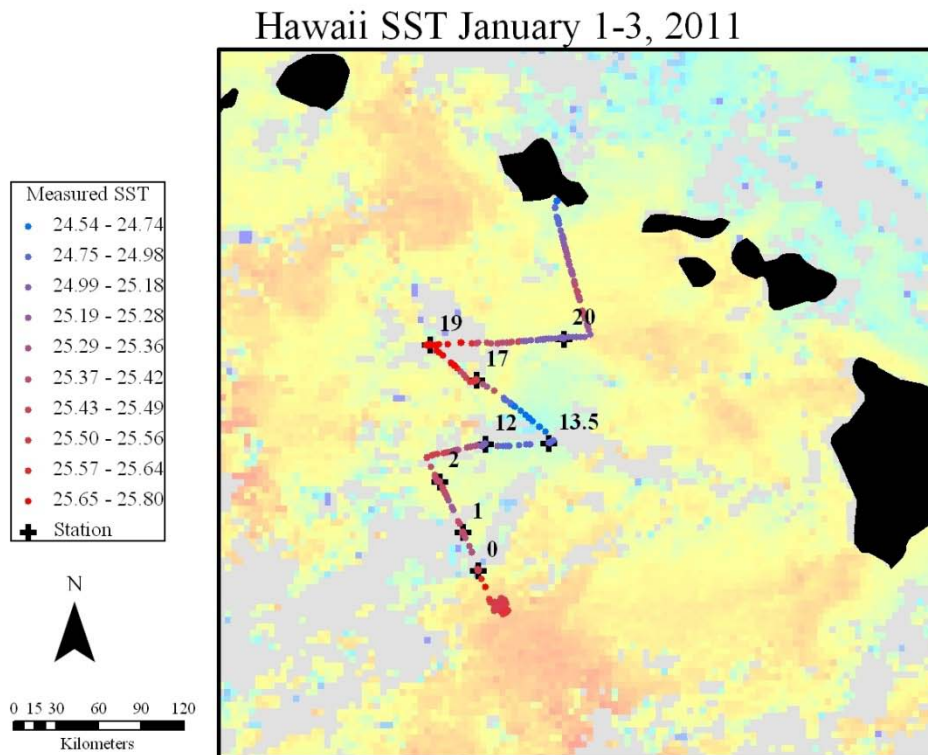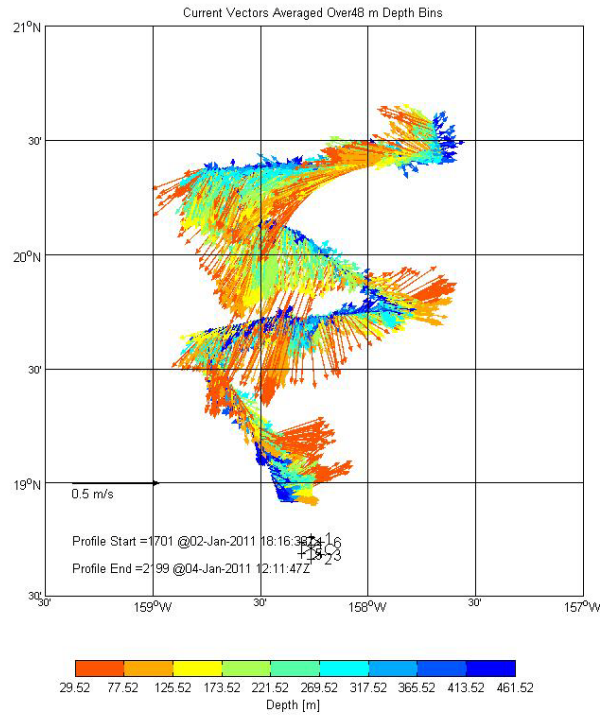
Fig. 2 ADCP current vectors along the eddy transect.

Sample collection

CTD casts using a Seabird 9-plus CTD equipped with a Wetlabs fluorometer were
made to a depth of 500 m at all stations. Water samples for nutrient and chlorophyll
analysis were taken from the surface and depths of 5 m, 50 m, the deep chlorophyll
maximum (DCM) varying from 85-125 mas shown by CTD fluorescence, 175 m, 250-
275 m, and 350-400 m. Chlorophyll samples were processed on board the ship, and
nutrient samples were frozen and processed at the University of Washington School of
Oceanography lab after the cruise using the Technicon Model AAll.

