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Zooplankton community structure in a cyclonic and mode-water eddy in the Sargasso Sea

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ABSTRACT

Mesoscale eddies are important suppliers of nutrients to the surface waters of oligotrophic gyres, but little is known about the biological response, particularly that of higher trophic levels, to these physical perturbations. During the summers of 2004 and 2005, we followed the development of a cyclonic eddy and an anti-cyclonic mode-water eddy in the Sargasso Sea. Zooplankton (> 150 μm) were collected across both eddies in 9 discrete depth intervals between 0 and 700 m. Comparison of the abundance of major taxa of mesozooplankton in the upper 150 m at eddy center and outside the eddies (day and night) indicated that the cyclone and mode-water eddy supported similar mesozooplankton communities, with several taxa significantly higher in abundance inside than outside the eddies, when compared with the Bermuda Atlantic Time-series Study site as representative of mean conditions. In both eddies copepod peak abundance occurred in the 50–100 m depth interval, coincident with the chlorophyll *a* maximum, suggesting elevated food concentration in the eddies may have influenced zooplankton vertical distribution. The two eddies differed in the strength of diel vertical migration of zooplankton, as indicated by the ratio of night:day abundance in the epipelagic zone, which was higher at the center of the mode-water eddy for most taxa. Over the sampling interval of 1–2 months, abundance of the three most common taxa (copepods, chaetognaths, and ostracods) decreased in the cyclone and increased in the mode-water eddy. This further supports previous findings that over the sampling period the cyclone was in a decay phase, while the mode-water eddy was sustaining nutrient fluxes and high phytoplankton concentrations. A more detailed analysis of community structure in the mode-water eddy indicated the 0–700 m integrated abundance of doliolids was significantly higher inside the mode-water eddy than outside. The presence of a mesopelagic (200–700 m) layer of lepadid barnacle cyprids in this eddy highlights the potential of eddies to transport and disperse biota. We conclude that when compared with average ambient conditions (as measured at BATS), mesoscale eddies can influence zooplankton behavior and alter zooplankton community structure which can affect food-web interactions and biogeochemical cycling in the open ocean.

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1. Introduction

The influence of physics on biology has been widely studied on both large and small scales. Within the scope of physical influence is what is known as the “internal

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weather of the sea”, or the oceanic mesoscale. Mesoscale physical features can change both the chemical and biological environment, which can alter biogeochemical cycles (McNeil et al., 1999). Mesoscale processes may be linked to the supply of new nutrients and elevated productivity in oligotrophic systems (Jenkins and Goldman, 1985). Recent studies of mesoscale eddies in the Sargasso Sea (McGillicuddy et al., 2007) and in the lee of the Hawaiian Islands (Benitez-Nelson et al., 2007) have shed new light on the complex physical (Dickey et al., 2008; Ledwell et al., 2008; Greenan, 2008), chemical (Noble et al., 2008; Bailey et al., 2008; Gabric et al., 2008), and biological (Bibby et al., 2008; Ewart et al., 2008; Goldthwait and Steinberg, 2008; Landry et al., 2008a; McAndrew et al., 2008) processes within these features.

Mesoscale eddies are important in controlling the structure and productivity of marine planktonic communities (Owen, 1981; Angel and Fasham, 1983; Mann and Lazier, 1991; Olson, 1991). However, relatively few studies have attempted a detailed quantification of the mesozooplankton community response to the passage of mesoscale eddies in oligotrophic systems such as the Sargasso Sea. Characterizations of mesozooplankton community structure (primarily in terms of zooplankton biomass) in mesoscale features have been conducted on Gulf Stream rings (The Ring Group, 1981; Wiebe, 1982; Davis and Wiebe, 1985; Hitchcock et al., 1985; Wormuth, 1985), the California Current system (Hauray, 1984; Bucklin, 1991; Huntley et al., 2000), the Haida eddies of the Gulf of Alaska (Mackas and Galbraith, 2002; Batten and Crawford, 2005; Mackas et al., 2005; Tsurumi et al., 2005), the Eastern Australian Current (Scott, 1981; Tranter et al., 1983), the Arabian and Black seas (Piontkovski et al., 1995; Arashkevich et al., 2002), the island-induced eddies of the North Atlantic (Hernández-León et al., 2001; Yebra et al., 2005), the Agulhas/Benguela system off southern Africa (Lutjeharms and Valentine, 1988; Pakhomov and Perissinotto, 1997), and the southeastern lee of the Hawaiian Islands (Landry et al., 2008b). However, there are relatively few studies that highlight eddy-induced changes in the zooplankton community (Davis and Wiebe, 1985; Tsurumi et al., 2005; Hernández-León et al., 2001; Landry et al., 2008b; Goldthwait and Steinberg, 2008).

In this study, we investigate the effects of two types of mesoscale eddies, a cyclone and a mode-water eddy, on mesozooplankton community taxonomic structure in the Sargasso Sea. Mesoscale eddies are ubiquitous in the Sargasso Sea, are roughly 150–200 km in diameter, and can persist from several months to more than a year (Richardson, 1993). The physical characteristics of both cyclonic and mode-water eddies are known to stimulate a biological response (Benitez-Nelson et al., 2007; McGillicuddy et al., 2007; Li and Hansell, 2008). The two target features of this study exhibited opposite rotational directions (counter-clockwise for the cyclone “C1”, and clockwise for the anticyclonic mode-water eddy “A4”) and opposite directions of displacement of the permanent thermocline (upwards for C1, and downwards for A4). However, both eddies were characterized by the shoaling of upper ocean isopycnals, resulting in nutrient injection into the euphotic zone (Li and Hansell, 2008; also see

Fig. 4 of McGillicuddy et al., 1999). This shoaling allows for the stimulation of both phytoplankton (Bibby et al., 2008; Landry et al., 2008a) and zooplankton (Goldthwait and Steinberg, 2008; Landry et al., 2008b) through upwelling of deep, nutrient-rich waters within the area occupied by the eddy. Mesoscale eddies in the Sargasso Sea can form from source waters in the north and east and propagate westward (Worthington, 1959; Brundage and Dugan, 1986; Siegel et al., 1999). There is also evidence from eddy nutrient profiles of C1 for more distant source waters in the southeastern Sargasso Sea (Li and Hansell, 2008).

Mesoscale eddies can influence zooplankton physiology (Boyd et al., 1978), species succession (Wiebe et al., 1976b), horizontal distribution (Wiebe et al., 1976b), and vertical distribution – both on a long-term (eddy lifetime) and on a diel cycle (Piontkovski et al., 1995). More recently, Goldthwait and Steinberg (2008) showed elevated mesozooplankton biomass, enhanced fecal pellet flux, and increased carbon export by diel vertical migration in cyclonic and mode-water eddies in the Sargasso Sea, but they did not address changes in individual taxa as a result of eddy perturbation. Similarly, in the subtropical Pacific, Landry et al. (2008b) show elevated mesozooplankton biomass, epipelagic abundance, and carbon export by migratory mesozooplankton inside cyclone *Opal* as compared to outside the cyclone.

By understanding how mesozooplankton community structure is affected by mesoscale eddies, we can further characterize the role that mesoscale eddies play in biogeochemical cycles. Changes in zooplankton taxa or abundance can control the flux of carbon and other elements to depth by resultant changes in grazing, fecal pellet size and sinking rates, and vertical migration behavior (e.g., Michaels and Silver, 1988; Steinberg et al., 2000). Understanding how mesoscale eddies affect zooplankton community structure will enhance our understanding of carbon cycling and sequestration, particularly in oligotrophic gyres where total biological production is thought to be relatively low.

2. Methods

2.1. Eddy characteristics

Two target eddy features were surveyed aboard the *R/V Oceanus*: a cyclonic eddy (C1) from 11 June–3 July and 25 July–12 August in 2004 (Fig. 1), and an anti-cyclonic mode-water eddy (A4) from 20 June–15 July and 7–25 August in 2005 (Fig. 2). Temperature and salinity sampling within the eddies characterized eddy C1 as an oblong feature with lateral extensions to the northeast and southwest. Eddy A4 was characterized as a relatively circular feature with a lens of 18 °C mode-water at its center (McGillicuddy et al., 2007). The deep chlorophyll *a* (Chl *a*) maximum occurred between 50 and 100 m in both eddies; however, both the location of highest Chl *a* concentration and the phytoplankton species composition differed between C1 and A4. Elevated fluorescence values occurred primarily along the periphery of eddy C1, particularly during the latter stages of sampling (Fig. 1). In contrast, the diatom bloom in eddy A4 was localized to

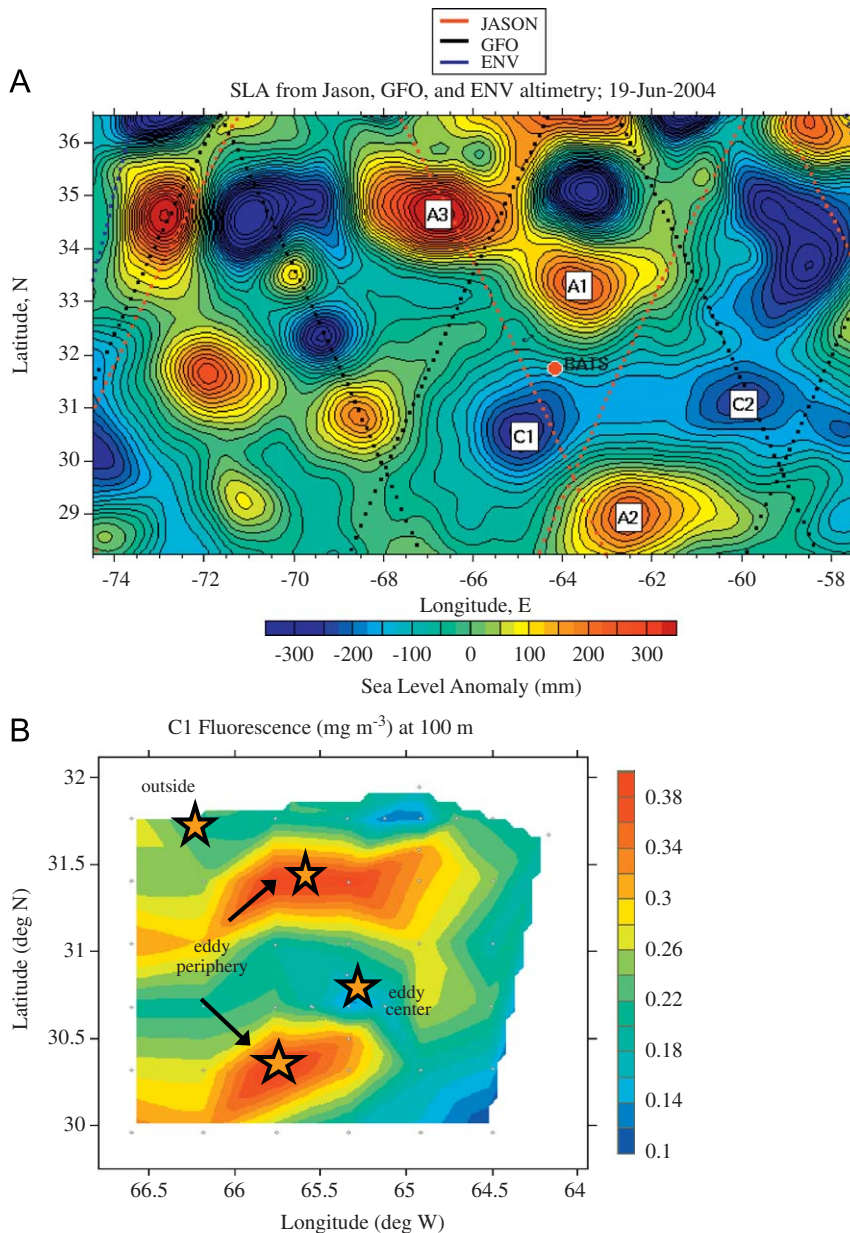


Fig. 1. Objective analyses of sea level anomaly (SLA) for June 19, 2004 (A), and fluorescence at 100 m depth of target eddy feature C1 (B). Several other eddy features (A1, A2, A3, C2) are noted in (A). Satellite ground tracks are shown for Jason (magenta), Geosat Follow-on (black), and ERS/ENVISAT (light blue). Access to these data in near-real time (Leben et al., 2002) facilitates the tracking of individual eddies and adaptive sampling in shipboard operations. Altimetric data provided by Ssalto/Duacs and distributed by AVISO with support from CNES. Stars in (B) represent approximate locations of MOCNESS tows (after McGillicuddy et al., 2007). Red circle indicates location of Bermuda Atlantic Time-series Study (BATS) site.

