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Zooplankton inside an Arctic Ocean cold-core eddy: Probable origin and fate

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ABSTRACT

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Keywords: Arctic Ocean Eddy Plankton Chukchi Sea Shelf-basin exchange In September 2004, an extensive survey of a cold-core eddy in the Canada Basin, western Arctic was carried out with high-horizontal-resolution physical and chemical sampling and lower-horizontalresolution biological sampling. The eddy was located over the continental slope north of the Chukchi Shelf and had a radius of \sim 8 km. Its core was centered at a depth of \sim 160 m. Water mass characteristics and the presence of copepods from the North Pacific Ocean (Neocalanus flemingeri and Metridia pacifica) demonstrated that the core contained water of Pacific origin. Vertical distributions of zooplankton were associated with the physical structure of the water column. For most taxa, concentrations in the eddy core were elevated compared with those in similar density water in the surrounding Basin. Based on tracer-age estimates and previous observations of eddy formation, the eddy is believed to have been formed during the previous spring/summer from the Chukchi shelfbreak jet. Surprisingly, the eddy also contained elevated abundances of Arctic-origin copepods (Metridia longa and Calanus glacialis). Analysis of a shelf-basin transect occupied in the region in August 2004 showed that these species were present in high abundances in relatively shallow water (50 m) inshore of the shelfbreak due to upwelling of deeper basin water, and copepods, onto the shelf in response to easterly winds. If the formation of the observed eddy occurred during, or shortly after, a period of such winds, upwelled Arctic-origin copepods on the shelf might have been entrained into the feature. Our observations suggest that formation and subsequent migration of such eddies may provide a mechanism for transporting zooplankton from the Chukchi Shelf into the interior Canada Basin. The periodic input of high abundances of zooplankton from productive shelf areas could affect food webs in the less productive basin.

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DEEP-SEA RESEARCH

PART I

1. Introduction

The extensive continental shelves surrounding the Arctic Ocean occupy over one-third of its area, connect it to subarctic regions, and can impact the deeper regions of the basin. In the western Arctic, the broad and shallow Chukchi shelf links the Pacific and the Arctic Oceans. Waters flowing through the Chukchi Sea are significantly modified during their transit, via atmospheric forcing and interaction with the sediments, and play a significant role in the stratification and circulation of the Arctic Ocean (Aagaard et al., 1981). The Chukchi Sea is also a region of intensive biological productivity, which provides nutrients and biota important to the Arctic ecosystem (Ashjian et al., 2005; Codispoti et al., 2005).

The productivity and plankton composition of the pelagic ecosystem of the western Arctic are regulated by (1) physical forcing mechanisms and hydrographic characteristics of the waters transiting through Bering Strait and over the Chukchi and Beaufort shelves to the Arctic Ocean (Springer et al., 1987; Grebmeier and Harvey, 2005); (2) changes in sea ice including ice extent and thickness, timing of ice melt/thaw cycles, and location of the ice edge (Hansen et al., 2003); and (3) shelf–basin exchange processes between the Chukchi and Beaufort Seas and the adjacent Canada Basin (Ashjian et al., 2005; Kadko and Muench, 2005). In this paper, we investigate the role that one particular shelf–basin exchange mechanism might play in the transport of zooplankton into the Arctic Basin, and the possible effects this may have on the shelf and basin ecosystems and their respective food webs. The mechanism in question is eddy formation from the boundary current that flows along the edge of the Chukchi shelf.

1.1. Hydrography of the Chukchi and Beaufort Seas and Canada Basin

Several distinct water masses from the Pacific Ocean enter the Chukchi Sea through Bering Strait, with a total average volume transport of 0.8 Sv (Roach et al., 1995) (Fig. 1). On the western side, the inflow is dominated by Anadyr water that has the lowest temperatures, highest densities and highest nutrient concentrations (Walsh et al., 1989). The Bering Shelf water is a mixture of Bering Sea water with less-saline, cold water resident on the



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Fig. 1. Representation of the dominant Arctic and sub-arctic copepods (at same magnification) and the mean circulation over the Chukchi and Beaufort Seas. The three main branches of Pacific-origin water from west to east are Anadyr Water (AW), Bering Shelf Water (BSW) and Alaskan Coastal Water (ACW).

northern Bering shelf (Coachman et al., 1975). Adjacent to Alaska, the Alaskan Coastal water is easily identified by its warm summer temperature and relatively low salinities and nutrient concentrations (Coachman et al., 1975). Although there is large variability over a range of timescales, most of the inflowing waters continue northward over the Chukchi shelf where they undergo modifications through physical, chemical, and biological processes. Recent models (Winsor and Chapman, 2004) and observations (Woodgate et al., 2005; Weingartner et al, 2005) indicate that Pacific-origin waters follow three general pathways determined largely by the bathymetry of the Chukchi shelf. The two main branches are channeled by Herald Canyon on the western shelf and by Barrow Canyon on the eastern shelf, while a third branch flows northward through the gap between Herald and Hanna Shoals (known as the Central Channel). The modified Pacific waters reach the shelfbreak of the Canada Basin, and, according to modeling studies (Winsor and Chapman, 2004; Spall, 2007), much of the flow turns eastward to form a shelfbreak current along the upper slope of the Chukchi and Beaufort Seas. Observational evidence supports the existence of such an eastward-flowing shelfbreak jet (Pickart, 2004; Mathis et al., 2007; Nikolopoulos et al., 2009). However, the jet is highly variable and readily reverses due to easterly, upwelling-favorable winds (Münchow et al., 2006; Nikolopoulos et al., 2009).

1.2. Zooplankton and food webs of the study area

The zooplankton community on the Chukchi and Beaufort shelves reflects the mixture of water masses of Pacific and Arctic origin (Fig. 1). Small-sized copepods such as *Oithona similis* and *Pseudocalanus* spp. numerically dominate the zooplankton community of these continental shelves. This prevalence of small copepod species subsequently leads to proliferation of benthic organisms because most of the primary production sinks to the bottom, as is the case in the southern Chukchi Sea where benthic communities of high biomass exist (Grebmeier and Dunton, 2000). In contrast, the presence of large-bodied copepods over the shelf enhances the pelagic ecosystem. From the south, Pacific waters transport large copepods such as Neocalanus spp. and Calanus marshallae (Springer et al., 1989), and the flow from the Arctic Ocean onto the shelves carries other large copepods such as Calanus hyperboreus, Calanus glacialis, and Metridia longa (Johnson, 1958; Thibault et al., 1999). By virtue of their abundance and high lipid content (Sargent and Falk-Petersen, 1988) these large copepods are of major importance in Arctic food webs, and although there are still some uncertainties about their effects on shelf ecosystems (Lane et al., 2007), it is clear that some of these copepod species feed on the shelf-derived primary production (Plourde et al., 2005) and require mechanisms to return to the basin to undergo diapause (Conover, 1988; Conover and Huntley, 1991). Offshore transport is necessary for some Arctic copepod species to complete their life cycle, and variability in offshore transport can play a significant role in modifying the shelf and basin ecosystems.