Zooplankton samples were collected at all stations. Samples for Stations 0, 1, 17,
and 19 were collected during daylight, while samples for Stations 2, 12, 13.5, and 20
were collected at night. Samples 1-20 were collected using a 60-cm diameter bongo net

equipped with a 333-µm mesh net. Nets were towed obliquely from 500 m depth at a speed of 1.5 knots h^{-1}. The sample at Station 0 (OUT) was collected using a 1-m, 330-µm net towed vertically from 550 m. Winch failure at Station 12 left the net at a depth of 78 m for approximately 60 minutes, the net was then hand-lifted vertically to the surface, and current speed was used to estimate flow volume. Both flow meters from the cruise were lost at sea during an earlier study, so an attached depth sensor was used to determine the time of each tow and estimate filter volume at all stations. Samples were preserved in the field using a 5% buffered formalin solution.

Zooplankton samples were processed in a laboratory, and settling volume was estimated in a 250-mL graduated cylinder. Samples were diluted to 10 times the settling volume, and two 5-mL subsamples were analyzed. Total abundance of organisms m^{-3} was calculated from the analyzed fraction. The sample from Station 0 was mistakenly spilled in the laboratory sink during processing by another researcher prior to counting for this study. The p-trap of the sink was removed and it is believed all organisms were recovered.

Results

Hydrographic survey

SST varied from 25.67°C at OUT Station 19 to 24.86C at the center (Station 13.5). CTD casts to 500 m at all stations showed cool temperature surfaces shoal approaching the center of Enakai (Fig 3a). The DCM shoaled from 130 m at OUT Station 0 to 86-96 m at the estimated center of the eddy (Fig. 3b). Fluorescence at the DCM peaked at the eddy periphery, reaching 0.3184 mg m^{-3} at a depth of 121 m at Station 2, and 0.2879 mg m^{-3} at 110.7 m depth at Station 20. Maximum fluorescence at the center

was 0.1963 mg m^{-3}, matching the DCM fluorescence value at 130 m depth at OUT

Station 0. The lowest DCM fluorescence of 0.1658 mg m^{-3} occurred at OUT station 19 at

110 m depth. The pattern of fluorescence maxima at the periphery in combination with

relatively low fluorescence at the center of the eddy suggest at donut shape with a radius

of approximately 80-90 km.

Fig. 3 a and b
Temperature (a)
and
fluorescence (b)
distribution
across the eddy
transect.
Transect was
made in a zig-
zag pattern.
Distance from
center is used to
approximate a
straight transect
across the eddy.
Depth is in
meters,
temperature is
in °C, and

fluorescence in mg m^{-3}. Distance is in kilometers from beginning of transect at Station 0.
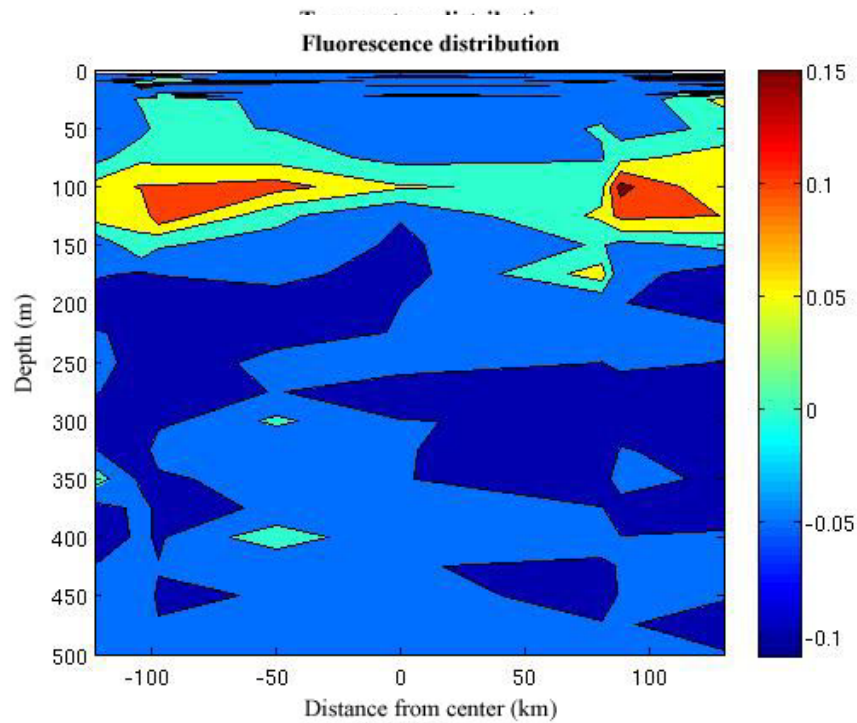
Nutrient analysis