within ca. 20–30 km of eddy center (Fig. 2) (McGillicuddy et al., 2007; Bibby et al., 2008). Analysis of the phytoplankton assemblage indicated *Prochlorococcus* spp., *Synechococcus* spp., pelagophytes, and prymnesiophytes constituted the largest percentage of Chl *a* in the deep chlorophyll maximum of eddy C1, while analysis of the phytoplankton assemblage in eddy A4 indicated extremely high Chl *a* values associated with a bloom of the chain-forming diatom *Chaetoceros* spp. (McGillicuddy et al., 2007; Bibby et al., 2008). This large diatom bloom

was unique to eddy A4, as high numbers of diatoms were not observed in eddy C1.

2.2. Zooplankton sampling

Zooplankton were collected during the day and night at the center and outside of both eddies, and additionally at the periphery of C1. Daytime tows were conducted between 1000 h and 1400 h and nighttime tows between

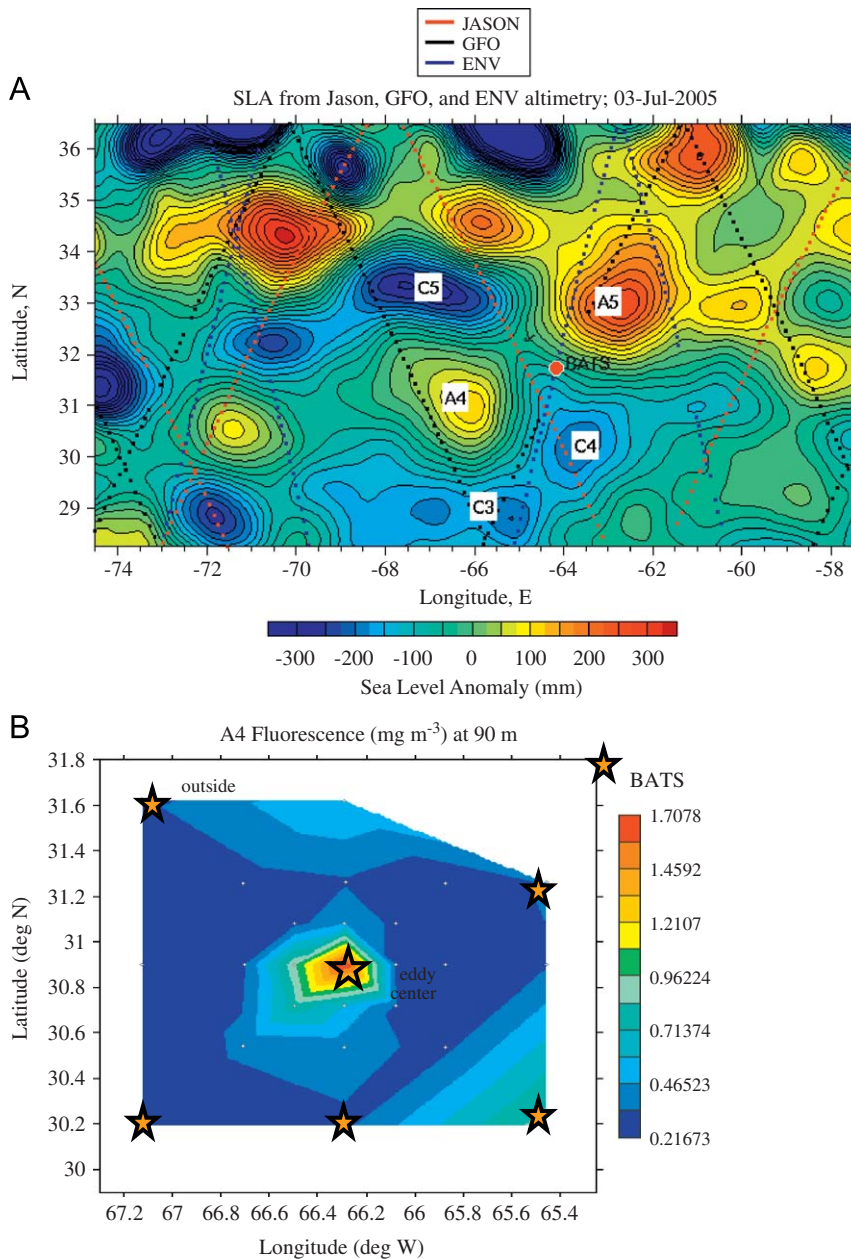


Fig. 2. Objective analyses of sea level anomaly (SLA) for July 3, 2005 (A), and fluorescence at 90 m depth of target eddy feature A4 (B). Several other eddy features (A5, C3, C4, C5) are noted in (A). Satellite ground tracks are shown for Jason (magenta), Geosat Follow-on (black), and ERS/ENVISAT (light blue). Access to these data in near-real time (Leben et al., 2002) facilitates the tracking of individual eddies and adaptive sampling in shipboard operations. Altimetric data provided by Ssalto/Duacs and distributed by AVISO with support from CNES. Stars in (B) represent approximate locations of MOCNESS tows (after McGillicuddy et al. 2007). Red square indicates location of Bermuda Atlantic Time-series Study (BATS) site.

2200 h and 0200 h (local time). Because of the enhanced fluorescence on the periphery of cyclonic eddy C1, tow locations were designated as either “center”, “periphery”, or “outside”. Tows conducted in anti-cyclonic mode-water eddy A4 were designated as either “center” or “outside” because of the localized nature of the diatom bloom at eddy center. “Outside” eddy tow locations were not designated strictly on a standard distance from eddy center, but rather on examination of shipboard physical

and chemical data that indicated those stations to be outside the eddy’s inner core (Acoustic Doppler Current Profiler, XBT, and CTD profiles). Therefore, stations designated as “outside” of eddies C1 and A4 are not equidistant from eddy center, nor are they necessarily unaffected by presence of the eddies. Indeed, our data show that these “outside” stations may be better termed “edge” stations, insofar as they appear to be under the influence of the eddies or perhaps eddy-eddy interactions.

Zooplankton were collected as described in Goldthwait and Steinberg (2008) using a Multiple Opening and Closing Net Environmental Sensing System (MOCNESS) with 9 sampling nets of 150 μm mesh mounted on a 1 \times 1 m frame (Wiebe et al., 1976a). The following discrete depth intervals were sampled on the upcast: 0–50, 50–100, 100–150, 150–200, 200–300, 300–400, 400–500, 500–600, and 600–700 m. Each net deployment lasted \sim 2–2.5 h with nets sampling for the final \sim 1.3 h. Fifteen MOCNESS tows were conducted in eddy C1 (2004), and 21 in eddy A4 (2005). Because of the larger sample size, we conducted a more detailed analysis of zooplankton community structure with depth in mode-water eddy A4.

Upon recovery nets were rinsed with seawater and the cod ends were removed. The contents of each cod end were then split using a Folsom plankton splitter with half preserved in 4% borax-buffered formaldehyde for analysis of community structure, and the other half size fractionated for biomass using methods similar to Landry et al. (2001) and Madin et al. (2001). For biomass results, see Goldthwait and Steinberg (2008).

The BATS summer zooplankton samples used to define mean conditions in this study were collected on BATS cruises during the months of June, July, and August, 2004 and 2005. The samples were collected by BATS scientists according to the methods described by Madin et al. (2001), using a 1 m², 202 μm mesh net towed obliquely through the mixed layer to an approximate depth of 200 m. This slightly larger mesh size could lead to more effective sampling of larger taxa, or underestimation of 150–200 μm zooplankton, such as small copepods, in the BATS summer samples as compared with the MOCNESS (150 μm mesh). The former bias was not apparent in the data set as there were no significant differences in the epipelagic abundance of some key large taxa (e.g., euphausiids, ANOVA $p > 0.05$) between BATS and the eddies (also see Results). Additionally, results from an attempt to remove the latter bias in a comparison of zooplankton biomass between the eddies and BATS in which the smallest (< 0.5 mm) size fraction was excluded from the analysis indicated significantly higher biomass associated with the eddies vs. BATS (Goldthwait and Steinberg, 2008). However, we can not rule out that some individual taxa that fall within the 150–200 μm size range (e.g., small copepods) may have been underestimated in BATS summer samples. Preserved (5% buffered formaldehyde) quarter-split samples of BATS summer tows were analyzed by the methods of this study. BATS day and night samples were averaged to determine summer mean (June–August) zooplankton abundance for each sampling year (2004, 2005). Six daytime BATS zooplankton samples were enumerated each year (2004, 2005). For nighttime tows, 6 samples for 2005 and 5 samples for 2004 were enumerated.

2.3. Taxonomic community structure analysis

Preserved samples were analyzed using an Olympus SZX12 stereo dissecting microscope under dark and light field illumination. Zooplankton were identified to major

taxa (e.g., calanoid copepods, non-calanoid copepods, chaetognaths), with some conspicuous taxa identified to genus or species. Copepods were separated into two groups, calanoid and non-calanoid, the latter comprising poecilostomatoid, cyclopoid, and harpacticoid copepods. Each sample was gently rinsed through two nested sieves (2000 and 150 μm). All animals collected on the 2000 μm sieve were identified and enumerated. Animals remaining on the 150 μm sieve were subsampled with a Stempel pipette (5 ml) before identification and enumeration. A minimum of 100 animals were identified in the 150–2000 μm fraction, resulting in examination of 1/320–1/2 of the total abundance of zooplankton collected per sample.

2.4. Vertical structure

In order to determine the presence and extent of vertical migration of the various taxa at each sampling location, we calculated two diagnostics: (1) night:day (N:D) abundance ratios in the upper 150 m (eddy C1 and A4), and (2) night vs. day change in weighted mean depth of zooplankton abundance (eddy A4). The former provides an indicator of the fraction of zooplankton that migrate (migration “strength”), and the latter quantifies vertical extent of the migration. N:D ratio was calculated by integrating the abundance of a given taxon over the upper 150 m (number of individuals m⁻²) and dividing the average night value by the average day value. (A night:day abundance ratio near 1 suggests no vertical migration). Weighted mean depth (m) was calculated as:

$$\text{WMD} = \frac{\sum (n_i \times z_i \times d_i)}{\sum S(n_i \times z_i)}$$

where d_i is the depth of a sample i (center of the depth interval, m), z_i is the thickness of the depth interval (m), and n_i is the density of individuals in the depth interval (number of individuals m⁻³) (Andersen et al., 2004, 1997, 2001; Steinberg et al., 2008a). The vertical extent of migration (ΔWMD) was calculated as day WMD minus night WMD (m).

