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Influences of mesoscale anticyclonic eddies on the zooplankton community south of the western Aleutian Islands during the summer of 2010

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Mesoscale anticyclonic eddies have been observed south of the Aleutian Islands. Eddies farther east, in the Gulf of Alaska, are known to transport coastal water and coastal zooplankton to the offshore open ocean. The impacts of mesoscale anticyclonic eddies formed south of the western Aleutian Islands (Aleutian eddies) on the zooplankton community are not fully understood. In the present study, we describe zooplankton population structures within an Aleutian eddy and outside the eddy during July 2010. Based on the sea-level anomaly, the Aleutian eddy was formed south of Attu Island (172°54′E) in February 2010, and it moved southeastward in the next 5 months. Large oceanic copepods, *Neocalanus cristatus*, *Eucalanus bungii* and *Metridia pacifica* were more abundant inside the eddy than the outside. Inside the eddy, the life stage distribution of *N. cristatus* was more advanced than that outside, and *Neocalanus* spp. had accumulated more lipids. These conditions probably reflect the greater primary production in the eddy, production enhanced by nutrients

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advected into the eddy. The Aleutian eddy contained mostly oceanic copepods because it was formed in the offshore water and/or eddy–eddy interaction occurred after its formation. The sufficient food condition in the eddy presumably resulted in higher growth and survival rates of these oceanic copepods, resulting in the greater abundance, advanced development stages and greater lipid accumulation.

KEYWORDS: Aleutian eddies; calanoid copepods; mesoscale anticyclonic eddies; zooplankton

INTRODUCTION

The Alaskan Stream is the northern boundary current of the North Pacific Subarctic Gyre, flowing westward along the shelf break and the Aleutian Trench, south of the Alaska Peninsula and the Aleutian Islands (Favorite, 1967; Ohtani *et al.*, 1997; Reed and Stabeno, 1999). The Alaskan Stream connects the Alaskan Gyre, the Bering Sea Gyre and the Western Subarctic Gyre (Onishi, 2001).

Along the coasts of the Gulf of Alaska and the Aleutian Islands, several types of mesoscale anticyclonic eddies are known to be formed (Fig. 1A). Haida eddies appear west of Haida Gwaii (formerly called the Queen Charlotte Islands at 53°00′N, 132°00′W) and Alexander Archipelago (56°40′N, 134°05′W), and propagate northwestward into the central Gulf of Alaska (Crawford *et al.*, 2000; Crawford, 2002, 2005). Sitka eddies form off Sitka, Alaska (57°03′N, 135°19′W), and propagate northwestward (Crawford *et al.*, 2000; Rovegno *et al.*, 2009). Yakutat eddies appear in the northern Gulf of Alaska, off Yakutat, Alaska (59°45′N, 140°42′W), and move westward along the Alaskan Stream (Ladd *et al.*, 2005, 2007; Janout *et al.*, 2009). Kenai eddies form south of the Kenai Peninsula between 143 and 160°W, and propagate southwestward along the Alaskan Stream (Rovegno *et al.*, 2009; Lippiatt *et al.*, 2011; Ueno *et al.*, 2012). These eddies do not cross the 180° meridian (Ueno *et al.*, 2009). Anticyclonic eddies called Alaskan Stream eddies appear in the Alaskan Stream region between 157 and 169°W, south of the Alaska Peninsula and Aleutian Islands (Ueno *et al.*, 2009). The Alaskan Stream eddies usually move westward for 1–5 years and sometimes cross the 180° meridian and reach the Western Subarctic Gyre. Mesoscale anticyclonic eddies also form in the western Alaskan Stream region (Rogachev *et al.*, 2007; Rogachev and Shlyk, 2009). These eddies form in the region between the 180° meridian and Near Strait (about 170°E) and are called Aleutian eddies. Many of the Aleutian eddies move southwestward, and reach the Western Subarctic Gyre.