At depths greater than 175 m, nutrients including silicate, phosphate, and nitrate

and nitrite (N+N) generally increased approaching the eddy center. Nutrients in the

euphotic zone followed the opposite pattern, generally decreasing approaching the center

of the eddy and increasing toward the periphery (Fig. 4).

Silicic acid reached maximum concentration of 52.25 μM at a depth of 400 m at

C2, the former center of the eddy (not shown). Si(OH)$_4$ spiked at Station 20 on the

periphery of the eddy, where it reached 21.9 μM at the DCM at 115 m depth, and 36.37 μM at 400 m depth. The lowest Si(OH)$_4$ concentration of 1.65 μM was found at 5 m depth at OUT Station 19, and remained below 3 μM to depths greater that 175 m.

Phosphate concentration of 0.04 μM was lowest at the center of the eddy at the DCM. [PO$_4$] maxima of 2.13 μM at a depth of 400 m and 1.25 μM at a depth of 275 m and occurred at Station 20 at the eddy periphery.

Nitrate and nitrite [N+N] at 250-275 m depths increased from

4.2-7.7 μM at the OUT stations to 12.8 μM approaching the center of the eddy. Sampled

[N+N] concentration of 33.54 μM reached a maximum at a depth of 400m at Enakai's

center (not shown). At depths shallower than 130 m, [N+N] decreased approaching the
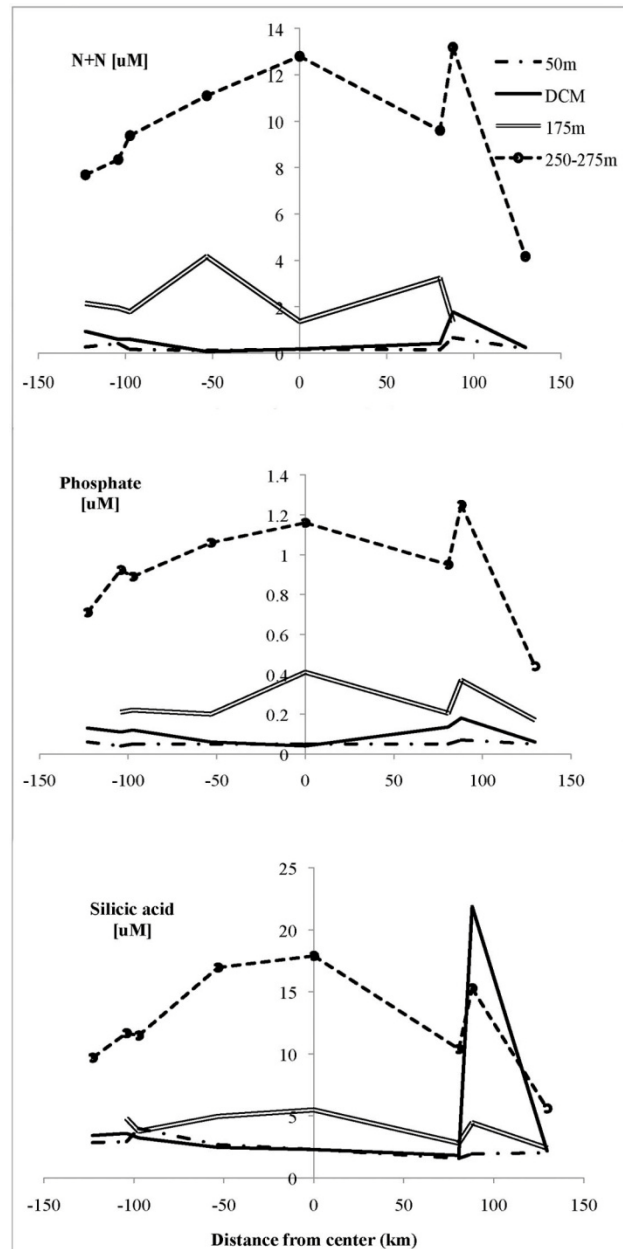
center of the eddy. Lowest [N+N] of 0.07 µM was calculated at the DCM at a depth of

100 m depth at 53.3 km from the center (Station 12).