2.5. Statistical analysis

Comparisons between locations (center vs. periphery vs. outside for eddy C1, or center vs. outside for eddy A4) within an eddy were done using 3-factor repeated measures ANOVAs (data were sorted by depth, location, and time of day: see Results for details). Where data did not fit the normality and homogeneity of variance assumptions of the ANOVA, data were transformed using square root, log, arcsine, or inverse transformations. Additionally, we used a community composition cluster analysis (Mackas and Sefton, 1982; Mackas, 1984) to test for differences in epipelagic zone (0–150 m) taxonomic abundance between the aforementioned locations; and additionally between the individual eddies and the BATS site. We assumed an a priori level of significance of $\alpha = 0.05$ for all comparisons.

3. Results

3.1. Eddy-eddy comparison in the epipelagic zone

Zooplankton abundance was integrated over the upper 150 m of the water column to compare the epipelagic abundance of major taxa between the two eddies (cyclone C1 versus mode-water eddy A4). There were no significant differences between the two eddies in abundance of any taxonomic group when eddy center and outside the eddies were compared during the day or night ($p > 0.05$, 3-way ANOVA, cluster analysis) (Figs. 3, 4, 5). There is no eddy vs. eddy comparison at periphery stations because the eddy periphery was only sampled in eddy C1 in 2004.

The contribution of each taxonomic group to the total zooplankton community was also determined for the epipelagic zone (upper 150 m) in each eddy. In both eddies, copepods made up ~75–95% of the total community at all locations sampled. In order to compare the taxonomic composition between eddy types (C1 versus A4) in more detail, we examined the non-copepod zooplankton, which largely comprised four other taxonomic groups (chaetognaths, ostracods, pteropods, and siphonophores) (Fig. 6). The non-copepod zooplankton taxa were also similar between the two eddy types (C1 vs. A4).

Comparison of the N:D ratio between the two eddy types suggests a more active migration across major taxa in mode-water eddy A4 compared to cyclone C1, as 11 out of 16 of the identified taxonomic groups in the center of the mode-water eddy A4 had higher N:D ratios than in the center of cyclone C1, including the most abundant taxon, the copepods (Table 1).

3.2. Anti-cyclonic mode-water eddy A4

3.2.1. Copepods

As expected, copepods were the most abundant taxa of zooplankton present day and night, both inside and outside of eddy A4. There was no significant difference in abundance of copepods inside vs. outside of eddy A4 at any depth ($p > 0.05$, ANOVA), although at the depth range of peak abundance (50–100 m), both calanoid and non-calanoid copepod abundances appear higher at eddy center (Fig. 7). As a broad taxonomic group, copepods did not exhibit a strong diel vertical migration at eddy center or outside the eddy (Table 1). This relatively low N:D ratio was further supported by less than a one meter day-night change in WMD (Table 1). Certainly some individual copepod taxa such as *Pleuromamma* spp. (Calanoida) were strong migrators. The abundance of *Pleuromamma* spp. copepods in the epipelagic zone increased from near zero in the day to 0.3 individuals m^{-3} at night both inside and outside the eddy. This increase in nighttime abundance was supported by high N:D ratios, as well as an order of magnitude increase in Δ WMD (Table 1). There was however, no significant difference in abundance of *Pleuromamma* spp. inside vs. outside the eddy ($p > 0.05$ ANOVA).

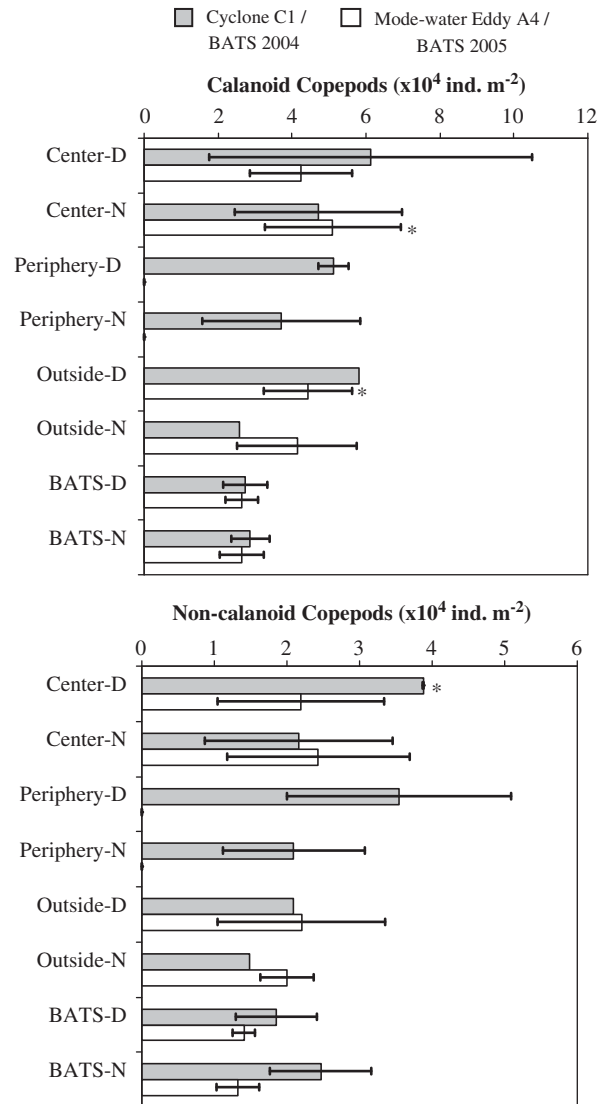


Fig. 3. Comparison of epipelagic zone (0–150 m) integrated abundance of copepods between cyclone C1, mode-water eddy A4, and 2004/2005 BATS summer means, for daytime and nighttime tows at eddy center, periphery, outside the eddy, and at BATS. Gray bars represent cyclone C1, except at BATS where they represent the 2004 summer mean. White bars represent mode-water eddy A4, except at BATS where they represent the 2005 summer mean. Values are mean (\pm 1 s.d.) of integrated abundance (C1, $n = 2$, except for outside station $n = 1$; A4, center and outside day $n = 4$, center and outside night $n = 5$; BATS 2004/2005, $n = 6$). Periphery stations were not sampled in eddy A4 (see text for explanation). * Represents significant ($p < 0.05$ ANOVA) difference from BATS abundance.

3.2.2. Other Crustacea

After the copepods, ostracods were the next most abundant group of crustaceans, making up between 5% and 75% of the non-copepod zooplankton community (Fig. 8). Ostracod abundance appeared higher outside the eddy at nearly all depths, but the results were not significant ($p > 0.05$ ANOVA) (Fig. 9). Ostracods exhibited pronounced diel vertical migration that was stronger at

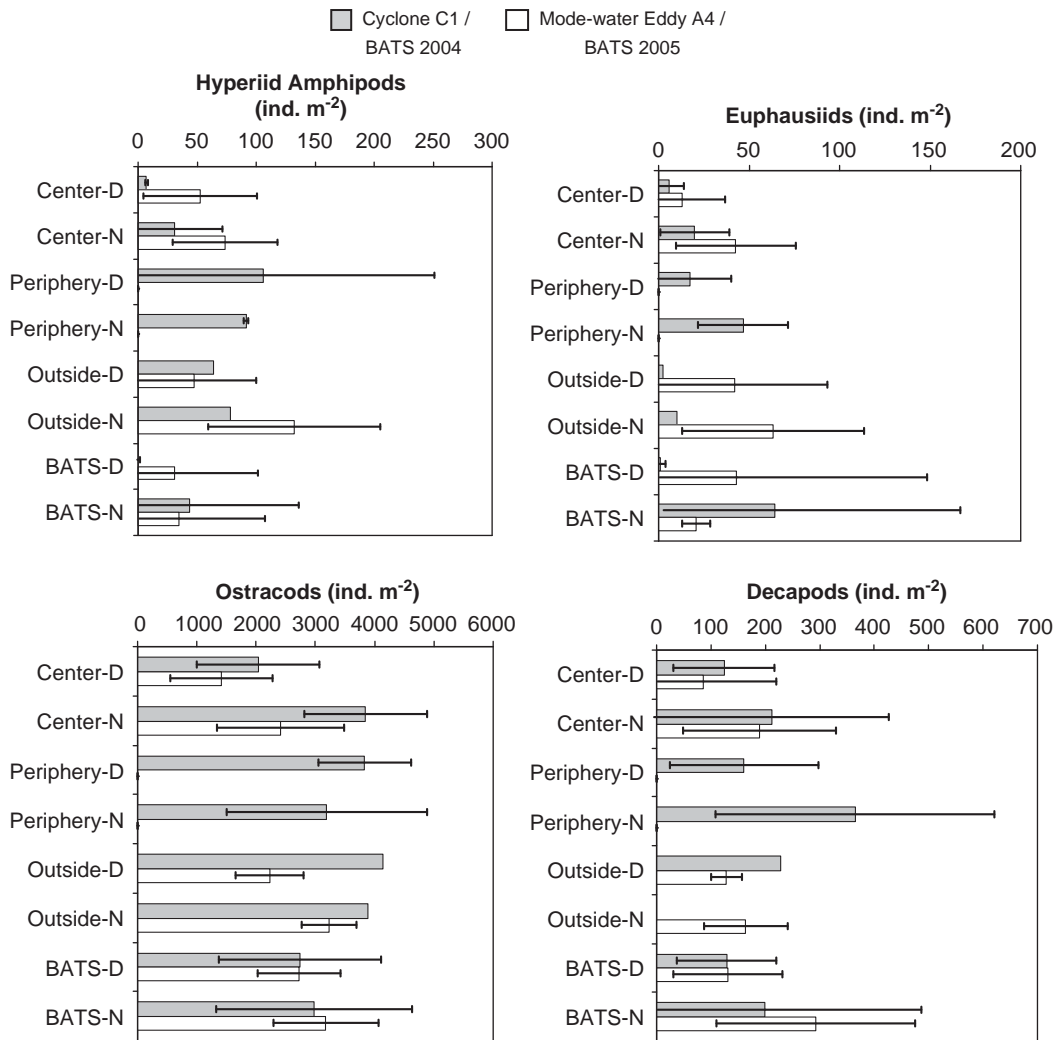


Fig. 4. Comparison of epipelagic zone (0–150 m) integrated abundance of crustaceans other than copepods between cyclone C1, mode-water eddy A4, and BATS, for daytime and nighttime tows at eddy center, periphery, outside the eddy, and at BATS. Figure as described in Fig. 3.

eddy center (higher N:D ratio) but was similar in vertical extent (Δ WMD) inside and outside the eddy (Table 1).

Decapods were the next most abundant group of crustaceans, constituting up to 4% of the non-copepod zooplankton community (Figs. 8 and 9). This group was dominated primarily by *Lucifer* sp. and a variety of decapod larvae and sergestids. As a group, decapods exhibited strong diel vertical migration at eddy center (Table 1). Outside the eddy, both N:D ratio and Δ WMD of decapods were considerably lower, suggesting enhanced vertical migration inside the eddy (Table 1).