1.3. Seasonal ice variation

An important process influencing water mass exchange and productivity in the region is ice cover. Annual cycles of freezing and melting sea ice alter the physical properties of waters flowing over the shelves and can impact the biota of the region by reducing the quantity of photosynthetically active radiation at the surface of the water column. Ice formation begins in shallow areas in October (Arrigo and Dijken, 2004), and after that the ice edge advances rapidly, covering the Chukchi Sea. By late February it is at the shelfbreak of the Bering Sea (Grebmeier et al., 1995). During the coldest months, the seasonal flow of Pacific water through Bering Strait and across the Chukchi Shelf is reduced (Coachman and Aagaard, 1988; Roach et al., 1995), and over the shelves, brine formation and cooling modify the winter resident water (Weingartner et al., 1998; Woodgate et al., 2005). Ice melt begins in April and continues until the ice extent reaches a seasonal minimum in September. During this time, phytoplankton blooms follow the receding ice edge and rapidly deplete the nutrients in shelf waters recently exposed to light, and, at the ice edge, productivity increases (Smith and Sakshaug, 1990; Hill and Cota, 2005). High rates of primary production extend from May to August and this results in increased abundance of most zooplanktonic taxa in summer and fall (Smith and Schnack-Schiel, 1990). These highly productive areas formed during the summer are important habitats for birds, fish, and mammals in the Arctic (Dickson and Gilchrist, 2002; Bengtson et al., 2005).

1.4. Shelf-basin exchange mechanisms

The lateral exchange of biological, chemical, and physical properties between shelf and basin can impact ecosystem characteristics and biogeochemical processes of both regions (Walsh, 1995). That such exchange takes place is readily apparent by the significant amount of Pacific water observed seaward of the Chukchi and Beaufort shelves in the interior Canada basin (e.g., Shimada et al., 2001; Steele et al., 2004). Numerous mechanisms are believed to be responsible for this transfer of mass and properties from the shelf to the basin. One process involves the flow of water through canyons. Early studies suggested that some portions of the dense, Pacific winter water was directed down Barrow canyon and entered directly into the Arctic Basin (Coachman and Barnes, 1961; Garrison and Becker, 1976). Another mechanism is wind-forced upwelling (e.g. Münchow and Carmack, 1997). Pacific-origin storms can lead to a strong Ekman circulation with offshore flow in the upper layer and deep onshore flow of Arctic basin water onto the shelf (e.g., Pickart et al., 2006). These events are most prevalent in the fall and winter months (Nikolopoulos et al., 2009) during the active storm season (Wilson and Overland, 1986). However, summertime upwelling events do occur (as discussed later in the paper).

A third shelf-basin exchange mechanism involves the formation and advection of small-scale eddies. Observations from icecamps and drifting buoys indicate that the Canada basin is populated with a large number of subsurface eddies (Manley and Hunkins, 1985; Plueddemann and Krishfield, 2009). Most of the features are anti-cyclones embedded in the halocline and are comprised of Pacific-origin water (Muench et al., 2000). This indicates that they are not formed in the basin interior and likely originate from the edges of the Chukchi and Beaufort shelves. Both warm- and cold-core eddies (relative to the ambient surrounding water) have been observed, although the latter seem to be more prevalent (Plueddemann and Krishfield, 2009). Isotope half-lives (Kadko et al., 2008) and tracer distributions (Muench et al., 2000) imply that the eddies range in age from weeks to over a year.

There is increasing evidence that the eddies in the southern Canada Basin originate from the shelfbreak current (e.g., Manley and Hunkins, 1985; Pickart et al., 2005). Spall et al. (2008) show that, at least during spring and early summer, the potential vorticity distribution of the current satisfies the necessary conditions for baroclinic instability. Using observations from a mooring array, Spall et al. (2008) modeled the shelfbreak jet, which quickly becomes unstable and forms a large number of predominantly anti-cyclonic, cold-core eddies. The characteristics of the model eddies closely match those observed from the drifting buoys. Shipboard hydrographic/velocity transects have revealed such cold-core eddies being formed from the shelfbreak current west of Barrow Canyon along the edge of the Chukchi Sea (Pickart et al., 2005; Mathis et al., 2007).

In this paper, we integrate physical and chemical properties with zooplankton distributions that were obtained during a survey of a cold-core eddy in September 2004 in the Chukchi Sea. We argue that this feature originated at the shelfbreak by showing that biophysical properties in its core are similar to biophysical properties of the shelfbreak region at the estimated time of formation. We begin with a presentation of the physical and chemical properties of the water column and the vertical distribution of zooplankton across a shelf-basin transect in the Chukchi Sea occupied in summer 2004. Among other things, this provides a quantitative description of the shelfbreak jet. This is followed by a description of a cold-core, anti-cyclonic eddy observed later that year. We interpret the water mass properties and species composition in the eddy using the summer boundary current transect as a proxy of the conditions present at the time the eddy was generated. Finally, we estimate the grams of carbon of zooplankton that might be transported annually into the Arctic Ocean via such eddies, and discuss the potential effects that this shelf-basin exchange process can have on the shelf and basin food webs.

2. Methods

The data used in this study were collected on two cruises to the Chukchi and Beaufort Seas and the adjacent Canada Basin on the USCGC *Healy*, in summer from July 17 to August 26, and in early-fall from September 2 to October 1, 2004. The cruises were part of the Western Arctic Shelf Basin Interactions (SBI) program. In summer, stations were located along transects from the Chukchi or Beaufort shelves to the slope waters of the Canada Basin. The West Hanna Shoal (WHS) transect was occupied between August 18 and 24, 2004 (Fig. 2) and provides background on the physical structure and zooplankton distribution of the water column across the shelf-basin boundary. A subsurface, cold-core, anti-cyclonic eddy was sampled over the slope of the Chukchi Sea between September 25 and 26, 2004 (Fig. 2). The sampling in both seasons of 2004 was carried out under unusually ice-free conditions.

2.1. Collection and analysis of hydrographic data

The SBI Service Group provided the hydrographic data from conductivity-temperature-depth (CTD) casts and water samples at all stations. The hydrographic sampling protocols are described by Codispoti et al. (2005) and are only briefly summarized here. The physical (temperature and salinity), chemical (nutrients), and biological (chlorophyll a) data were collected using modified WOCE/JGOFS protocols. The hydrographic sampling system was comprised of a Sea Bird Electronics (SBE) 911+ CTD mounted on a 24-place rosette with 10-L Niskin bottles. All instruments were calibrated according to WOCE methods and samples were analyzed using quality control protocols that meet WOCE standards. The estimated accuracy for temperature is 0.001 °C. For salinity the accuracy ranges from 0.002 (deep water) to 0.01 (mid-depth). Prior to the eddy CTD section, the feature was mapped using expendable CTDs (Fig. 2B), with an accuracy of 0.02 °C and 0.04 for temperature and salinity, respectively (see Kadko et al., 2008). Vertical sections were constructed for various properties, including potential temperature and density (referenced to the sea surface), transmissivity and nutrients.