Fig. 4 Silicic acid, phosphate and nitrate + nitrite [N+N] at depths of 50 m, the deep
chlorophyll maximum (DCM), 175 m, and 250-275 m by distance from eddy center.

Chlorophyll-a and phaeopigments

Chlorophyll-a (Chl-a) in the DCM at a depth of 125 m reached a maximum of

0.116 µg L^{-1} at 104.1 km from the center of the cyclone. Minimum Chl-a of 0.0 µg L^{-1}

was found at the 250 m depth at 104.1 km and 122.9 km from the center. Phaeopigments

reached a maximum of 0.14 µg L^{-1} at a depth of 100m, 53.3 km from Enakai's center.

The phaeopigment minimum of 0.0 µg L^{-1} was measured at 50 m depth 129.6 km from

the center.

Fig. 5 Phaeopigments (a), chlorophyll-a (b), and zooplankton abundance by radial
distance from center of eddy.
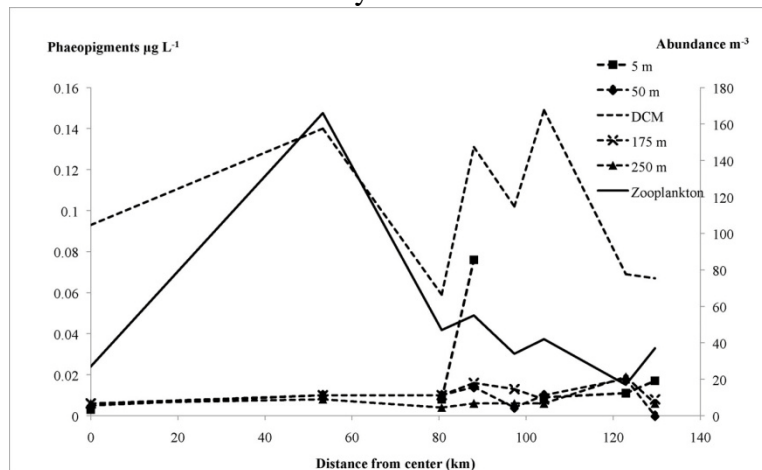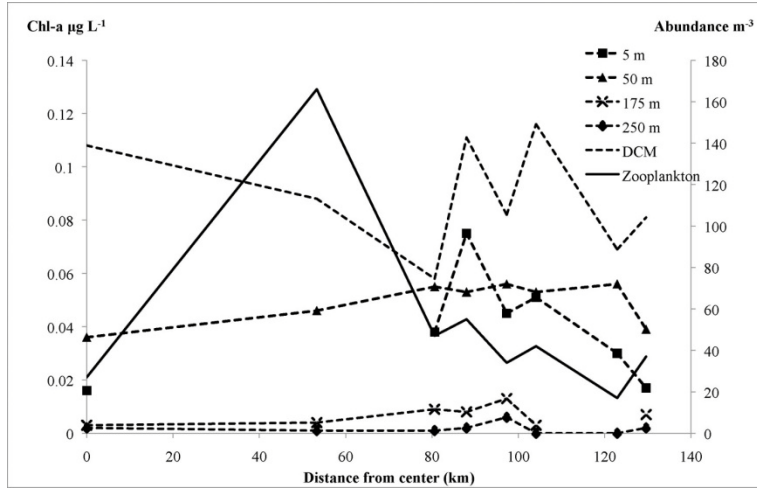
Zooplankton results

Table 1 Average zooplankton abundance and SST for IN and OUT eddy stations. Station 12 is not included in this calculation.