Mesoscale anticyclonic eddies observed in the Alaskan Stream and the Alaska Current regions (Fig. 1A) are thought to transport significant mass of coastal water to the offshore open ocean. For example eddies in the Gulf of Alaska bring coastal water (which is warm, has a low salinity and is rich in nutrients and iron) to the offshore oceanic region (Crawford, 2005; Lippiatt *et al.*, 2011; Brown *et al.*, 2012). Satellite images show that these eddies have high surface chlorophyll and primary production from spring through summer (Crawford *et al.*, 2005, 2007). Alaskan Stream eddies are also high in chlorophyll and hence primary production (Ueno *et al.*, 2010). A recent study of a Haida eddy showed that the phytoplankton assemblage in the eddy was dominated by diatoms, but as the eddy drifted away from the coast, the amount of diatoms significantly decreased (Peterson and Harrison, 2012). Phytoplankton diversity inside that eddy was greater than in waters outside in autumn during the eddy's later evolution (Peterson *et al.*, 2011). These mesoscale anticyclonic eddies are thought to influence strongly the density of phytoplankton in the central subarctic North Pacific (Ueno *et al.*, 2010).

Mesoscale anticyclonic eddies with high primary production in the Alaskan Stream region are thought to influence the zooplankton, which could in turn support higher trophic levels and enhance fish production. The zooplankton in Haida eddies has been reported to have a mixed community of coastal and oceanic species at the point of formation, and then the abundance of coastal species gradually decreases over time (Mackas and Galbraith, 2002; Mackas *et al.*, 2005). Analysis using a continuous plankton recorder of mesoscale anticyclonic eddies in the Gulf of Alaska also showed that coastal calanoid copepods are abundant inside them transporting these coastal species offshore (Batten and Crawford, 2005). Thus, the impacts of mesoscale anticyclonic eddies in the Gulf of Alaska on zooplankton communities have gradually come to be understood. However, the influences of Aleutian eddies south of the western Aleutian Islands on their entrained zooplankton communities are not fully understood.

In the present study, we compared vertical profiles of hydrography and the zooplankton communities between waters inside and outside of an Aleutian eddy for the first