Euphausiids and hyperiid amphipods were the least abundant of the crustaceans (Fig. 8). Both of these groups tended to have peak abundances in nighttime tows outside the eddy, although abundances were not significantly different inside vs. outside the eddy ($p > 0.05$ ANOVA) (Fig. 9). Euphausiids and hyperiid amphipods both exhibited marked diel vertical migration, with euphausiids migrating more strongly at eddy center and hyperiid amphipods migrating more strongly outside the eddy (Table 1).

Migrating hyperiid amphipods included members of the family Scinidae and *Phronema* spp. Other than *Pleuromamma* spp., gammarid amphipods exhibited the most pronounced diel vertical migration (N:D ratio and Δ WMD) of all the taxonomic groupings at eddy center (Table 1).

Cyprid stage larvae of the lepadid barnacle *Lepas pectinata* were found in night and daytime tows between 200 and 700 m at all stations in abundances that exceeded the abundance of many of the other crustacean groups (Fig. 9). Peak abundance was between 500 and 600 m, and cyprids were absent from tows shallower than 200 m (Fig. 9). Barnacle cyprids made up as much as ~32% of the zooplankton abundance between 200 and 700 m (Fig. 8). Although samples from > 150 m were not fully enumerated for cyclonic eddy C1, a cursory microscopic survey of samples from the 500–600 m depth interval indicated the presence of *Lepas pectinata* cyprids at all sampling locations in abundances similar to those found in mode-water eddy A4. The cyprids did not vertically migrate (Table 1).

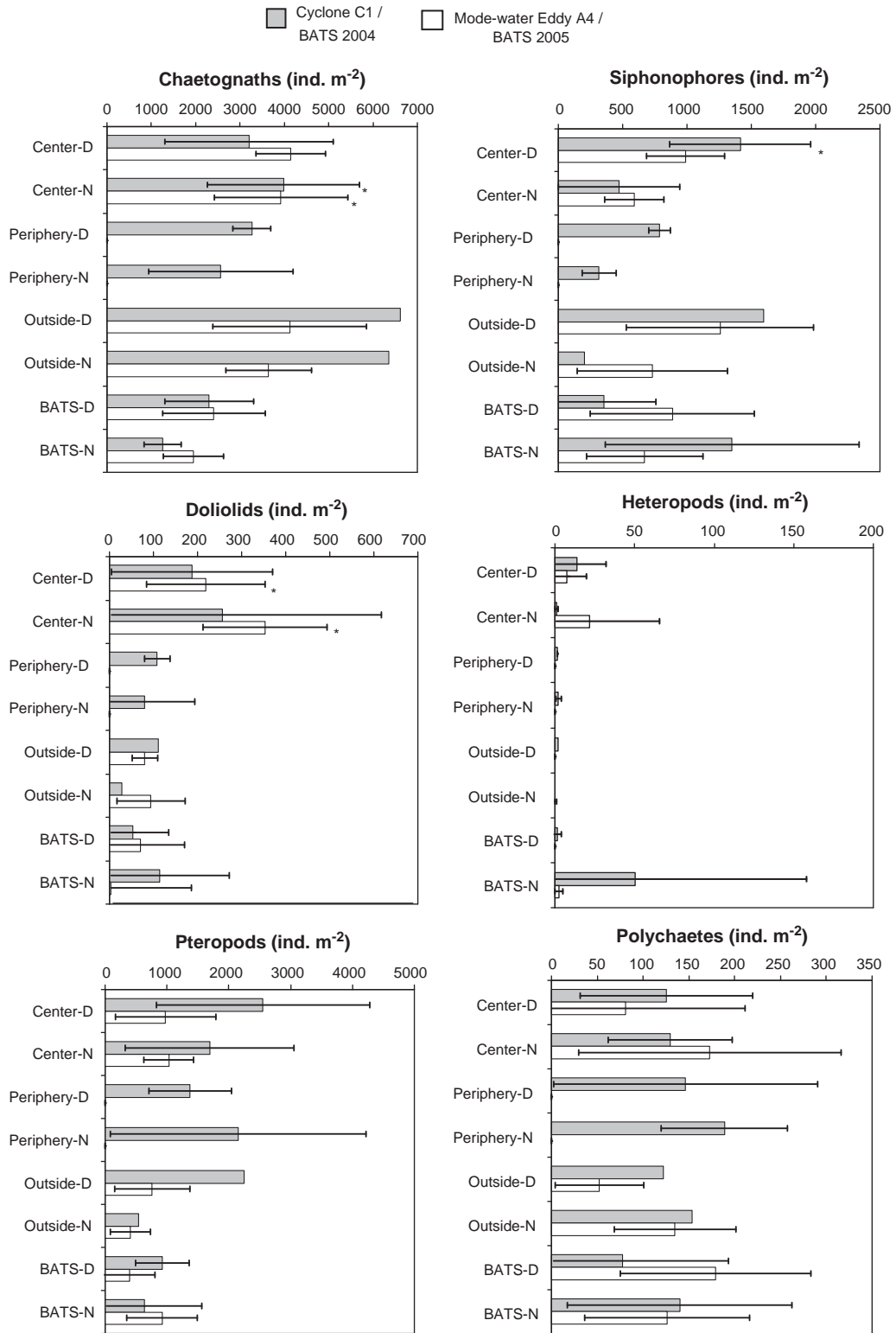


Fig. 5. Comparison of epipelagic zone (0–150 m) integrated abundance of gelatinous zooplankton between cyclone C1, mode-water eddy A4, and BATS, for daytime and nighttime tows at eddy center, periphery, outside the eddy, and at BATS. Figure as described in Fig. 3.

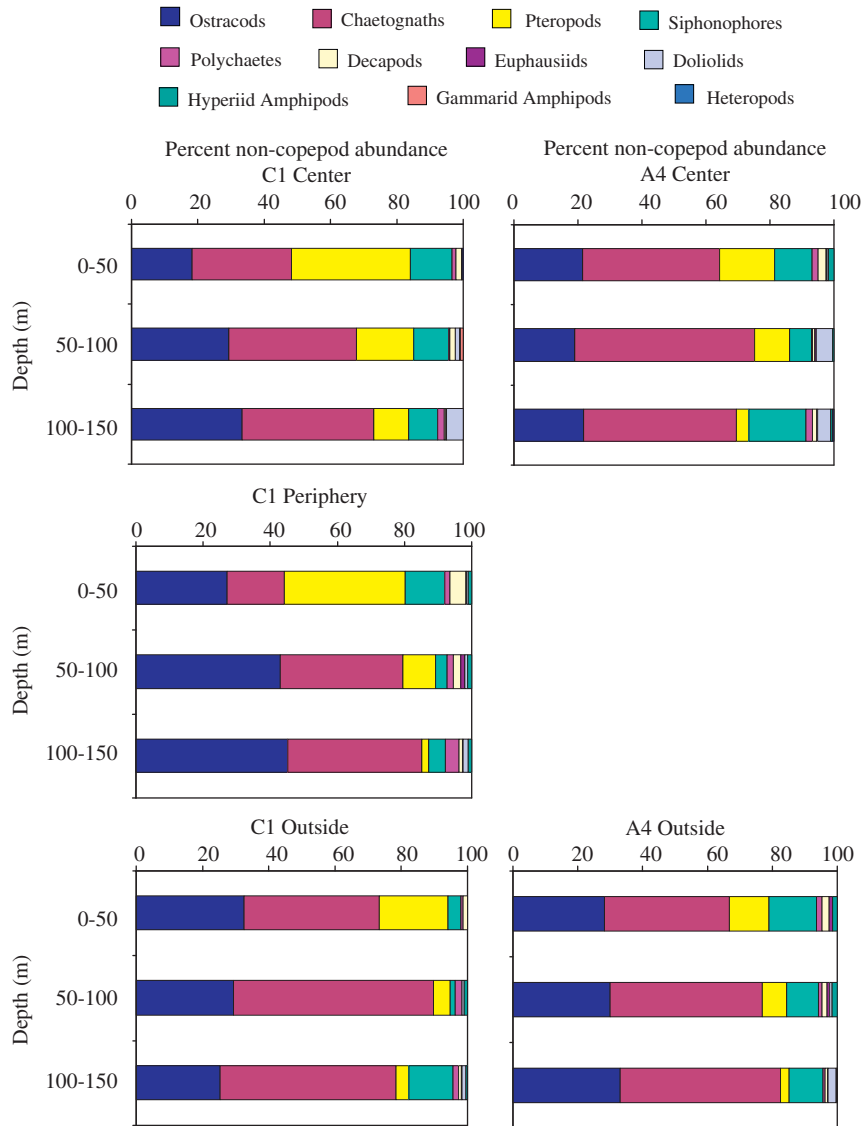


Fig. 6. Percent abundance of epipelagic non-copepod zooplankton in cyclone C1 and mode-water eddy A4. Abundance is mean of day and night tows for each depth interval. Periphery stations were not sampled in eddy A4 (see text for explanation).

3.2.3. Gelatinous zooplankton

Chaetognaths were the third most abundant taxa in the surface waters (~4–10% of the total community) and were the most abundant gelatinous zooplankton taxon sampled (Fig. 8). The vertical distribution of chaetognaths closely follows that of the copepods (Figs. 7 and 10). Chaetognaths as a broad taxonomic group did not exhibit pronounced diel migration, as evidenced by a low N:D and negative day-night changes in WMD (Table 1). Cnidarians, such as siphonophores, were also common in the tows, making up as much as 22% of the non-copepod zooplankton community (Fig. 8). Most siphonophores sampled were calycophoran (families Abylidae and Diphyidae). Siphonophores peaked in abundance in the surface waters, with abundance reduced by ~75% below 150 m

(Fig. 10). Similar to chaetognaths, siphonophores did not exhibit diel migration (Table 1). There was no significant difference in siphonophore or chaetognath abundance inside vs. outside the eddy ($p > 0.05$) (Fig. 10).

Doliolids were the only pelagic tunicate present in tows with abundance > 1 individual m^{-3} (larvaceans were virtually absent from tows and were probably damaged beyond recognition). Doliolid abundance peaked between 50 and 100 m (Fig. 10). In the surface waters, doliolids appear more abundant at eddy center than outside, but this difference was not significant ($p > 0.05$ ANOVA) (Fig. 10). Doliolids migrated more strongly at eddy center vs. outside the eddy (Table 1). Doliolids were the only taxonomic group that showed significantly higher integrated water column abundance (0–700 m) at eddy center

Table 1
Diel vertical migration indices for major taxa of zooplankton in C1 and A4.