In order to analyze the boundary current structure at the WHS line we made use of the shipboard ADCP data collected during the cruise. In particular we used the Healy's 75 kHz narrow band data



Fig. 2. (A) Study area in the Chukchi and Beaufort Seas. The Beaufort slope moored array discussed in the text is denoted by the star. (B) Enlarged view of study area, showing the hydrographic and biological stations occupied by the USCGC Healy in summer and fall 2004. The summer West Hanna Shoal (WHS) line consisted of eight hydrographic stations of which five had concurrent zooplankton sampling. The eddy survey in fall consisted of 11 hydrographic stations with zooplankton sampling at every other station.

for the WHS section. The data were first de-tided using the Oregon State University 5 km resolution Arctic tidal model (Padman and Erofeeva, 2004), in an effort to remove the dominant barotropic tidal signals. Encouragingly, the predicted tidal currents were very small (<2 cm/s) at this location and time. After subtracting out the tidal currents, the latitude and longitude of the ADCP ensembles were projected along a regression line that included the positions of the CTD stations (this was necessary because some of the ADCP data were collected while the ship drifted on station). Then the component of velocity normal to the regression line was gridded using Laplacian–Spline interpolation (cross-stream resolution of 2 km, vertical resolution of 5 m).

Since we are interested in the geostrophic flow of the boundary current, and since there were no ADCP data shallower than 20 m or near the bottom (due to the normal blanking associated with the surface and bottom), we computed the absolute geostrophic velocity for the WHS line by referencing the thermal wind shear to the projected ADCP velocity. Unfortunately the coarse CTD spacing (range 10–35 km)—in particular the fact that there was only one CTD station on the shelf—made this problematic. To get around this we objectively interpolated the CTD temperature (T) and salinity (S) data to fill in the gaps (cross-stream resolution of 10 km, vertical resolution of 10 m), then computed a vertical section of thermal wind shear from the

gridded *T* and *S* fields. Finally, the thermal wind velocities were referenced using the laterally averaged (gridded) ADCP data between each 10-km point. (At each location along the section the reference velocity was computed over the common depth range of the thermal wind and ADCP velocities.) As a consistency check on this approach we note that the absolute geostrophic velocity section so computed and the original ADCP velocity section, are very similar in structure.

2.2. Collection and analysis of zooplankton data

We obtained distributions of zooplankton using a MultiNet^(B) fitted with 150-µm mesh nets at five of the eight stations of the WHS shelf-basin transect in summer and at six of the 11 stations across the eddy in fall (see Fig. 2B). We focus on samples collected in the upper 300 m. In summer, zooplankton sampling intervals varied according to bottom depth. In fall, sampling intervals were 0–50, 50–100, 100–150, 150–200 and 200–300 m. After collection, the sample was poured through a 150-µm mesh sieve to remove seawater and then preserved in 95% ethyl alcohol for enumeration and identification in the laboratory. Information on the zooplankton sampling and analysis is summarized in Table 1.

Zooplankton samples were enumerated at the University of Miami's Rosenstiel School of Marine and Atmospheric Science. Net samples for taxonomic enumeration were split several times in a Folsom splitter, and three aliquots were counted for each taxonomic category identified. Organisms were identified to the lowest possible taxonomic level. For the copepods C. glacialis and M. longa each developmental stage was counted individually. For O. similis and Oncaea spp. adult females, adult males and all copepodid stages were counted. For Pseudocalanus spp. adult females, adult males and copepodid stages C5-C4 were counted, whereas copepodid stages C3-C1 were grouped with unidentified calanoid copepodites. The identification of chaetognaths, appendicularians, gastropods and other planktonic taxa was carried out only to broad taxonomic levels. Abundance in terms of individuals per cubic meter (ind/m³) was estimated for each category by dividing the number counted by the fraction of the sample counted for that category and dividing the result by the volume of water filtered (Table 1).

We used displacement volumes (Ahlstrom and Thrailkill, 1963) to estimate zooplankton carbon (Wiebe et al., 1975; Wiebe, 1988). The displacement volume (DV) in terms of ml/m³ was used to calculate zooplankton carbon (C) using

$Log (DV) = -1.434 + 0.820 \, Log (C)$

(Wiebe et al., 1975; Wiebe, 1988).

Wet displacement volumes were run after 2 years of preservation, hence plankton shrinkage due to preservation should have stabilized and been constant for all samples (Ahlstrom and Thrailkill, 1963). In addition, our samples were dominated by copepods which show the least volume loss with time (Ahlstrom and Thrailkill, 1963; Wiebe et al., 1975).

The lower-horizontal-resolution zooplankton data in the eddy transect (i.e. only one sample was collected inside the eddy), relative to the higher horizontal resolution physical and chemical observations, limited our interpretations. No statistical analyses were possible to demonstrate that changes in abundance were significant or that associations with environmental parameters were quantitative. However, consistent trends in the zooplankton distributions, combined with detailed descriptive physical and chemical oceanographic data, provide support to our assertions regarding the nature of the eddy and the conditions in which it was formed.

Table 1Zooplankton sampling and analysis data.