	OUT	IN	StDev
Average abundance m^{-3}	27	41	11.17
Average SST	25.56	25.2	0.22

Zooplankton abundance peaked at 53.3 km from the center of the eddy (Fig. 5). The abundance of 166 organisms m^{-3} at this station was 3 times larger than the abundance of organisms at any other station. Lower abundance of 27 organisms m^{-3} was counted at the center (station 13.5). The lowest calculated abundances of 17 organisms m^{-3} and 37 organisms m^{-3} were found at stations 0 and 19, both OUT stations.

Fig. 6 (a) Zooplankton abundance m^{-3}, unorthodox tow at Station 12 is shaded. Station 13.5, the center, is at the 0 distance mark. (b) Zooplankton abundance m^{-3} using 78 m depth and hypothetical vertical tows at all stations.
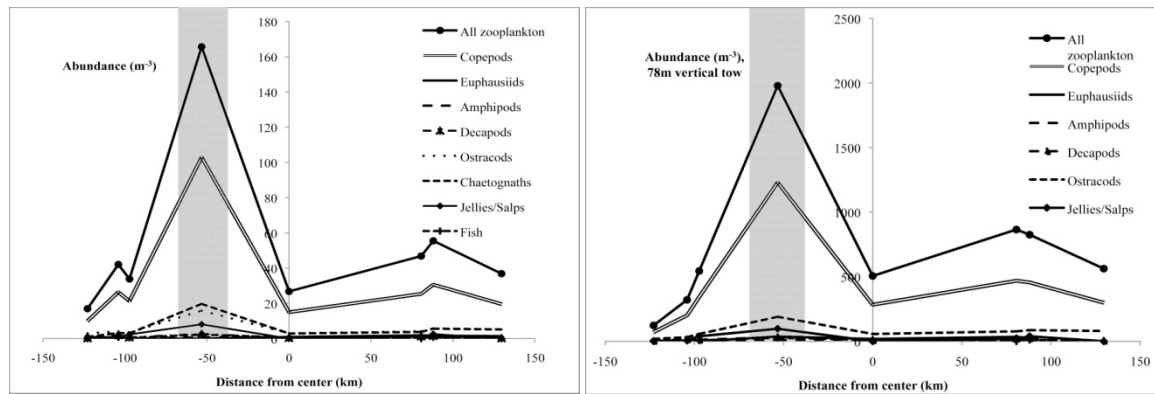
Number of organisms m^{-3} was recalculated at each station as if samples were collected using a 78 m vertical tow (Fig. 6b). The reduced the flow volume of 88.2 m^3 for all samples should have eliminated the influence of depth as a factor in organism abundance. Although the relative abundance of 1980 organisms m^{-3} at Station 12 is roughly double the next highest abundance of 865 organisms m^{-3} at Station 17, it remains significantly higher than the abundance of organisms at any other station. It may, therefore, be reasonable to include this sample in data analyses. Average abundance at IN eddy stations was conservatively 1.5 times that of OUT eddy station, and may be as much as 2.5 times higher if abundance from Station 12 is included in the calculation.

Table 2 Average zooplankton abundance and SST for IN and OUT eddy stations calculated as if all collections were towed vertically from 78 m depth. Station 12, where mechanical failure occurred, is included in this calculation.

	OUT	IN	StDev
Average abundance m^{-3}	342	840	594.72
Average SST	25.56	25.2	0.22

Zooplankton length was measured in mm, and copepod biomass was estimated using individual copepod weights in µg C from Roman et al. (2002). Weights were averaged between measurements listed for the TT007 and TT011 cruises to 2.8 µg C for copepods of 0.2-0.5 mm length, 19.95 µg C for copepods of

0.5-1.0 mm length, 53.6 µg C for copepods of 1.0-2.0 mm length. Weight of 97.7 ug C

for copepods of 2.0-3.0 mm length was calculated using linear analysis (Fig. 7).