Eddy and taxon	Center N:D ratio in surface 150 m		Periphery N:D ratio in surface 150 m			Outside N:D ratio in surface 150 m			
CYCLONE C1	n = 2/2		n = 2/2			n = 1/1			
Calanoid copepods	0.8		0.7			0.4			
<i>Pleuromamma</i> spp.	26.2		98.2			22.6			
Non-calanooid copepods	0.6		0.6			0.7			
Ostracods	1.9		0.8			0.9			
Decapods	1.7		2.3			<0.1			
Euphausiids	3.4		2.7			4.4			
Hyperiid amphipods	3.3		0.9			1.2			
Gammarid amphipods	– ^a		– ^a			– ^a			
Chaetognaths	1.2		0.8			1.0			
Siphonophores	0.3		0.4			0.1			
Doliolids	1.4		0.7			0.3			
Salps	– ^a		0.3			5.5			
Pteropods	0.7		1.6			0.2			
Heteropods	0.1		1.4			<0.1			
Polychaetes	1.0		1.3			1.3			
Barnacle Cyprids	– ^b		– ^b			– ^b			
Eddy and taxon	Center N:D ratio in surface 150 m	Outside N:D ratio in surface 150 m	Center WMD Day (m)	Center WMD Night (m)	Center ΔWMD (m)	Outside WMD Day (m)	Outside WMD Night (m)	Outside ΔWMD (m)	
MODE-WATER EDDY A4	n = 5/4		n = 4		n = 5			n = 5	
Calanoid copepods	1.2	0.9	163	130	33	146	123	23	
<i>Pleuromamma</i> spp.	76.4	64.4	587	91	496	580	93	487	
Noncalanooid copepods	1.1	0.9	184	146	38	162	145	17	
Ostracods	1.7	1.4	221	167	54	193	138	55	
Decapods	2.2	1.3	150	50	100	98	66	32	
Euphausiids	3.3	1.5	311	191	120	178	97	81	
Hyperiid amphipods	1.4	2.8	116	63	53	181	84	97	
Gammarid amphipods	19.5	– ^a	533	167	366	264	191	73	
Chaetognaths	0.9	0.9	92	99	–7	99	106	–7	
Siphonophores	0.6	0.6	91	127	–36	88	105	–17	
Doliolids	1.6	1.2	139	138	1	136	152	–16	
Salps	3.7	0.1	221	53	168	119	109	10	
Pteropods	1.1	0.5	164	89	75	115	109	6	
Heteropods	2.9	– ^a	124	125	–1	304	133	171	
Polychaetes	2.1	2.6	226	139	87	204	149	55	
Barnacle Cyprids	– ^b	– ^b	524	489	35	526	479	47	

N:D ratio – Ratio of night:day taxon abundance integrated over the surface 0–150 m. Ratio was computed after abundance values were averaged across all tows at each location. WMD – Weighted mean depth for day and night (see methods). ΔWMD – Vertical extent of the migration, calculated as day WMD minus night WMD. Dash (–) indicates not determined (see footnote for explanation). Sample size, n, (day/night) is indicated at head of each column.

^a Either did not occur in 0–150 m layer in day (i.e., N:D undefined) or at night (i.e., N:D = 0).

^b Did not occur.

vs. outside the eddy for both day ($p = 0.006$, ANOVA) and night ($p = 0.05$ ANOVA) tows. Salps were highest in abundance outside the eddy, and generally decreased in abundance with depth (Fig. 10). Despite their patchy depth distribution, salps appear to be migrating more strongly at eddy center than outside the eddy (Table 1).

Of the pelagic gastropods (pteropods and heteropods), heteropods (mostly of the families Atlantidae and Pterotracheidae) were present in relatively low abundance ($<1 \text{ ind. m}^{-3}$) and were more common in eddy center vs. outside (Fig. 11). The pteropods were dominated by Thecosome (shelled) pteropods of the families Limaciniidae and Cavoliniidae and were relatively numerous in surface waters ($\sim 10 \text{ ind. m}^{-3}$) (Fig. 11). Gymnosome

(shell-less) pteropods were rare at all locations and depths. Pteropods were most abundant in the epipelagic zone and decreased with depth at both locations (Fig. 11), yet constituted as much as 20% of the non-copepod zooplankton community (Fig. 8). Diel vertical migration of pteropods was negligible at eddy center and absent outside the eddy; however, the vertical extent of migration was greater at eddy center than outside (Table 1).

Polychaetes, mostly of the families Alciopidae and Tomopteridae, exhibited a mesopelagic peak (100–200 m) in abundance in the day, which shoaled to 0–50 m at night (Fig. 11). Thus diel vertical migration was pronounced, and polychaetes exhibited some of the largest changes in vertical extent of migration of the taxa sampled (Table 1).

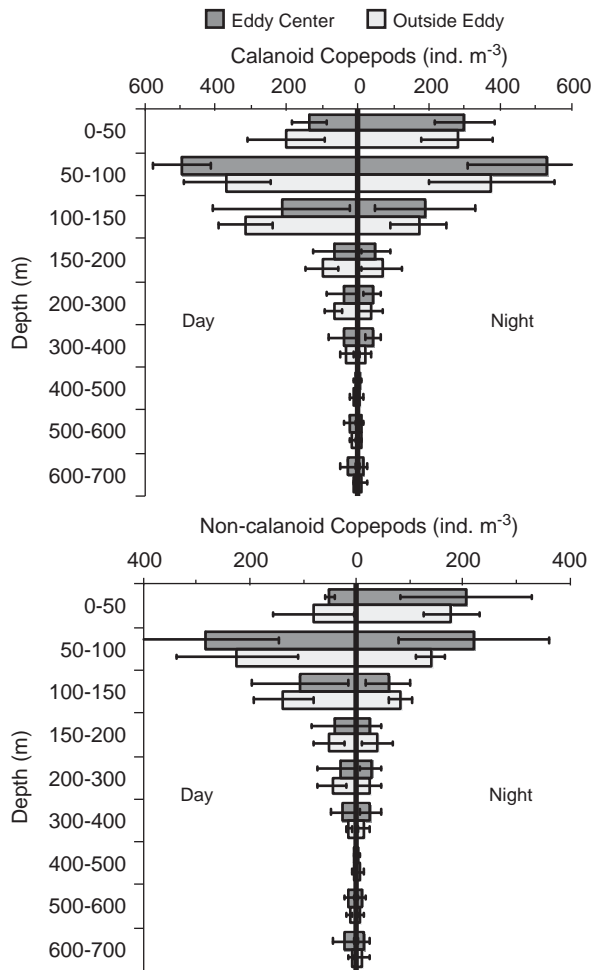


Fig. 7. Day/night profiles of copepod taxonomic abundance at the center and outside of mode-water eddy A4. Values are mean (± 1 s.d.) of $n = 4$ for center/outside day and $n = 5$ for center/outside night. Note abundance scales differ by taxonomic group, and depths are 50 m intervals in the top 200 m, and 100 m thereafter.

3.3. Changes in zooplankton abundance over time

This study also provided the unique opportunity to monitor changes in the zooplankton community over the eddy lifecycle, as sampling of these eddies extended over 43–62 days. Total epipelagic zooplankton abundance (depending on location and time of day) in cyclone C1 decreased by ~ 14 –56% over a period of 43 days, and increased by ~ 13 –250% in mode-water eddy A4 over a period of 62 days.

In both eddies we examined in more detail the changes in epipelagic abundance over time for the three most abundant taxonomic groups (total copepods, chaetognaths, and ostracods). In cyclone C1 decreases in abundance at eddy center for the three groups ranged from 47–60% (Fig. 12), and decreases at the periphery ranged from 16–62% (Fig. 12). Total copepod abundance decreased in cyclone C1 over time at all sampling locations and times of day. Outside eddy stations were not examined as

there was a short time span between samples. While slight increases in abundance were noted for chaetognaths and ostracods in daytime tows at eddy periphery, decreases in abundance over time were seen for these two groups in daytime tows at eddy center as well as nighttime tows at periphery stations.

Conversely, in mode-water eddy A4, abundance of these three groups increased from 20–343% at eddy center and remained relatively constant over the duration of sampling outside the eddy (Fig. 13). Total copepod abundance increased during both day and night at eddy center. While slight decreases in abundance were observed for chaetognaths and ostracods in nighttime tows at eddy center, these two groups increased in abundance in daytime tows at eddy center. Total water column abundance (0–700 m) for the three groups tracked epipelagic abundance (0–150 m) over time in eddy A4 (data not shown).

3.4. Zooplankton abundance relationship with chlorophyll distribution

In both eddy C1 and A4, the deep chlorophyll maximum fell within the depth range sampled by the 50–100 m net (usually ~ 80 –90 m) (McGillicuddy et al., 2007). Analysis of zooplankton abundance in the centers of eddy A4 and eddy C1 indicated that 4 and 6, respectively, of the 14 broad taxonomic groups sampled (i.e., excluding *Pleuromamma* spp. copepods and barnacle cyprids) during day and nighttime tows had peak abundances in the 50–100 m depth interval. Zooplankton sampled during day and nighttime tows outside both eddies also showed elevated abundances in the 50–100 m depth interval (5, for A4, and 9 for C1, of the 14 groups sampled). Importantly, groups with elevated abundance in the Chl maximum included the most numerous herbivorous taxa, the copepods (both inside and outside the eddy). However, there was no significant relationship found between surface-integrated (0–150 m) zooplankton abundance (by taxonomic group) and surface-integrated (0–140 m) chlorophyll concentration at any location or sampling time in either eddy (regression $p > 0.05$). Lack of correlation in these vertically-integrated quantities is not surprising, given that the eddy-induced perturbation in nutrient availability and autotrophic activity is mostly confined to the deep chlorophyll maximum, which occupies a relatively small fraction of the depth intervals sampled.

3.5. Comparison with BATS

A comparison of epipelagic zooplankton abundance of the various taxa indicated some significant differences between mean conditions at the BATS site and eddy C1. Daytime abundances of both non-calanoid copepods and siphonophores at eddy C1 center were significantly higher ($p = 0.02$, $p = 0.04$, respectively, ANOVA) than the daytime BATS summer mean (Figs. 3, 5). In addition, nighttime chaetognath abundance at eddy center was higher ($p = 0.04$ ANOVA) than the nighttime BATS summer mean

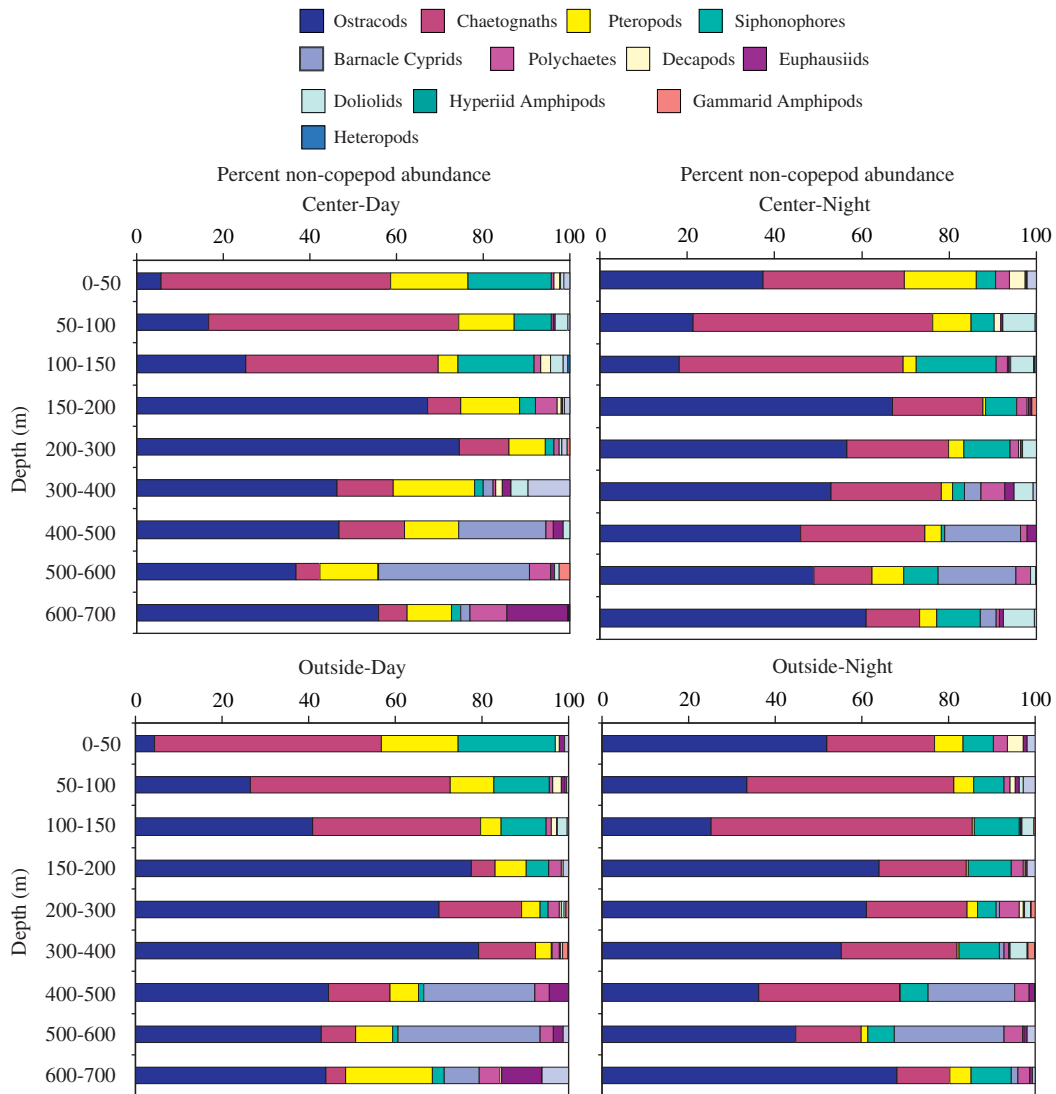


Fig. 8. Percent abundance of non-copepod zooplankton during day and night inside and outside mode-water eddy A4. Values are the mean of $n = 4$ (center/outside, day), or $n = 5$ (center/outside night).