Date	Latitude (°N)	Longitude (°W)	Sea beam depth (m)	Station number	Sample depth (m)	Volume filtered (m ³)	Percentage counted (%)	Zooplankton abundance (no. m ³)	Zooplankton biomass (mg C m ³)
18-Aug-04	73.901	157.854	3760	52	300-100	56	23	124	N/A
18-Aug-04	73.901	157.854	3760	52	100-0	28	18	1029	N/A
19-Aug-04	73.480	159.610	2110	54	300-100	52	22	262	N/A
19-Aug-04	73.480	159.610	2110	54	100-0	25	3	3849	N/A
20-Aug-04	73.284	160.077	1135	55	300-100	51	11	414	N/A
20-Aug-04	73.284	160.077	1135	55	100-50	14	17	1248	N/A
20-Aug-04	73.284	160.077	1135	55	50-0	13	9	3184	N/A
22-Aug-04	73.102	160.506	217	58	200-150	13	22	315	N/A
22-Aug-04	73.102	160.506	217	58	150-100	12	22	413	N/A
22-Aug-04	73.102	160.506	217	58	100-50	9	13	1470	N/A
22-Aug-04	73.102	160.506	217	58	50-0	12	11	8316	N/A
25-Aug-04	72.737	161.301	52	60	40-0	10	6	5541	N/A
25-Sep-04	73.524	160.507	1470	121	300-200	28	100	101	3.68 ^a
25-Sep-04	73.524	160.507	1470	121	200-150	13	100	108	4.03 ^a
25-Sep-04	73.524	160.507	1470	121	150-100	14	100	165	5.23ª
25-Sep-04	73.524	160.507	1470	121	100–50	16	22	598	20.46
25-Sep-04	73.524	160.507	1470	121	50–0	17	11	1740	7.50
25-Sep-04	73.470	160.505	1473	123	300-200	37	100	55	2.62ª
25-Sep-04	73.470	160.505	1473	123	200-150	18	100	180	6.31ª
25-Sep-04	73.470	160.505	1473	123	150-100	23	100	105	5.64ª
25-Sep-04	73.470	160.505	1473	123	100-50	35	22	425	7.20
25-Sep-04	73.470	160.505	1473	123	50-0	22	11	2290	10.34
25-Sep-04	73.414	160.504	1068	125	300-200	34	100	77	2.90ª
25-Sep-04	73.414	160.504	1068	125	200-150	16	100	119	5.83*
25-Sep-04	73.414	160.504	1068	125	150-100	16	100	166	4.44ª
25-Sep-04	/3.414	160.504	1068	125	100-50	1/	100	225	8.16
25-Sep-04	/3.414	160.504	1068	125	50-0	22	22	1303	5.96
25-Sep-04	/3.362	160.496	980	127	300-200	26	100	122	4.03
25-Sep-04	/3.362	160.496	980	127	200-150	15	100	120	0.89
25-Sep-04	/3.362	160.496	980	127	150-100	12	100	149	2.71
25-Sep-04	/3.362	160.496	980	127	100-50	11	100	326	9.21
25-Sep-04	/3.362	160.496	980	127	50-0	14	22	2859	14.05
26-Sep-04	/3.30/	160.497	937	129	300-200	26	100	120	4.03
26-Sep-04	/3.30/	160.497	937	129	200-150	12	100	68	2.71
26-Sep-04	/3.30/	160.497	937	129	150-100	13	100	124	5.72
26-Sep-04	/3.30/	160.497	937	129	100-50	14	100	305	8.57
26-Sep-04	/3.30/	160.497	937	129	50-0	16	44	1135	20.46
26-Sep-04	/3.25/	160.484	625	131	300-200	51	100	4/	4.55
26-Sep-04	/3.25/	160.484	625	131	200-150	13	100	126	4.03
26-Sep-04	/3.25/	160.484	625	131	150-100	13	100	168	/.51
26-Sep-04	/3.25/	160.484	625	131	100-50	15	100	2/0	0.31
20-Sep-04	/3.25/	160.484	625	131	50-0	15	88	1164	30.08

^a Estimates used to calculate average zooplankton biomass inside eddy.



Fig. 3. Time series of zonal 10 m-wind speed from the Pt. Barrow, AK weather station. The time period of the WHS transect is indicated by the gray shading. Easterly winds are upwelling favorable.

3. Results

3.1. Summer shelf-basin section

The 2004 SBI summer cruise consisted of relatively wide station spacing that did not adequately describe spatially smallscale features such as eddies. As this study was not designated to determine the time and location of eddy formation, we cannot definitely answer the important question, what conditions existed at the formation site of the eddy? Nevertheless, we provide the WHS sections as background on the physical structure and zooplankton distribution of the shelfbreak current, which we believe are very similar to the source of the core water of the eddy observed in fall. The WHS section was occupied approximately 1 month before the eddy survey, and we note that the estimated age of the eddy (Kadko et al., 2008) was on the order of months. The timing of the WHS section is thus appropriate to identify the potential water mass and plankton community contained within the eddy.

3.1.1. Hydrography and state of the shelfbreak jet

During summer, the undisturbed shelfbreak jet tends to flow eastward along the edge of the Chukchi Sea (Pickart et al., 2005; Mathis et al., 2007; Spall et al., 2008). Depending on the precise season, and probably the severity of the preceding winter, the current advects either cold winter-transformed Chukchi/Bering Water (temperature <-1.65 °C) or summertime Chukchi/Bering Water (temperature \sim 0 °C). During the SBI summer 2004 cruise the current was advecting primarily the former. However, the WHS line was occupied during an easterly wind event. The event consisted of two separate wind peaks on the order of 5–10 m/s, with a lull in between (Fig. 3). The influence of this easterly wind is reflected in the structure of the shelfbreak jet at the time of the transect.

The vertical sections of potential temperature and absolute geostrophic velocity for the WHS transect are shown in Fig. 4, with the potential density overlaid. One sees that the boundary current has enhanced eastward flow on the outer-shelf and shelfbreak, with a second peak near 200 m on the upper slope. Offshore of this there is a westward-flowing surface-intensified jet of similar magnitude (centered at stations 56–57, Fig. 4B). This westward flow, together with the upward tilt of the deep isopycnals and the warm Atlantic Water present on the upper slope, is indicative of upwelling (e.g., Carmack and Kulikov, 1998). The combination of both eastward and westward flow is also consistent with the



Fig. 4. Vertical sections along the summer 2004 WHS transect (see Fig. 2B for location). The potential density contours (kg/m³) are overlaid on the colored (A) potential temperature and (B) absolute alongstream geostrophic velocity. Positive flow is eastward. The CTD station positions are indicated along the top.

velocity structure observed during upwelling events by a mooring array located farther to the east (in the Beaufort Sea) during SBI. Using an empirical orthogonal function (EOF) analysis, Nikolopoulos et al. (2009) showed that during periods of upwelling (easterly winds) the shelfbreak jet alternates between a reversed state (during the height of the storm) and a "recovered" state (after the storm ends). These two states are shown in Figs. 5A and B, respectively. Interestingly, the recovered state contains a secondary velocity maximum similar in structure to the enhanced eastward flow in the WHS velocity section near 200 m.

To investigate this further, we regressed the zonal 10-m wind speed record from the meteorological station at Point Barrow, AK with the EOF modal amplitude time series from Nikolopoulos et al. (2009). Not surprisingly, the two time series are significantly correlated at the 95% confidence level. Based on this relationship, it implies that the reversed boundary current in Fig. 5A corresponds to strong easterly winds (order 15 m/s) and the recovered boundary current (Fig. 5B) occurs when the winds are weakly out of the west (3-5 m/s). The EOF configuration that corresponds most closely with the structure of the boundary current observed during the WHS transect is shown in Fig. 5C. Keeping in mind that the mooring array was located on the Beaufort slope some 300 km to the east of the WHS line, and that the mooring data are from 2002 to 2003, the similarity is striking (compare Figs. 5C and 4B). Using the above regression, the corresponding value of the EOF modal amplitude in Fig. 5C implies a wind speed of 5 m/s out of the east. This compares favorably with the mean easterly wind speed computed over the duration of the WHS velocity section (the shaded area in Fig. 3) of 5.6 m/s.