Fig. 7 Average weight in ug C per organisms from Roman et al. (2002), linear regression used to estimate weight of larger organisms.
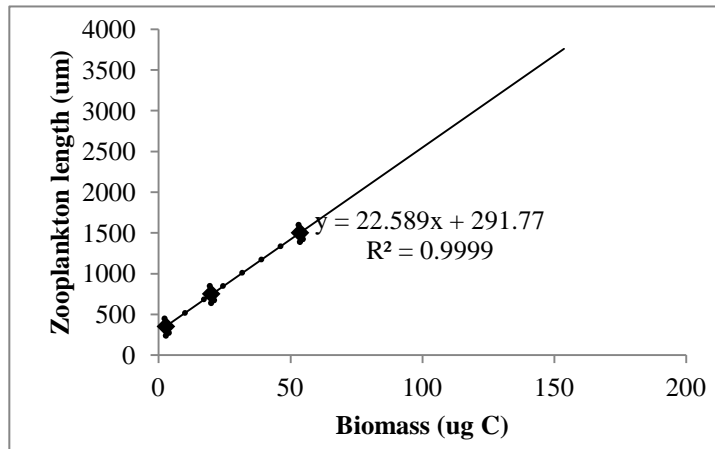
Estimated copepod biomass reached a maximum of 354.3 µg C m^{-3} at Station

12, 53.3 km from the center of the eddy. The lowest copepod biomass of 60.4 µg C

m^{-3} was found 63.4 km from the center of the eddy. Average copepod biomass at

OUT stations was estimated to be 180.5 µg C m^{-3} .

Table 3 Copepod biomass estimates at each station by distance from center of the eddy.

Distance from center (km)	Estimated copepod biomass (µg C m^{-3})
0	130.4
53.3	354.3
80.6	63.4
88	182.4
104.1	271.2
122.9	145.6
129.6	178.6

Discussion

Enakai's life history

       Cyclone Enakai was approximately 60 days old at the time of this survey and roughly elliptical rather than circular. Previous studies of eddies in the lee of Hawaii have examined mature cyclones of 3 months old in the case of cyclone Noah (Rii et al. 2008) and 1 month old in the case of cyclone Opal (Nencioli et al. 2008). Although of differing chronological ages when studied, both Noah and Opal were hypothesized to be in the mature or decay phase of their life cycles. Cyclone Enakai was still visible in the NAVOCEANO model on 14 Feb. 2011, but was much smaller and appeared to be dissipating, suggesting that cyclone Enakai was in a mature or decaying stage at the time of the TN260 survey.

       Observations of cyclone Opal found radial velocities varying between 40 cm s^{-1} and -30 cm s^{-1} across eddy transects. Radial velocities reverse direction at approximately 90 km from the eddy's center on both transects shown in Fig. 15 of Nencioli et al (2008). Although analysis of Enakai's current vectors is not complete at this writing, it is reasonable to anticipate similar patterns.

Enakai's chemical signatures

       Cyclone Enakai exhibited increased [N+N] concentration approaching the center at 175-400 m depths. The depth of the DCM varied from 130 m at OUT stations to approximately 90 m at the center. [N+N] at the DCM and shallower depths peaked 80-90 km from the center of the eddy (Fig. 7). Assuming eddy processes are roughly radially symmetric, this pattern of [N+N] spikes away from the center suggests a 'donut' of

nutrients penetrating the euphotic zone. This differs from the doming pattern of the

nutricline demonstrated by Bidigare et al. (2003) and suggests that some either

consumption by phytoplankton or transport by currents may be influencing radial nutrient

distribution in the euphotic zone.

Chl-a maxima coincided with [N+N] spikes at the periphery of the eddy.

Relatively high chl-a concentration at the center of the eddy co-occurred with low [N+N]

concentration, suggesting phytoplankton consumption may have depleted nutrients.

Phaeopigments are found in dead phytoplankton and may be abundant in zooplankton

fecal pellets (Roman et al.2002). High phaeopigment concentration of 0.093 μg L^{-1} in the

center of the eddy at the DCM suggests that primary productivity may have been higher

early in the eddy's life history. It is interesting to note that a phaeopigment maximum

coincides with the zooplankton maximum at 53.3 km from the center of the eddy (Fig. 5

a).

Zooplankton distribution

Zooplankton abundance was elevated by a factor of 1.5-2.5 at IN stations relative

to OUT stations. This is similar to results of previous studies that reported increased

abundance factors of 2-5 times inside eddies relative to outside (Landry et al. 2008; Eden

et al. 2009). A prominent spike in zooplankton abundance at 53.3 km from the center of

cyclone Enakai may be the result of the irregular sampling method caused by winch

failure at this station. However, a spike in abundance of 3 times the magnitude of any

other tow remained in the data after all abundances were recalculated using the flow

volume of a 78 m vertical tow, suggesting that a spike in abundance would be found at

this station if the same tow method had been used at all stations. This hypothesis is reinforced by the spike in phaeopigments at the same station, which may have resulted from zooplankton consumption and excretion of phytoplankton.