(Fig. 5). All other taxonomic groups showed no significant ($p > 0.05$ ANOVA) differences between eddy C1 and BATS (Figs. 3, 4, 5). Results from the cluster analysis performed to further investigate potential differences in epipelagic abundance between eddy C1 and BATS indicated no significant groupings by location.

Diel vertical migration of about half of the taxa (9 of the 16 groups examined) was stronger (higher N:D ratio) at the BATS site than at any location sampled inside or outside eddy C1 (Tables 1, 2). However, the N:D ratio of the most abundant taxonomic group (calanoid copepods) was similar between eddy C1 and BATS (Tables 1, 2).

A comparison of epipelagic zooplankton abundance of the various taxa at BATS (June–August, 2005) with mode-water eddy A4 (ANOVA) indicates significantly higher abundances at eddy center versus BATS for calanoid copepods (Fig. 3), chaetognaths (Fig. 5), and doliolids

(Fig. 5). For all other groups, there was no significant difference ($p > 0.05$) between eddy center, outside, and BATS (Figs. 3, 4, 5). Cluster analysis further indicated no significant groupings by location.

When indices of migration (N:D ratio) between the mode-water eddy and BATS are compared, about half (9 of the 16) of the taxonomic groups examined are migrating more strongly at eddy center vs. BATS (Tables 1, 2).

4. Discussion

4.1. Zooplankton communities in cyclones vs. mode-water eddies

Zooplankton community dynamics can be challenging to quantify given the patchiness that exists on various

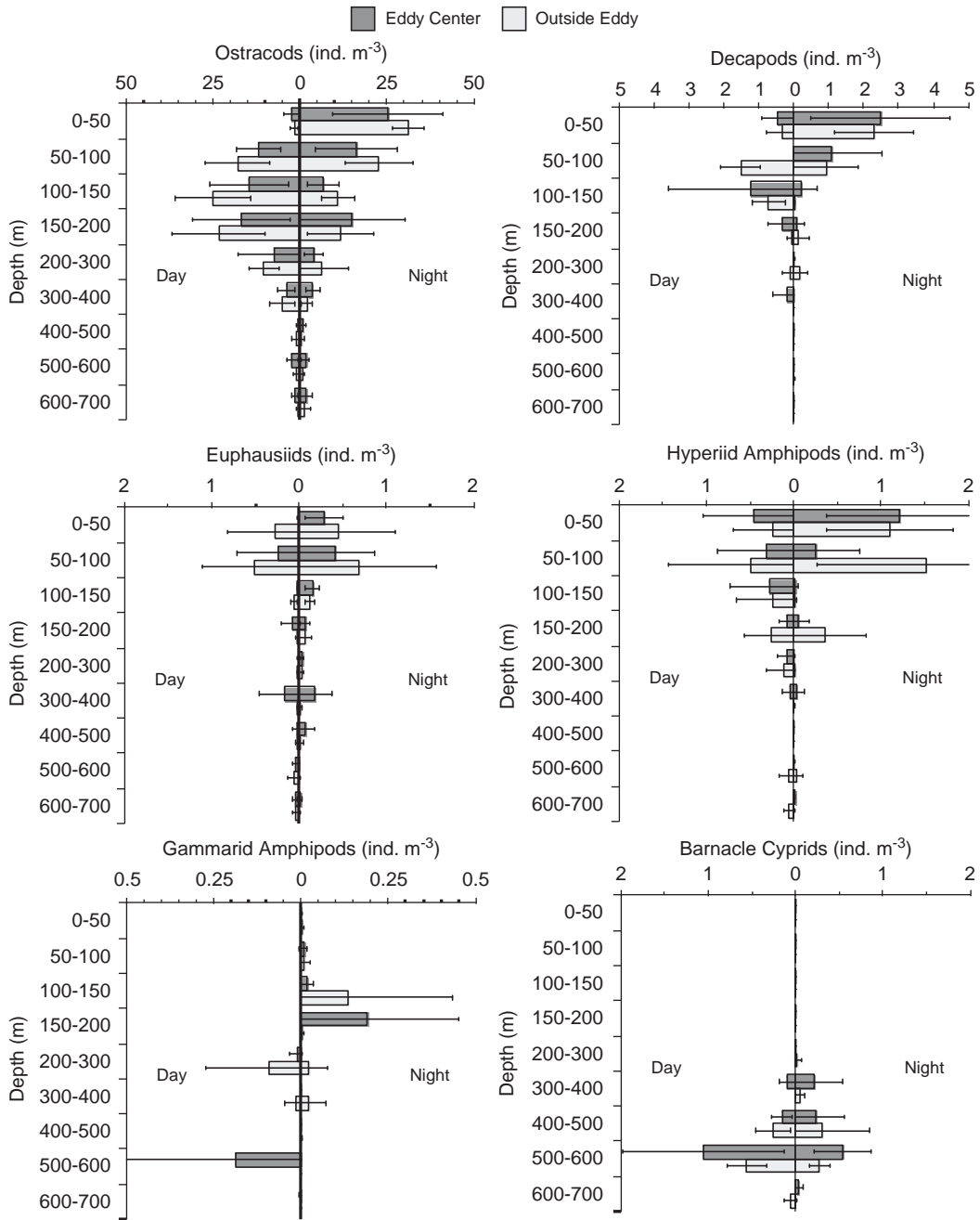


Fig. 9. Day/night profiles of other crustacean taxonomic abundance in the center and outside of mode-water eddy A4. Figure as described in Fig. 7.

temporal and spatial scales. A suite of biological and physical parameters can influence zooplankton patchiness, including population dynamics, advection, and behavior, all of which can be altered by the presence of mesoscale eddies (Huntley et al., 2000). Despite the considerable difference in both chlorophyll concentration and phytoplankton species composition (McGillicuddy et al., 2007; Bibby et al., 2008) between the two eddies, there were few significant differences between eddy types in abundance of the various zooplankton taxa. Goldthwait

and Steinberg (2008) also found similar zooplankton biomass in these two eddies, further indicating that both eddy types produced a similar broad zooplankton community response rather than a response from individual taxonomic groups. However, the broad taxonomic categories we used may have disguised changes in abundance of some individual species (see Section 4.5 below).

Given the potentially distinct source waters for the two eddies sampled herein (C1 from the southeastern Sargasso

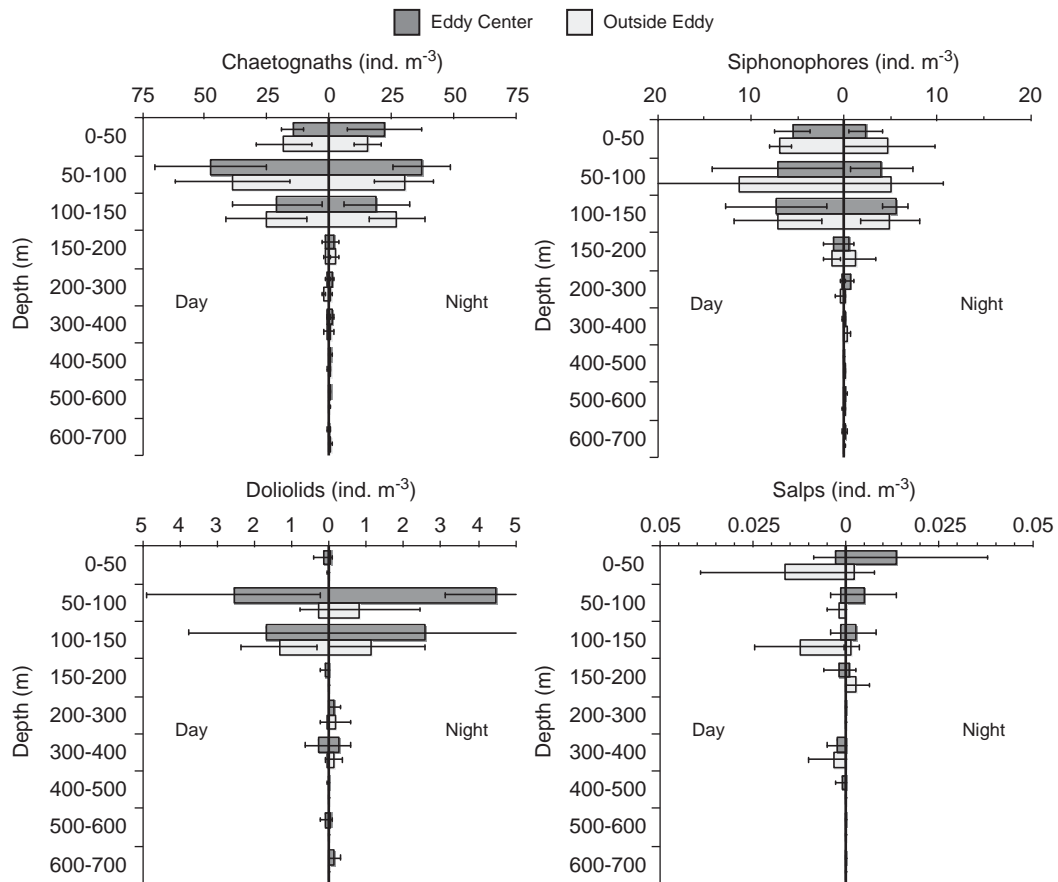


Fig. 10. Day/night profiles of gelatinous zooplankton taxonomic abundance in the center and outside of mode-water eddy A4. Figure as described in Fig. 7.

Sea, and A4 from the northern/eastern Sargasso Sea), their similarity in zooplankton community composition is somewhat surprising, particularly as other types of eddies, warm core and cold core Gulf Stream Rings, which originate from different source waters, support two different zooplankton communities (Wiebe et al., 1976a; Wiebe et al., 1976b; Ortnier et al., 1978; The Ring Group, 1981; Davis and Wiebe, 1985; Roman et al., 1985; Wormuth, 1985; Beckmann et al., 1987). Increases in abundance, as demonstrated for some of the common taxa in eddy A4, could be attributed to zooplankton enhanced growth and reproduction, as well as their aggregation in areas with high food densities (Huntley et al., 2000). Zooplankton generation times, especially those of the larger taxa, range from weeks (large copepods) to months (euphausiids) (Huntley et al., 2000). The lifespan of mesoscale eddies (several months to a year) may thus provide adequate time for zooplankton to exhibit a reproductive response (Huntley et al., 2000).