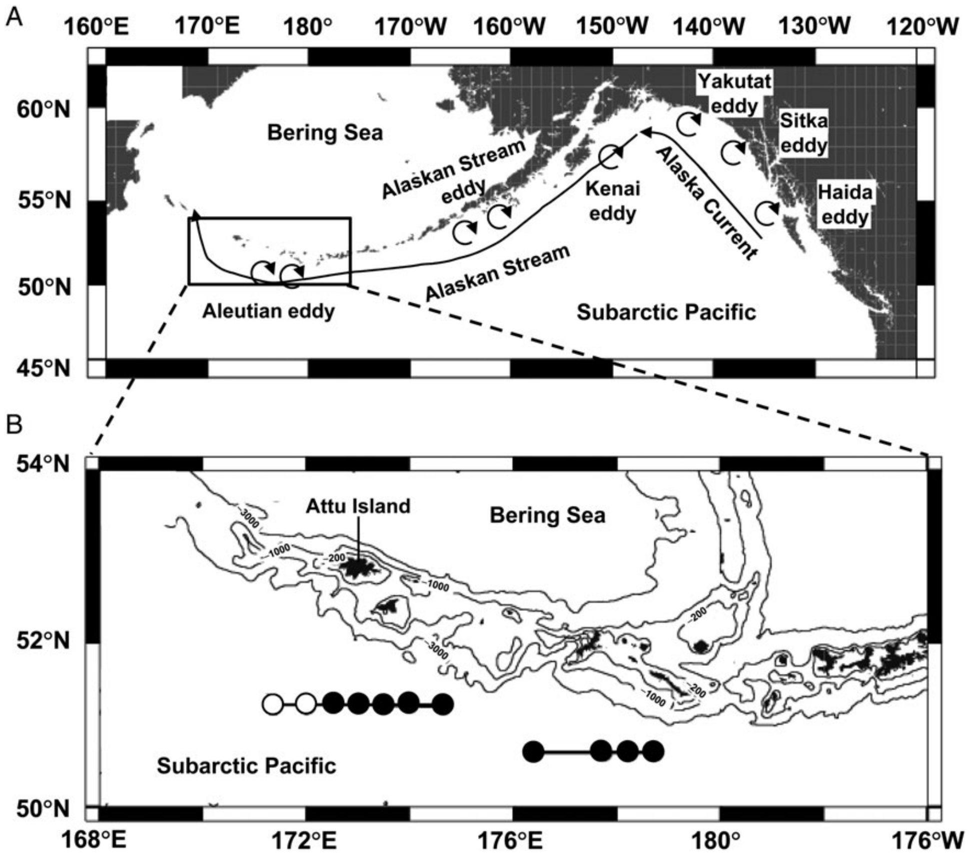

Fig. 1. The geographical distribution of mesoscale anticyclonic eddies along the Alaska Current and the Alaskan Stream in the subarctic Pacific (**A**). A box indicates the study area magnified in (**B**). Sampling stations along lines of mesoscale anticyclonic eddies during 7–8 July 2010 (B). Open and filled symbols in (B) indicate stations where XCTD and CTD casts were conducted, respectively.

time. Analyses of population structure and lipid accumulation of large oceanic calanoid copepods demonstrate the possible impacts of the eddy on the growth and nutritional condition of the copepods.

METHOD

Field study

Our field study was conducted at seven stations along 51°15′N from 171°21′ to 174°38′E and at four stations along 50°40′N from 176°24′ to 178°44′E on board T/S *Oshoro-Maru* of the Faculty of Fisheries, Hokkaido University, during 7–8 July 2010 (Fig. 1B). At each station, temperature, salinity and fluorescence were measured with a CTD (Sea-Bird Electronics, Inc., USA, CTD-SBE 9plus). At some stations, only temperature and salinity were measured with an XCTD (Tsurumi Seiki Co., Ltd., Japan). These hydrographic data have been published elsewhere (Hokkaido University, 2011).

Zooplankton samples were collected by vertical tows from 150 m to the surface using a 45-cm mouth diameter, 100 μm mesh size NORPAC net (Motoda, 1957) equipped with a flowmeter (Rigosha Co., Ltd., Japan). The net towing speed was 1 m s^{-1}. During each sampling, the wire angle was measured using a protractor, and the wire length was extended until the net reached the desired depth. Samples were immediately preserved in 5% formalin-seawater buffered with sodium tetraborate. The volume of water filtered was calculated from the flow metre reading.

Data and sample analyses

To evaluate the position of mesoscale anticyclonic eddies, delayed-time data of sea-level anomaly (SLA) in the period from the approximate date of eddy formation (6 January 2010) to the date of field sampling (7 July 2010) were downloaded from AVISO (Collecte Localisation Satellites, France; http://www.aviso.oceanobs.com; SSALTO/DUACS, 2012). The spatial resolution was 1/4° × 1/4°. The SLA data at 7-day intervals was used to track eddies. During summer, seawater expands due to the increase in water temperature, thus using raw SLA data, the SLAs in the whole region tend to be positive in summer and negative in winter (Ueno *et al.*, 2012). Accordingly, the weekly spatial mean state of the subarctic North Pacific north of 45°N, except for the marginal seas, was removed from each weekly map of SLA to compensate for seasonal steric effects (Ueno *et al.*, 2009, 2010, 2012). Eddies were tracked using the Okubo–Weiss parameter: W (Okubo, 1970; Weiss, 1991) calculated from the SLA data assuming geostrophy. In this analysis, we defined an area with $W < -2 \times 10^{-12}\ \mathrm{s}^{-2}$ as an eddy area (Chelton *et al.*, 2007). The eddy area and the position of the eddy centre were analysed, and the eddies were tracked in the same manner as by Henson and Thomas (Henson and Thomas, 2008); Inatsu (Inatsu, 2009) and Ueno *et al.* (Ueno *et al.*, 2012). The positions of eddy centres estimated from SLA data may have errors >50 km due to data resolution and eddy propagation (Ladd *et al.*, 2005, 2007).