It is interesting to note that, although peaks of chl-a and [N+N] coincide at approximately 88 km from center of cyclone Enakai, zooplankton abundance peaks at 53.3 m from the center. Here, I suggest two processes that may have influenced this pattern. First, eddy-induced upwelling reached the center of the eddy first, inciting a burst of primary productivity. Phytoplankton were consumed by zooplankton, leaving a high concentration of phaeopigments behind. As upwelling nutrients at the center were depleted, primary productivity moved radially outward in a donut-shaped patch, tracked by grazing zooplankton.

Second, zooplankton consumed phytoplankton at the center of the eddy, and were simultaneously advected outward by radial currents in the cyclone. Reversing radial velocities observed by Nencioli et al (2008) would serve to concentrate food patches. Vertical migration of zooplankton may have resulted in horizontal directional changes as they moved up and down in the water column. Although phytoplankton may depth regulate, they have little swimming ability. It is, therefore, likely that their movement was primarily controlled by eddy currents. Radial velocity of cyclone Opal varied between -10 cm s^{-1} and 20 cm s^{-1} at 100 m depth, the approximate depth of the DCM in cyclone Enakai. Averaged to 5 cm s^{-1}, phytoplankton from the initial bloom would have been advected to 88 m from the center in 20.3 days. If we assume that vertically migrating zooplankton spend 50% their time feeding near the DCM at 100 m and 50% their time at the 450-550 m depths observed in the ADCP backscattering layer, radial movement

induced by the cyclone would carry them from the center of the eddy to a distance of 53.3

km in around 24-25 days (Fig. 8). The 34.7 km distance between the zooplankton peak

and the phytoplankton peak would be covered in 17-18 days.

Fig. 8 Cartoon illustrating temporal and spatial distribution of zooplankton and
chlorophyll a (Chl-a) along Enakai's radius. The secondary x axis represents estimated
travel time from the center of the eddy.
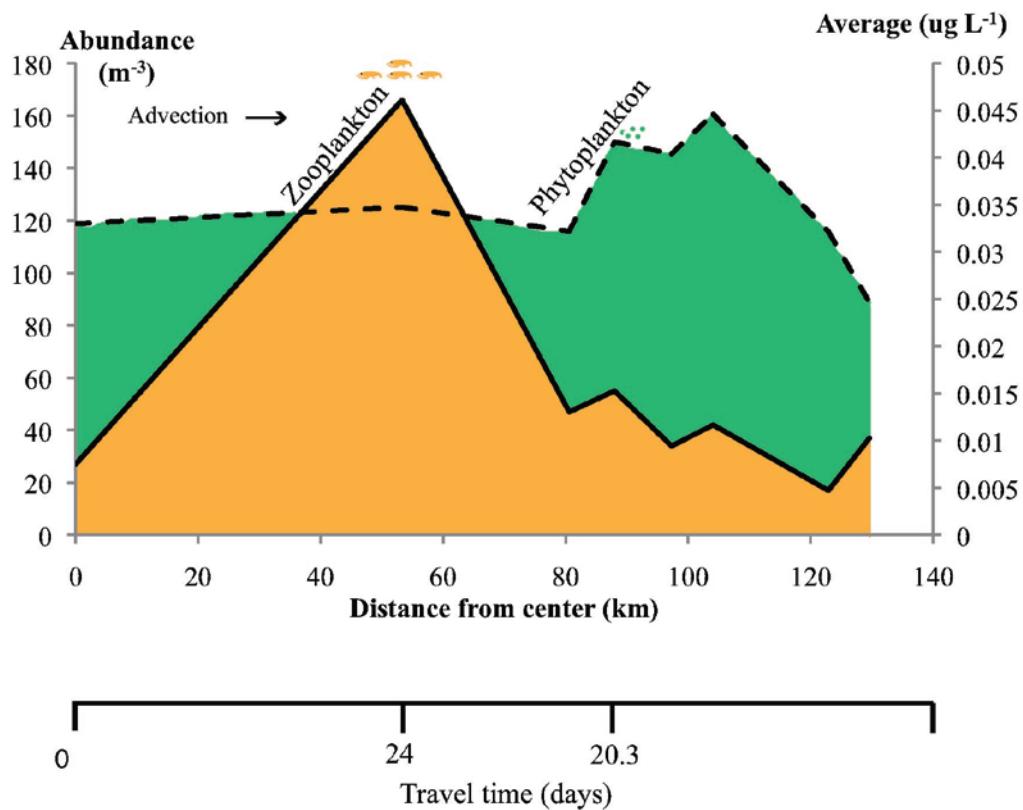
Using copepod biomass estimates (Table 3) of 354.3 μg C m^{-3} at 53.3 km from