While the abundance of the various taxa in the epipelagic zone was not significantly different between the eddy types, the strength of vertical migration (N:D ratio) was higher for about three quarters of the taxa inside and outside of the mode-water eddy (A4) compared to inside and outside the cyclone (C1). This could be

attributed to a difference in availability and type or size of phytoplankton prey between the two eddies. Higher availability of a more favored food (diatoms) may have caused zooplankton in mode-water eddy A4 to migrate more strongly. Similarly, Steinberg et al. (2008a) found stronger diel vertical migration (N:D ratio) in zooplankton sampled at a site dominated by large diatoms (station K2 in the subarctic North Pacific Ocean) as compared to a site dominated by picoplankton and cyanobacteria (station ALOHA in the subtropical North Pacific gyre). Zooplankton migratory behavior has also been shown to be influenced by food availability, such that as food availability decreases the vertical extent of zooplankton migration also decreases (Huntley and Brooks, 1982; Johnsen and Jakobson, 1987; Lampert, 1989). Because food was less limiting at the center of eddy A4 vs. the center of eddy C1, we would expect to see more pronounced (i.e., larger Δ WMD or N:D ratio) diel vertical migration associated with zooplankton at the center of mode-water eddy A4. However, because more pronounced migratory behavior occurred outside eddy A4 vs. outside C1 as well, the results can not be attributed solely to the presence of the diatom bloom inside eddy A4. Alternative explanations include (1) interannual differences (i.e., 2004 vs. 2005) in larger-scale Sargasso Sea zooplankton diel migration

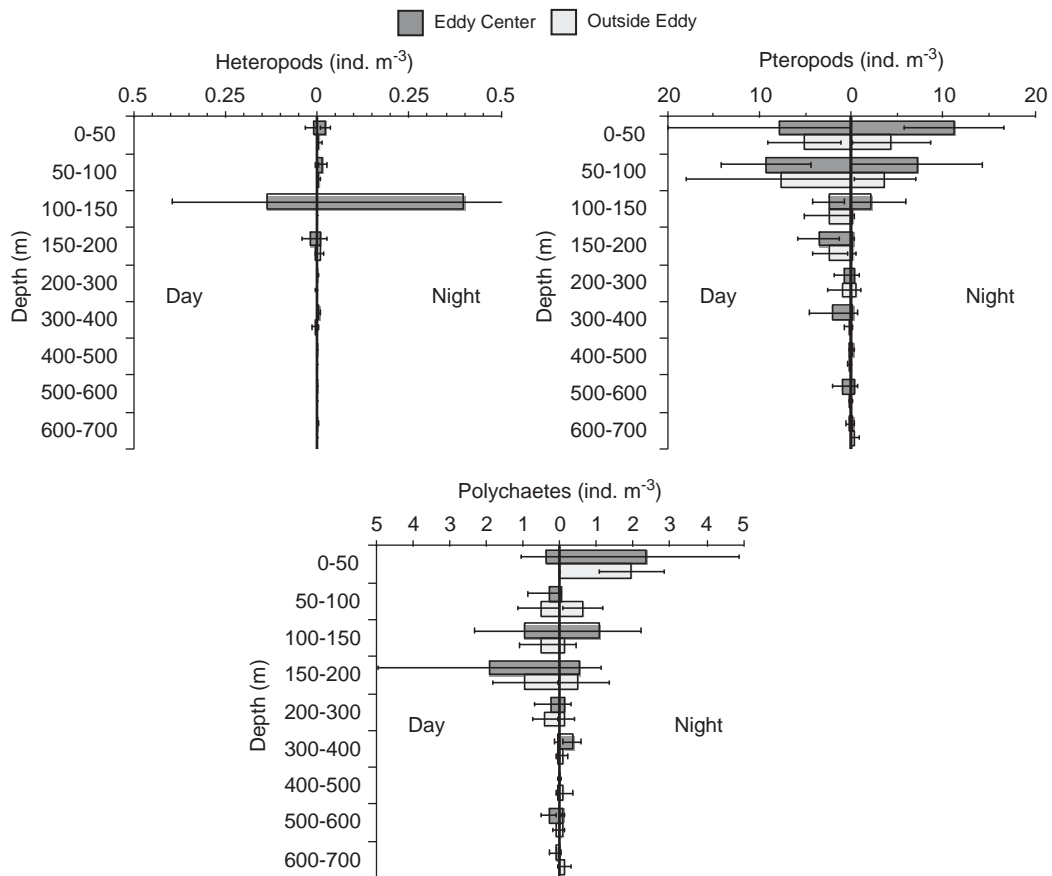


Fig. 11. Day/night profiles of gelatinous zooplankton taxonomic abundance in the center and outside of mode-water eddy A4. Figure as described in Fig. 7.

(e.g., Steinberg et al., 2000) and (2) differences in the ambient conditions outside the two eddies.

Although the vertically integrated abundance of different taxa both in and outside the eddy was not significantly correlated with vertically integrated Chl *a*, it is possible that several physical, chemical, and biological factors (current speed and direction, phytoplankton patchiness, predator abundance, etc.) could be combining to cause a peak in abundance coincident with the Chl *a* maximum for many of the taxa. It is also possible that the high variability in zooplankton abundance at eddy center (A4) could be related to the patchy distribution of the central diatom bloom, which was restricted to a small area (~20–30 km in diameter) (Bibby et al., 2008).

4.2. General vertical patterns in zooplankton community structure

Because zooplankton diel vertical migration tends to be more pronounced in areas of higher food availability, the higher strength of migration observed at the center and periphery of eddy C1 can likely be attributed to the elevated chlorophyll *a* values seen inside the eddy during early occupations of C1 (McGillicuddy et al., 2007) and in the periphery later on (Fig. 1B) (Huntley and Brooks, 1982;

Johnsen and Jakobson, 1987; Lampert, 1989). Given that Chl *a* concentrations were higher at the center of eddy A4 than outside the eddy and at BATS (McGillicuddy et al., 2007; Bibby et al., 2008), we may expect to see more pronounced zooplankton migration at eddy center. Sameoto (1984, 1986) also found that regions of elevated primary productivity were correlated with vertical biomass distributions, as some taxa may preferentially concentrate within the Chl *a* maximum. Both Herman (1983) and Castro et al. (1991) found that the dominant calanoid copepod species in their respective study areas tended to aggregate in the deep chlorophyll maximum.

4.3. General horizontal patterns in zooplankton community structure

At night, several taxa in eddy A4 center (e.g., calanoid and non-calanoid copepods, doliolids, pteropods and polychaetes) were more abundant than outside the eddy, particularly in the epipelagic zone. As mentioned above, elevated nighttime epipelagic abundances at eddy center for many taxa was most likely a result of enhanced zooplankton vertical migration in response to greater food availability. The central region of eddy A4 was exceptional in that it contained the highest primary production rates

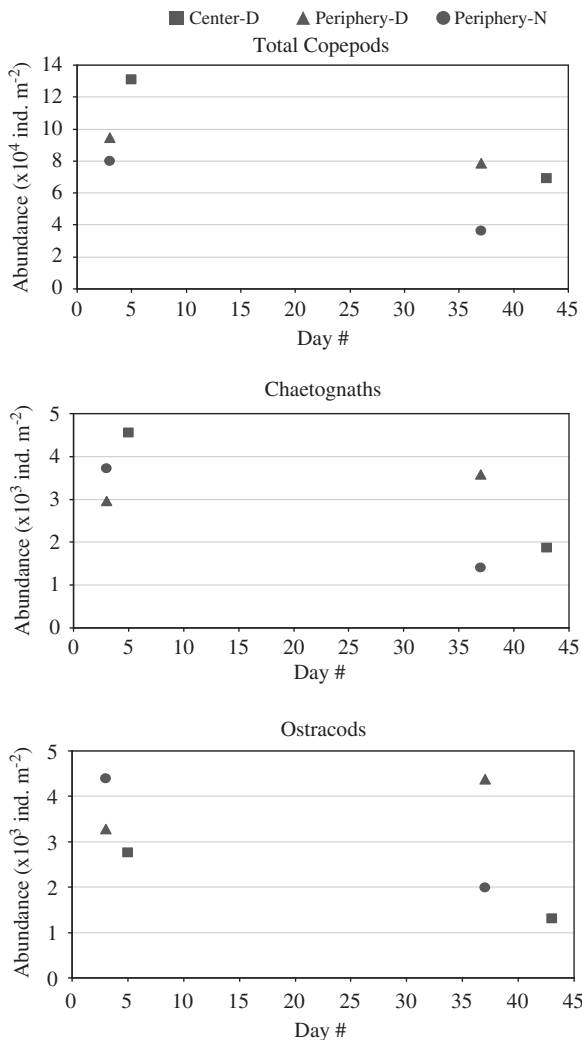


Fig. 12. Changes in epipelagic abundance of total copepods (calanoid+non-calanoid), chaetognaths, and ostracods over time during day and night in cyclone C1 center* and periphery, day 1 (22 June 2004) to day 43 (4 August 2004). No outside eddy comparison is shown as only one outside eddy station was sampled (i.e., no time lapse). *Excludes eddy center night because of short (3 day) interval between enumerated tows. Each point represents $n = 1$ (tow).

ever measured at 60–80 m relative to the BATS climatology (McGillicuddy et al., 2007). In addition, Goldthwait and Steinberg (2008) measured peak gut fluorescence for the migrating copepod *Pleuromamma xiphias*, higher fecal pellet carbon flux, and high, but variable, zooplankton biomass at eddy center. The significantly higher doliolid abundance at eddy A4 center vs. outside also suggests a response to improved food conditions within this eddy. Doliolids can reproduce asexually, allowing them to rapidly reproduce and form blooms in response to improved food conditions (Deibel, 1985, 1998; Gibson and Paffenhofer, 2002). While eddy A4 did persist long enough (several months) to allow sufficient time for other groups of zooplankton to reproduce, doliolids are

particularly well suited for taking advantage of the diatom bloom seen in eddy A4.

Landry et al. (2008b) saw similar increases in zooplankton biomass without significant changes in zooplankton community structure in a diatom-dominated cyclonic eddy in the lee of the Hawaiian Islands. The authors also propose a broad zooplankton community increase in the area perturbed by the cyclone, as opposed to specific taxonomic differences between sampling locations inside and outside of the eddy. Goldthwait and Steinberg's (2008) analysis of zooplankton biomass from these two eddies indicates that zooplankton samples from the BATS site were more representative of ambient conditions, and that when compared with BATS, both eddies had significantly higher biomass.

For most taxonomic groups in this study, the standard deviations of the zooplankton abundances at BATS were much smaller than at center and outside stations in eddy A4. This suggests that the mean conditions at the BATS site are more stable, and that the eddy stations were subject to a greater amount of physical, chemical, and biological variability due to the influence of the eddy. Therefore, our data indicate that the mean condition at BATS may be a more representative “outside eddy” station than the stations noted as outside stations, which may have been under the influence of the eddy at its edge, or were influenced by other eddies (eddy-eddy interaction). Because the Sargasso Sea is so densely populated with mesoscale eddies, it is difficult to discern the boundary between an eddy and its adjacent neighboring eddies.