To summarize, the WHS transect apparently captured the shelfbreak jet in a partially wind-driven state. One must keep in mind, however, that the transect took approximately 4 days to occupy, and hence the velocity and hydrographic fields represent a mixture in space in time. It is possible that the entire shelfbreak jet reversed at some point, with significant upwelling (although the lull in the wind speed during the middle of the occupation probably limited this to some extent). The occurrence of upwelling would explain why the coldest temperatures



Fig. 5. Reconstructed alongstream velocity from the SBI Beaufort slope mooring array (see Fig. 2A for location) using the upwelling EOF results of Nikolopoulos et al. (2009). In each case a particular value of the mode has been added back into the mean field to produce a realization. Positive flow is eastward, and the mooring locations are indicated along the top. (A) Realization corresponding to a strong easterly wind (modal amplitude equal to +1 standard deviation, see Nikolopoulos et al., 2009). (B) Realization corresponding to a weak westerly wind (-1 standard deviation modal amplitude). (C) Realization that most closely matches the calculated WHS absolute geostrophic velocity section. This corresponds to a moderate easterly wind (see text).

(associated with the winter-transformed water) do not coincide with the eastward shelfbreak flow (compare Figs. 4A and B); the shoreward advection of warmer water from the lower slope to the shelfbreak would moderate the temperatures there (see Pickart, 2004). We note that the hydrographic section occupied prior to the WHS line on the summer cruise (under variable westerly winds) showed a large amount of winter-transformed water on the outer-shelf and shelfbreak. The distributions of nutrients along the WHS transect show enhanced concentrations near the shelfbreak (Fig. 6). This is typical of the eastward-flowing shelfbreak jet in the Chukchi Sea as it advects winter-transformed Pacific-origin water (e.g. Weingartner et al., 1998; Pickart et al., 2005), and is consistent with the idea from models that the origin of the jet is the outflow from Herald Canyon. A hydrographic/ velocity survey of Herald canyon, carried out during the same time period of the 2004 SBI summer cruise, supports this notion (R. Pickart, pers. comm., 2006). We surmise that the upwelling during the WHS occupation did not impact the nutrient distributions near the shelfbreak as much as the temperature, because of higher ambient nutrient concentrations at depth and due to stirring up of regenerated nutrients from the sediments during the storm (consistent with the transmissometer data, not shown).

3.1.2. Zooplankton distribution

We identified several mesozooplankton categories on the WHS section, including 20 copepod species, 5 copepod genera, and 20 other categories where identification was made to the lowest taxonomic rank possible. Copepods were by far the most abundant group during the summer and fall periods. We will focus on two large Arctic copepods, *C. glacialis* and *M. longa*, one ubiquitous species, *O. similis*, and two copepod genera *Pseudocalanus* and *Oncaea* that are predominantly neritic and oceanic taxa, respectively. Other species of interest are *Acartia longiremis*, whose presence is indicative of coastal waters, and the Pacificorigin copepods *Metridia pacifica* and *Neocalanus flemingeri*.

We obtained distributions of zooplankton at five of the eight stations of the WHS shelf-basin transect in summer, 2004. Total zooplankton abundance decreased with depth with the highest abundance observed in surface waters (0-50 m) over the shelfbreak (8316 ind/m³, Fig. 7A). For waters of the same density, zooplankton abundance decreased with distance from the shelf (Fig. 7A). The cyclopoid copepod O. similis was the most abundant organism, especially over the shelf and in surface waters (Fig. 7B), and its distribution established the total zooplankton trend. The distributions of Pseudocalanus spp. and Oncaea spp. followed opposite patterns to each other. In the WHS section, Pseudocalanus spp. were numerous over the shelf and present in relatively low numbers at the most offshore station (Fig. 7C). An important feature of the distribution of this copepod genus was the high abundance in subsurface waters (50-100 m) associated with the shelfbreak current (Fig. 7C). In the same subsurface waters, Oncaea spp. were present in low numbers, and were only numerically important in surface waters (0-100 m) over the slope and basin (Fig. 7D), an expected distribution since Oncaea spp. are characteristic of polar waters and are commonly found at bottom depths up to 2000 m in the Arctic Basin (Heron et al., 1984).

Interestingly, the Arctic copepods *C. glacialis* and *M. longa* were found in significant numbers in the region of the shelfbreak and even on the shelf (Figs. 7E and F). This is another indication that upwelling occurred during the easterly wind event as the section was being occupied, consistent with the velocity results discussed above. *M. longa* is a basin species, capable of pronounced diel vertical migrations, and intrinsic to the Arctic Ocean and its surrounding seas (Brodskii, 1967). The high concentration of this copepod on the upper slope at station 58 is where the upslope



Fig. 6. Summer 2004, West Hanna Shoal vertical section. The potential density contours (kg/m³) are overlaid on the colored vertical sections of (A) silicate (µMol/L), (B) nitrate (µMol/L), and (C) phosphate (µMol/L). Hydrographic stations are plotted as white circles (see Fig. 2B).

flow would be strong during upwelling (Pickart et al., 2006), and it is consistent with the upward tilt of the Atlantic water isotherms (warmer than 0 °C) at this location (Fig. 4A).

The enhanced concentration of *M. longa* at the shoreward-most station implies that the upwelled water penetrated onto the shelf (Fig. 7E). Arctic water also was indicated by the presence of *C. glacialis* in subsurface waters (50–100 m) at station 58. We suspect that the concentration decreases near the bottom of this station because this species is found at shallower ambient depths in the interior basin (Fig. 7F). Copepodids of another Arctic copepod, *C. hyperboreus*, were also abundant in subsurface waters over the shelfbreak (8 ind/m³, data not shown). It is expected that these Arctic species would not normally be found in significant quantities in the undisturbed, eastward-flowing shelfbreak jet (i.e. under non-upwelling conditions).

3.2. Eddy section

Roughly a month after the summer section was occupied, a subsurface, anti-cyclonic eddy was sampled in the vicinity of the WHS section (Fig. 2B). The core of the feature contained cold, winter-transformed Chukchi/Bering water, similar to that being advected by the shelfbreak jet during the earlier cruise. Isotope half-lives, oxygen concentrations and respiration rates within the eddy indicated an age on the order of months (Kadko et al., 2008). We infer, therefore, that the eddy was spawned from the shelfbreak jet sometime during spring/summer 2004. While we are unable to determine the precise area and time of formation, it

is reasonable to use the WHS section, in particular station 58 (in the depth range 50–100 m) as a source function to interpret the physical and chemical structure of the eddy and its zooplankton distribution.