the center of the eddy and an average of 180.5 μg C m^{-3} at OUT stations, the mean

growth rate (g) of 2.25 mmol C m^{-2} d^{-1}, and mortality rate (m) of 2.2 mmol C m^{-2} d^{-1} from

Zhang et al (2002) results in a 13.5 day time period for copepod biomass of this size to

develop. This estimate roughly agrees with the travel time estimate of 24 days to the

zooplankton peak at 53.3 km from the center of the eddy.

It seems likely that multiple processes are responsible for the observed patterns of

chl-a and zooplankton distribution across the eddy. Both nutrient depletion at the center

of the eddy and radial advection of phytoplankton and zooplankton may be responsible

for patches of organism concentration. If radial velocities are found in Enakai similar to

those observed in cyclone Opal, directional reversals are likely and may serve to further

enhance radial concentration of both phytoplankton and zooplankton. Reproduction may

also play a role in observed patterns of zooplankton abundance. Examination of

phytoplankton community structure across the eddy is likely to provide additional insight

into processes influencing the temporal and spatial distribution of organisms along

Enakai's radius. Data collected during the TN260 study of Enakai may be used to model

the effects of eddy processes on plankton distribution, further illuminating the ecological

significance of eddies in oligotrophic oceans.

Conclusions

Average zooplankton abundance within cyclone Enakai was 1.5-2.5 times higher

than at control stations outside the eddy. Nutrient, chl-a, and zooplankton exhibit a radial

pattern of distribution, with peaks in zooplankton abundance lagging behind chl-a peaks

by 17-18 days. Several effects of eddy processes may be responsible for patchiness.

Those include eddy-induced upwelling, radial advection, and concentration by reversing

radial currents. Reproduction may also play a role in eddy patchiness. It seems likely that

trophic cascades echo outward from the center of the eddy in waves of primary

productivity followed by waves of secondary productivity. Further study of eddy

ecosystem dynamics should include phytoplankton community structure, deeper

sampling of zooplankton, study of life stage composition along the eddy's radius, and

examination of the influence of eddy currents on the distribution of food patches.

Observations of an eddy over time would illuminate eddy life histories and their

significance in oligotrophic ecosystems.

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Appendices

Appendix 1, Zooplankton abundance by taxa

	E0	E1	E2	E12	E13.5	E17	E20	E19
Copepod	10	26	21	103	15	25	31	20
Euphausid	0	0	0	0	1	2	2	1
Adult	0	0	0	1	0	1	0	0
Furcilia	0	1	0	2	0	1	1	0
Calyptopis	0	0	0	0	0	0	0	1
Amphipod	0	1	0	1	1	0	1	0
Crustacea	0	0	0	0	0	0	0	0
Decapod	0	2	1	3	0	1	2	0
Ostracod	3	4	4	16	3	4	6	5

Chaetognath	1	3	3	20	3	4	6	5
Mollusca	0	0	0	0	0	0	0	0
Gastropoda	0	0	0	0	0	1	0	0
Pteropoda	0	1	1	0	1	1	0	0
Heteropoda	0	0	0	0	0	0	0	0
Annelid	0	0	0	0	0	0	0	0
Jellies/Salps	1	1	2	8	0	1	3	0
Larvacean	0	1	0	0	0	0	0	0
Fish	0	1	0	2	1	0	1	0
Eggs	3	2	1	9	2	5	4	3
Other	0	0	0	0	0	0	0	0
Total	17	42	34	166	27	47	55	37