Eddy lifecycle also plays an important role in the distribution of zooplankton. Mode-water eddy A4 was still in a “bloom phase”, and macronutrients were being consistently supplied to the surface waters through upwelling for the entire duration of sampling (June–August) (McGillicuddy et al., 2007; Ledwell et al., 2008; Li and Hansell, 2008). Conversely, cyclonic eddy C1 was in a “decay phase.” Although its altimetric history indicated a recent intensification prior to sampling (McGillicuddy et al., 2007), during our observations eddy center was characterized by subsiding isopycnals and a transition from a local maximum to a local minimum of chlorophyll *a*. The contrasting phases of the two eddies are further supported by the temporal trends in zooplankton abundance. Decreases in epipelagic abundance over a ~1 month period of the three most abundant taxa in eddy C1 indicate that zooplankton abundance was presumably driven by the “decay phase” portion of eddy C1's lifecycle. Conversely, increases in epipelagic abundance over a ~2 month period for the same three taxa in eddy A4 suggest that the zooplankton community was responding to the sustained, high levels of macronutrients being supplied to the surface waters through upwelling and the resultant diatom bloom. Goldthwait and Steinberg (2008) saw similar results in their analysis of zooplankton biomass over the same time interval in both of these eddies. Most notably, zooplankton biomass was elevated throughout the summer in eddy A4, while zooplankton biomass reached a peak in late June and decreased slowly throughout the remainder of the summer sampling period in eddy C1.

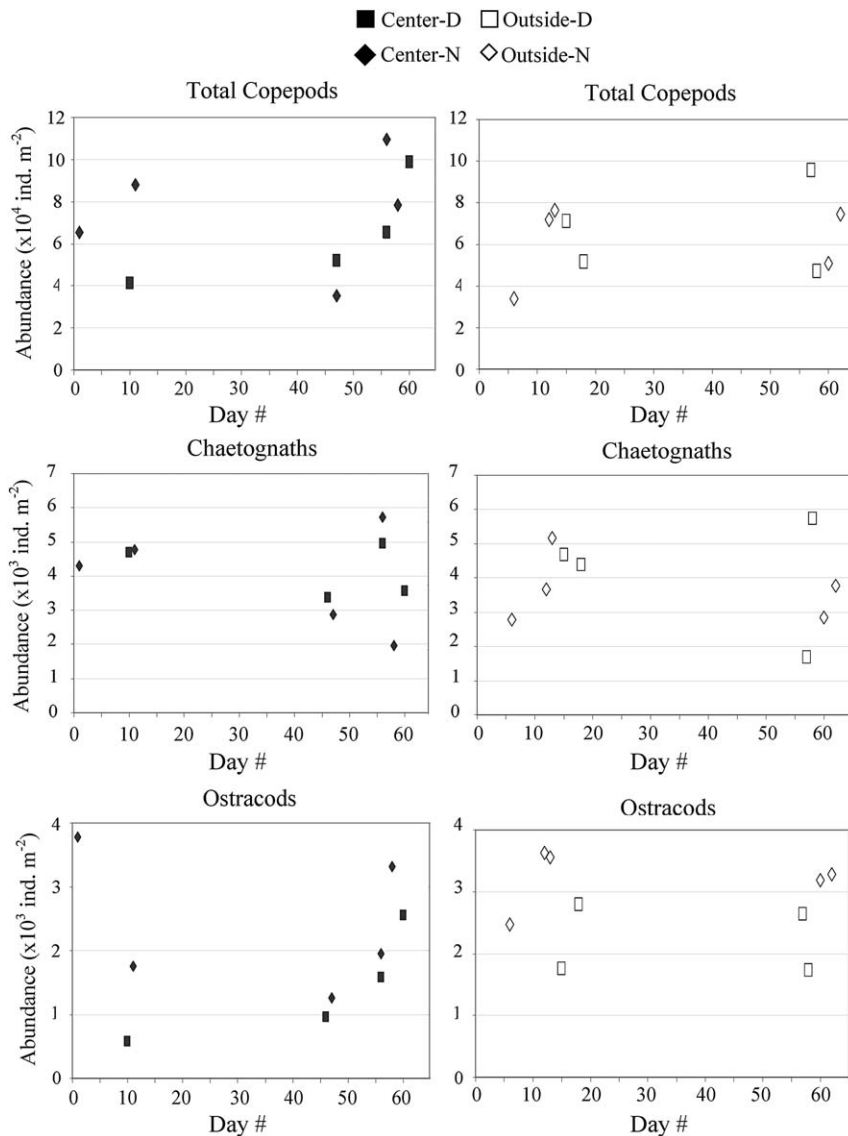


Fig. 13. Changes in epipelagic abundance of total copepods (calanoid+non-calanoid), chaetognaths, and ostracods over time during day and night tows at mode-water eddy A4 center and outside, day 1 (25 June 2005) to day 62 (25 August 2005). Each point represents $n = 1$ (tow).

4.4. Potential for transport and aggregation of zooplankton

Barnacle cyprids found at depth (200–700 m) in both eddies indicate the potential for these eddies to act as a transport and dispersal mechanism for larvae. *Lepas pectinata* is a common North Atlantic barnacle found in the Sargasso Sea, where the adults are most commonly found associated with floating debris, especially *Sargassum* spp. seaweed (Moyse, 1987). Little is known about the life history of this species of barnacle; however Conway et al. (1990) observed similar depth distribution patterns and abundance of *L. pectinata* cyprids in zooplankton tows from the Sargasso Sea near Bermuda and in the Azores frontal region of the North Atlantic Ocean. Cyprids were abundant both inside and outside the

eddies, indicating that their mesopelagic distribution is a widespread phenomenon rather than an eddy-induced effect. Conway et al. (1990) propose that the most likely explanation for this depth distribution in colder, deeper waters is an ontogenetic migration designed to reduce metabolism and extend life expectancy for settlement and metamorphosis to adulthood in a more favorable time of year. Entrainment and transport within these eddies would presumably be beneficial to the barnacles, providing the surface-feeding larval stages (nauplii) with a higher, consistent food source in the epipelagic zone, as well as providing the non-feeding larval stages (cyprids) in the mesopelagic zone with greater dispersal potential, as opposed to larvae outside the eddies.

Table 2

Diel vertical migration indices for major taxa of zooplankton at BATS.

Location and taxon	N:D ratio in surface 150 m	N:D ratio in surface 150 m
BATS Summer Mean	2004 n = 5/6	2005 n = 6/6
Calanoid copepods	1.0	1.0
<i>Pleuromamma</i> spp.	– ^a	– ^a
Non-calanoid copepods	1.3	0.9
Ostracods	1.1	1.2
Decapods	1.5	2.2
Euphausiids	55.1	0.5
Hyperiid amphipods	93.5	1.1
Gammarid amphipods	9.6	0.9
Chaetognaths	0.5	0.8
Siphonophores	3.8	0.8
Doliolids	2.2	– ^b
Salps	2.0	2.0
Pteropods	0.7	2.3
Heteropods	30.9	– ^b
Polychaetes	1.8	0.7
Barnacle Cyprids	– ^b	– ^b

N:D ratio – Ratio of night:day taxon abundance integrated over the surface 0–150 m. Ratio was computed after abundance values were averaged across all tows at each location. Dash (–) indicates not determined (see footnote for explanation). Sample size, n, (day/night) is indicated at head of each column.

^a Either did not occur in 0–150 m layer in day (i.e., N:D undefined) or at night (i.e., N:D = 0).

^b Did not occur.

4.5. Sampling considerations

While we conducted a large number of MOCNESS tows in order to obtain sufficient replication, there was still considerable variability in the data. Zooplankton abundance can fluctuate considerably over small temporal and spatial scales (Angel et al., 1982; Angel and Pugh, 2000); thus, it is conceivable that by the time our nets reached the surface, the ship may have drifted out of the patch of zooplankton we were sampling at depth. Another consideration is the broad taxonomic groups we used to characterize zooplankton abundance, which likely limited our ability to resolve spatial differences within each eddy as well as differences between eddy types. There are over 326 species of copepods (all orders, 0–2000 m) found in the Sargasso Sea near Bermuda (Deevey and Brooks, 1977) and considerable diversity found in most other taxonomic groups (Deevey, 1971; Deevey and Brooks, 1971). A species-level analysis of the present data, although time-intensive, may elucidate some of the factors contributing to the high variability in abundance of major taxa.

In addition to inherent variability in the data set, there are a number of potential errors associated with estimating abundance and biomass of zooplankton with nets (Angel and Pugh, 2000). These include underestimation of fragile or patchy gelatinous zooplankton, daytime net avoidance, vertical migration to depths deeper than the lowest sampling depth, and the inherent patchiness of plankton communities due to passive or active aggregation and rapid reproduction and growth (Steinberg et al., 2008a). While several gelatinous taxa such as

siphonophores, chaetognaths, and polychaetes were well represented in our samples, groups such as larvaceans and hydrozoan medusae were not. Larvaceans are common in summer at BATS (pers. obs.), and hydrozoan medusae were abundant in separate surface tows taken during this study. These groups were likely destroyed beyond recognition, especially in our deeper nets in the MOCNESS (Steinberg et al., 2008a). Furthermore, other taxa such as bloom-forming salps are patchy (Madin et al., 2006) and could be missed (Angel and Pugh, 2000; Roman et al., 2002). Daytime net avoidance appears negligible in our study, with a ~6% increase in 0–700 m integrated abundance at night vs. day at A4 eddy center. Patchiness of phytoplankton in both eddies sampled (McGillicuddy et al., 2007; Bibby et al., 2008) could have led to patchiness of zooplankton, resulting in variable abundance. Lastly, future studies will need to carefully delineate the boundaries between eddies so sampling locations represent distinct conditions.

4.6. Conclusion and potential eddy effects on biogeochemical cycling in the Sargasso Sea

Eddy-mediated changes in zooplankton community structure and behavior could have important implications for the functioning of oligotrophic food webs and the transfer of particulate organic matter to depth, thus affecting carbon sequestration in the deep ocean (Buesseler et al., 2008; Goldthwait and Steinberg, 2008; Steinberg et al., 2008b; Verdeny et al., 2008). Sustained presence of elevated macronutrient levels, particularly in eddy A4 (Li and Hansell, 2008), resulted in a shift to larger phytoplankton species, which in turn is predicted to favor an export food web dominated by larger zooplankton (Michaels and Silver, 1988; Legendre and Le Fevre, 1995). There is some evidence to support a shift toward an export-dominated food web in eddy A4 as we saw increases in zooplankton abundance over time at eddy center, coupled with elevated diel vertical migration at eddy center, and elevated copepod and doliolid abundances relative to the BATS summer mean. Furthermore, Goldthwait and Steinberg (2008) saw increased fecal pellet flux in the interiors of both eddies as well as enhanced active carbon transport by diel vertical migration (i.e., consumption of C in surface waters which is metabolized at depth) at the periphery (cyclone) and center (mode-water eddy) over the BATS summer mean (1994–2005). Increases in active carbon transport have also been observed in a cyclonic eddy near Hawaii (Landry et al., 2008b) and an anticyclonic eddy near the Canary Islands (Yebra et al., 2005). The elevated abundance of zooplankton, coupled with enhanced fecal pellet production and stronger diel vertical migration of many taxa at eddy center, would thus increase the efficiency of the biological pump in waters under eddy influence.

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