3.2.1. Eddy core properties

The eddy survey is described in Mathis et al. (2007) and Kadko et al. (2008) and is only briefly summarized here. After locating the feature using expendable bathythermographs (XBTs), a rapid high-resolution survey was carried out using expendable CTDs (XCTDs) along with the shipboard ADCP. The XCTD grid was approximately 30 km on a side with 5 km resolution and took roughly 24 h to complete (Fig. 2B). This provided a threedimensional snapshot of the eddy (for a lateral view of the feature see Fig. 9 of Mathis et al., 2007). Immediately following this, a transect was occupied through the center of the eddy using the shipboard CTD package, including water samples and net tows. From this survey, it was determined that the eddy had a radius of ~8 km and its core was located at an approximate water depth of 160 m (Fig. 8) on the continental slope, centered over the 1000 m isobath. Inside the eddy core, silicate ($>40 \mu Mol/L$, Fig. 8A), nitrate (> 15 μ Mol/L, Fig. 8B) and phosphate (> 2 μ Mol/L, Fig. 8C) concentrations were the highest for the section. Also, the eddy core had low temperatures ($< -1.7 \circ C$, Fig. 9A). The eddy core had very similar physical (temperature and density) and chemical (silicate, nitrate, phosphate) properties to the shelfbreak jet observed in summer (Figs. 4 and 6), characteristic of Pacificorigin water (see also Pickart et al., 2005).



Fig. 7. Summer 2004, West Hanna Shoal vertical distribution of zooplankton abundances (ind/m³). The potential density contours (kg/m³) are overlaid on the vertical sections of (A) total zooplankton, (B) *Oithona similis*, (C) *Pseudocalanus* spp., (D) *Oncaea* spp., (E) *Metridia longa*, and (F) *Calanus glacialis*. Numbers indicate abundance values. Stations where zooplankton samples were collected are plotted as black triangles (see Fig. 2B).

The ADCP data showed relatively high echo intensities at the eddy core when compared with waters of similar density outside the eddy (not shown). This observation and the low transmissivity found at the eddy core (84%, Fig. 9B) suggest that different sized particles were confined inside the eddy and actively transported by it. Low chlorophyll a (Fig. 9C) and phaeopigment concentrations (data not shown) at the eddy core suggest that phytoplankton cells were not transported in significant numbers to the Arctic Basin by this subsurface eddy. It is possible that phytoplankton cells were not present at the time and place of formation of the eddy or that grazing by copepods within the eddy subsequently reduced cell concentration prior to our sampling.

3.2.2. Distribution of zooplankton

The sections presented in Figs. 10A–F represent the first observations of the vertical distribution of mesozooplankton across an eddy in the western Arctic. While the bulk of the zooplankton was above 50 m (Fig. 10A), there was a clear signature in the eddy: within the central density range of the feature $(26.5-26.8 \text{ kg/m}^3)$ the zooplankton abundance was higher at the eddy core $(180 \text{ ind/m}^3, \text{Fig. 10A})$ than outside the influence of the eddy $(108 \pm 23 \text{ ind/m}^3, N = 5)$. As observed earlier in the summer cross-shelf section, *O. similis* was the most abundant organism in surface waters and its distribution dictated the total zooplankton distribution. We observed a sharp decline in *O. similis* abundance with depth and slightly elevated numbers at the eddy core $(23 \text{ ind/m}^3, \text{Fig. 10B})$ in comparison to waters of the same density outside the eddy $(12 \pm 3 \text{ ind/m}^3, N = 5)$. Similar vertical distribu-

tions for *Pseudocalanus* spp. and *Oncaea* spp. were found. Inside the eddy core, *Pseudocalanus* spp. (37 ind/m³, Fig. 10C) and *Oncaea* spp. (33 ind/m³, Fig. 10D) abundances were higher than they were in waters of the same density outside the eddy $(18\pm 6 \text{ ind/m}^3, N = 5 \text{ and } 14\pm 4 \text{ ind/m}^3, N = 5$, respectively). In the upper 100 m, the abundances of the two genera were associated with elevated chlorophyll *a* concentrations (Fig. 9C); although not a perfect match, abundances were generally higher at stations with elevated chlorophyll *a* values.

The spatial distributions of the Arctic copepods M. longa and C. glacialis were particularly interesting. As discussed above, their presence at the shelfbreak during the summer WHS section was likely the result of wind-driven upwelling (Figs. 7E and F). The high abundance of *M. longa* at the eddy core $(46 \text{ ind/m}^3, \text{Fig. 10E})$ compared to its average abundance in waters of the same density outside the eddy $(29 \pm 9 \text{ ind}/\text{m}^3, N = 5)$ implies that the particular formation event that spawned the observed eddy occurred near a time of enhanced easterly winds. We note that the hydrodynamic instability hypothesis for the formation of the eddies does not require the presence of wind. For example, the study of Spall et al. (2008) focused on periods of low wind speed, and the observed potential vorticity structure of the Beaufort shelfbreak jet during these periods satisfied the necessary conditions for instability. Their corresponding model boundary current (whose structure agreed well with the observations) readily formed eddies.

One explanation for the enhanced concentration of *M. longa* in the eddy is that a storm occurred just prior to the eddy formation event, resulting in Arctic-origin water being present in the boundary current and hence entrained into the feature. This is



Fig. 8. Fall 2004, eddy vertical section of chemical properties. The potential density contours (kg/m³) are overlaid on the colored vertical sections of (A) silicate (μ Mol/L), (B) nitrate (μ Mol/L), and (C) phosphate (μ Mol/L). Hydrographic stations are plotted as black circles (see Fig. 2B).

not an unreasonable scenario based on the high frequency of storms in this part of the western Arctic (even during spring and summer, Spall et al., 2008). Another possibility, however, is that the observed eddy formed as a direct result of the wind forcing. As described in Spall (1995), when a water parcel moves from the onshore side of the current towards the offshore side (which happens occasionally in any time-varying system) the resulting potential vorticity anomaly can initiate an eddy spin-up process. There are different mechanisms that could cause such a crossshore diversion of water. In the first scenario (after the storm is over) it could be due to meandering of the current; in the second scenario, the cross-stream perturbation might result from the wind-induced circulation. This latter mechanism for eddy formation in the western Arctic remains to be explored.

The vertical distribution of *C. glacialis* in the eddy was also similar to its distribution in the shelfbreak summer section. In summer, *C. glacialis* was highly abundant in subsurface waters (50–100 m) on the upper slope (Fig. 7F), and in fall it was also abundant in the top part of the eddy (Fig. 10F). In the upper part of the water column above this, its distribution seems



Fig. 9. Fall 2004, eddy vertical section of physical and biological properties. The potential density contours (kg/m³) are overlaid on the colored vertical sections of (A) potential temperature (°C), (B) transmissivity (%), and (C) chlorophyll *a* (μ g/L). Hydrographic stations are plotted as black circles (see Fig. 2B).

to be related to chlorophyll *a* concentrations (Fig. 9C). The other Arctic copepod, *C. hyperboreus*, was observed in low numbers ($\sim 1 \text{ ind/m}^3$, data not shown) with higher numbers at depths below 200 m. Its vertical distribution was not associated with the physical structure of the eddy.

3.2.3. Biomass

Zooplankton biomass (Fig. 11) was most elevated in the upper 50 m at stations closer to the shelf (stations 129 and 131), and in subsurface waters (50–100 m) at the farthest offshore station (station 121). In surface water, high abundances of all zooplankton types were responsible for the elevated biomass. In subsurface waters at station 121, the large-bodied copepod *C. glacialis* probably accounts for much of the increase in biomass of zooplankton observed. Deeper in the water column, zooplankton biomass was higher near the eddy core (6.31 mg C/m³, Fig. 11) when compared with similar density water outside the eddy $(3.50 \pm 1.83 \text{ mg C/m}^3, N = 5)$. The eddy center contained elevated numbers of the large copepods *M. longa* and *Paraeuchaeta glacialis* and other large zooplankton including amphipods and



Fig. 10. Fall 2004, eddy vertical section of zooplankton abundances (ind/m³). The potential density contours (kg/m³) are overlaid on the vertical sections of (A) total zooplankton, (B) *Oithona similis*, (*C) Pseudocalanus* spp., (D) *Oncaea* spp., (E) *Metridia longa*, and (F) *Calanus glacialis*. Numbers indicate abundance values and the abundance inside the eddy is highlighted in bold. Stations where zooplankton samples were collected are plotted as white triangles (see Fig. 2B).



Fig. 11. Fall 2004, eddy vertical section of zooplankton biomass (mgC/m^3). The potential density contours (kg/m^3) are overlaid on the vertical section zooplankton biomass. Numbers indicate biomass estimates and the biomass inside the eddy is highlighted in bold. Stations where zooplankton samples were collected are plotted as white triangles (see Fig. 2B).

chaetognaths. *C. hyperboreus* was relatively sparse but, due its large size and lipid reserves, it possibly contributed to a significant fraction of the observed biomass.

4. Discussion

Our study has presented the vertical distribution of zooplankton across an eddy in fall 2004 over the Chukchi slope of the Arctic Ocean and offers an explanation on the origin of the physical, chemical, and biological characteristics of its core. We argue that the feature originated from the shelfbreak jet in the preceding spring/summer, likely after a period of upwelling. To further elucidate the role of eddies in the Arctic ecosystem, we now provide some insights concerning their source region, likely trajectories, and lifetimes. Knowledge of these processes and circulation patterns is essential to determine their impact on the distribution of various zooplankton species and their role in the transport of carbon in terms of zooplankton biomass. Our limited data (a single transect through an eddy) make it difficult to assess the significance of eddies to the regional food webs. Trends in the data, however, suggest that eddies might provide a mechanism for transporting certain species of zooplankton from the shelf region into deep waters that could affect food webs in the less productive basin.

4.1. Mesoscale features and copepod distributions

The zooplankton distribution patterns presented above are consistent with advection of secondary production from the shelf to the basin by mesoscale features (see also Ashjian et al., 2005). The shelfbreak and the eddy center were particularly interesting with elevated abundances of several taxa. The high abundances of zooplankton inside the eddy are explained by their high numbers in subsurface waters at the shelfbreak from where the eddy likely originated. Pseudocalanus individuals were present in high numbers in surface waters over the shelf, in subsurface waters at the shelfbreak, and inside the eddy; an expected distribution for a genus that is predominantly coastal with a poorly studied shelf-basin gradients (Corkett and McLaren, 1978). The genus Pseudocalanus is scarce and patchy in the Arctic basin where it is generally considered an expatriate from the surrounding neritic waters, especially the Chukchi Sea where it is common (Johnson, 1958; Brodskii, 1967; Corkett and McLaren, 1978; Horner and Murphy, 1985; Hopcroft et al., 2005; Lane et al., 2007). Records of Pseudocalanus spp. from the central parts of the basin probably represent populations carried offshore by surface currents, filaments and eddies of the type discussed here. These populations may survive temporarily by feeding under ice (Conover et al., 1986; Runge and Ingram, 1991), but it is unlikely that they are sustained over long periods in basin waters. The absence of the genus in some surveys, and its scarcity and patchiness in the more central parts of the basin, may have resulted from variability in the mesoscale processes responsible for its transport from the continental shelves.

The significant number of Arctic-origin Calanoid copepods observed over the Chukchi Shelf and upper slope during the summer cruise was likely the result of upwelling. The persistent occurrence of these species over the Chukchi Shelf (Johnson, 1958: English and Horner, 1977; Plourde et al., 2005; Campbell et al., 2009) suggests that on-shelf intrusions of Arctic Ocean water are common events. Frequent reversals of flow have been observed at Barrow Canyon (Mountain et al., 1976; Münchow and Carmack, 1997; Weingartner et al., 1998), possibly related to canyon dynamics. At the same time, the mooring data from the Beaufort SBI array (Fig. 2A) reveal that the shelfbreak jet reverses quite often at that location: during the first year alone there were 27 major upwelling events over the course of the year (R. Pickart, unpubl. data). It is likely that similar wind-driven processes occur to the west of Barrow Canyon along the shelf edge of the Chukchi Sea, consistent with the results presented here. Such transport of Arctic biota onto the shelves should be modulated seasonally. Although easterly winds do occur in spring and summer (e.g., Fig. 3; see also Spall et al., 2008), the majority of the upwelling storms in the Beaufort Sea (and likely the Chukchi Sea) seem to be Pacific-origin cyclones (Pickart et al., 2006) whose frequency increases in the fall and winter months (Terada and Hanzawa, 1984). Such seasonal variability is particularly important in the Arctic where zooplankton life cycles and distributions are also strongly seasonal, and alterations in the physical transport processes of zooplankton can potentially drive large matchmismatch variations in distribution and community structure of both zooplankton and their predators (Mackas and Coyle, 2005).

4.2. Preliminary estimate of offshore transport of carbon by eddies

Based on the large number of eddies observed in the Canada Basin (Manley and Hunkins, 1985; Plueddemann and Krishfield, 2009), the potential vorticity structure of the shelfbreak jet (Pickart, 2004; Spall et al., 2008), and direct observations of eddies emanating from the current (Pickart et al., 2005), it is likely that hydrodynamic instability of the shelfbreak jet and subsequent eddy formation is a major contributor to shelf-basin exchange in the western Arctic. This is supported by the recent study of Spall et al. (2008) who investigated the behavior and dynamics of the shelfbreak current during the spring and early summertime period using the SBI Beaufort slope moored array data and a high-resolution primitive equation model. During this period the current advects winter-transformed Chukchi/Bering water, and the corresponding isopycnal structure results in a potential vorticity distribution that satisfies the necessary conditions for baroclinic instability. The observed energy transfer in the boundary current was dominated by baroclinic conversion from the mean to the eddies-consistent with baroclinic instability-and the model boundary current produced a large number of cold-core, anti-cyclonic eddies of the type considered here.

Previous work implies that approximately 100-200 cold-core eddies are formed every year (Pickart et al., 2005; Plueddemann and Krishfield, 2009), or 1-2 eddies per day over the 6-month time period from early-spring to early-fall. Such a high formation rate is supported by the model results of Spall et al. (2008). In addition, the tracer budget presented by Spall et al. (2008) indicates that roughly half of the original boundary current water (the model equivalent of Pacific water) is fluxed into the basin interior via the eddies. This cross-slope flux is accomplished by the self-advection of dipole pairs. In particular, when the eddies are first formed, the anti-cyclones have cyclonic partners and together the eddy pairs propagate offshore. Since the cyclones are concentrated in the upper layer, however, they tend to spin down quickly (see also Ou and Gordon, 1986), leaving just the anticyclone. This explains why subsurface, anti-cyclonic eddies are prevalent in the observations. In the model of Spall et al. (2008), the eddies ultimately become entrained into the interior Beaufort Gyre and are advected to the west. This is consistent with the observations of Plueddemann and Krishfield (2009). Based on the locus of studies to date then, it seems that the cross-slope flux of Pacific water via eddies is significant.

To get an idea of the flux of zooplankton due to this process we did the following simple calculation. Following Mathis et al. (2007) we assume that roughly 100 cold-core eddies are formed each year. To calculate the average zooplankton biomass in a single eddy we used nine biomass estimates (see Table 1) and obtained an approximation of the grams of carbon (gC) of zooplankton contained inside the particular eddy sampled here. Taking an average eddy volume to be 25 km³ (Pickart et al., 2005), based on the average zooplankton biomass inside the observed eddy (4.52 mg C/m³), the implied total annual carbon export to the basin equals 1.1×10^8 gC/year. This represents less than 0.01% of the 1.8×10^{12} gC of zooplankton believed to be transported annually into the Chukchi Sea through Bering Strait (Springer et al., 1989).

This large discrepancy could be due to a variety of factors. The first possibility is that other mechanisms, such as wind-driven Ekman flow or canyon currents, are the dominant mechanisms of off-shelf flux of secondary production (e.g., Ashjian et al., 2005). It should be kept in mind, however, that we have sampled only a single eddy, and it is difficult to assess how representative this particular feature is in terms of zooplankton inventory. For example, it was argued above that an upwelling event likely preceded the formation of the eddy in question. If this were the case, the secondary current from much of its Pacific-origin zooplankton prior to the spawning of the eddy. Another consideration is the seasonal timing of the eddy formation in

relation to the phytoplankton bloom, which could strongly influence the zooplankton content of the eddy. It is also worth pointing out that the central station in our fall eddy transect (station 124, Fig. 9A) did not include zooplankton measurements, which likely biases our estimate low.

Alternatively, it could be inferred from our calculation that much of the influx of zooplankton biomass from the Pacific is either consumed or deposited into the sediments before it reaches the northern Chukchi shelfbreak. In this case, while the eddies may be highly efficient at transporting any zooplankton off the shelf, the available biomass in the boundary current may be minimal to begin with. Unfortunately, due to the sparse sampling of zooplankton in the region, it is not possible at this point to determine which of these scenarios is correct. The preliminary estimate presented here, together with previous distribution data (Lane et al., 2007), suggest that eddies may not be important for exporting significant amounts of shelf-derived zooplankton to the Arctic Basin. However, our fall transect did reveal anomalous concentrations of various zooplankton within the eddy, and there are reasons to believe that our inventory estimates of Pacificorigin zooplankton are biased low compared to eddies formed under weak wind forcing. It is also worth mentioning that warm core eddies, containing summertime Chukchi/Bering water, may play a role in the off-shelf transport of zooplankton. However, at this point there have been no biological measurements taken within this type of feature.

4.3. Structure and functioning of Arctic food webs

Recent work indicates the structure and functioning of Arctic food webs is conditioned by trophic pathways and can be modified by transport mechanisms (Grebmeier et al., 2006; Hirche et al., 2006). Our observations support the view that upwelling events and the formation of eddies provide mechanisms for on-shelf and off-shelf advection of mesozooplankton. One of the surprises of our study was the enhanced concentrations of the basin-origin zooplankton C. glacialis and M. longa within the eddy, seemingly due to the occurrence of upwelling near the time of formation of the feature. A natural guestion to ask is whether the transport by eddies of these species back into the Arctic interior can impact the fate of primary production in the basin. To address this we must determine if these populations were actively feeding or in diapause in the case of C. glacialis. The vertical distribution of *M. longa* may be explained by its foraging behavior as this copepod feeds on marine snow and diatom particles, which are observed in high concentrations in the shelfbreak current (Ashjian et al., 2005) and thus inside the eddy. The proposed behavior is reasonable as M. longa has an omnivorous diet (Haq, 1967), is characterized by extensive diel vertical migrations (Brodskii, 1967) and is predominantly found below 100 m (Smith, 1988). In this sense, its life cycle strategy is different from that of C. glacialis.

C. glacialis occupied the upper 100 m where it was likely feeding on large diatoms cells (Mullin, 1963). Further down the water column and inside the core, *C. glacialis* was grazing on other potential food sources such as microzooplankton (Campbell et al., 2009). Although there was some variability in the vertical distribution of individuals, the general species-specific patterns suggested active feeding. Recently, Olli et al. (2007) proposed that, given the low standing stock al algal biomass, the grazing capacity of expatriated mesozooplankton could affect the fate of primary production in the central Arctic. *C. hyperboreus, C. glacialis*, and, to a lesser extent, *M. longa* dominate the mesozooplankton biomass of the Arctic Ocean (Smith and Schnack-Schiel, 1990; Kosobokova and Hirche, 2000; Ashjian et al., 2003) and have significant

grazing impacts on the phytoplankton biomass of the shelf and basin environments (Campbell et al., 2009). Based on these observations, the maintenance of populations of large copepods in the basin, through reintroduction from the more productive shelf regions via eddies, could influence primary productivity over the Arctic Basin.

5. Conclusions

The physical, chemical, and biological characteristics of a coldcore eddy observed in fall 2004 in the western Arctic were described. The vertical distributions of copepods showed distinct patterns that were associated with the physical structure of the water column and the origin and life strategies of each species or genus. The core of the eddy was characterized by enhanced concentrations of both Arctic- and Pacific-origin zooplankton. The feature likely originated the previous summer/spring, presumably after an upwelling event in the shelfbreak current of the Chukchi Sea. A simple estimate of the annual offshore flux of zooplankton biomass due to such eddies is much less than that believed to be advected through Bering Strait. This suggests that either the observed eddy was atypical in terms of zooplankton contentpossibly due to the influence of upwelling—or that most of the influx of zooplankton through Bering Strait does not make it to the shelf edge. Nonetheless, our observations support the view that upwelling events and eddies provide mechanisms for on-shelf and off-shelf advection of mesozooplankton, which can impact the fate of primary production on the shelves and basins.

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