In the laboratory of Hokkaido University, each zooplankton sample was mixed well, and a 1/10 subsample was taken using a large bore pipette. The subsample was observed under a dissecting microscope, and calanoid nauplii, cyclopoid copepods, poecilostomatoid copepods, large oceanic calanoid copepods, small calanoid copepods and other zooplankton taxa were sorted and counted. Calanoid copepods were identified to species according to Brodskii (Brodskii, 1967), Frost (Frost, 1974, 1989) and Miller (Miller, 1988). Among calanoid copepods, large oceanic species, *Neocalanus cristatus*, *N. plumchrus*, *Eucalanus bungii* and *Metridia pacifica* are known to account for 70% of the mesozooplankton biomass in the subarctic North Pacific (Ikeda *et al.*, 2008). For these species, every copepodid stage (C1–C6) was counted. In addition, female and male identifications were made for C4–C6 stages of *E. bungii* and *M. pacifica*. *Eucalanus bungii* nauplii, which differ morphologically from other species and are easily identifiable (Johnson, 1937), were also counted. *Metridia pacifica* performs diel vertical migration in the subarctic Pacific during summer (Hattori, 1989; Padmavati *et al.*, 2004; Yamaguchi *et al.*, 2004; Takahashi *et al.*, 2009). The C6 females of *M. pacifica* are more abundant near the surface at night than during the day, which affects its apparent population structure and the zooplankton community structure. Saito *et al.* (Saito *et al.*, 2011) calculated the day: night ratio of *M. pacifica* C6F abundance in this region, and this ratio was used to convert night-time values to daytime values. For large copepods, the mean population stage was calculated using the following equation,

$$\mathrm{MS} = \frac{\sum_{i=1}^{6} i \times N_i}{\sum_{i=1}^{6} N_i},$$

where MS is the mean population stage, i is the copepodid stage (1–6), and N_i is the abundance (ind. m^{-2}) of each stage (Marin, 1987). For *E. bungii*, whose nauplii were counted, a nauplius was treated as stage 1, and MS was calculated using the value of each copepodid stage plus one, i.e. C1 was considered as 2. For C5 individuals of *N. cristatus*, *N. plumchrus* and *E. bungii*, the lipid accumulation was scored as three levels (1: no lipid, 2: some lipid, 3: full of lipid) (Kobari and Ikeda, 1999, 2001; Tsuda *et al.*, 1999, 2004; Shoden *et al.*, 2005), and the mean lipid score was calculated. The integrated mean temperature and phytoplankton fluorescence in the 0–150 m profiles, total zooplankton abundance, the abundance and mean population stage of large oceanic calanoid copepods and the mean lipid score of the C5 individuals were compared between the sampling lines using Mann–Whitney U-tests.

RESULTS

Hydrography

Based on the SLA data in the sampled area, the 51°15′N (western) line crossed an anticyclonic eddy with an SLA of 10–35 cm and a diameter of ~200 km (Fig. 2A). Along the 50°40′N (eastern) line, an anticyclonic eddy with an SLA of 10–25 cm was observed north of the westernmost station, but this line did not cross the eddy. We named the 51°15′N line crossing the mesoscale anticylonic eddy the "Eddy line" and the 50°40′N line the "Non-eddy line."

The eddy observed along the Eddy line was first detected in mid-February 2010 south of Attu Island (eddy centre: 52°10′N, 172°20′E) (Fig. 2B and C). This eddy gradually increased in area (Fig. 2D) as it moved southeastward during the next 5 months and reached the sampling area (near 51°10′N, 172°50′E) on 7 July 2010. The SLA near the eddy centre, representing the strength of the eddy, increased continuously, and the area oscillated at 1- to 2-month periods overlain on a general increase from ~7000 to ~18 000 km^2 (Fig. 2D). Figure 3A shows vertical profiles of temperature along the Eddy line and the Non-eddy line. Between 171.35°E (solid black circles) and 173.49°E (open red triangles) along the Eddy line, a subsurface cold water mass (3.0–4.0°C at 26.3–26.8σ_θ) was observed at 80–200 m. A somewhat warmer water mass (4.0–4.5°C at 26.5–27.5σ_θ) was also seen in this section at 200–500 m depth. In contrast, this warm water mass (4.0–4.5°C) spreads from 50 to 350 m between 174.00 and 174.64°E. The temperature–salinity relation also separated the water mass into cold and warm volumes between 26.2 and 26.6σ_θ (Fig. 3B). Unlike the Eddy line, subsurface cold or warmer water

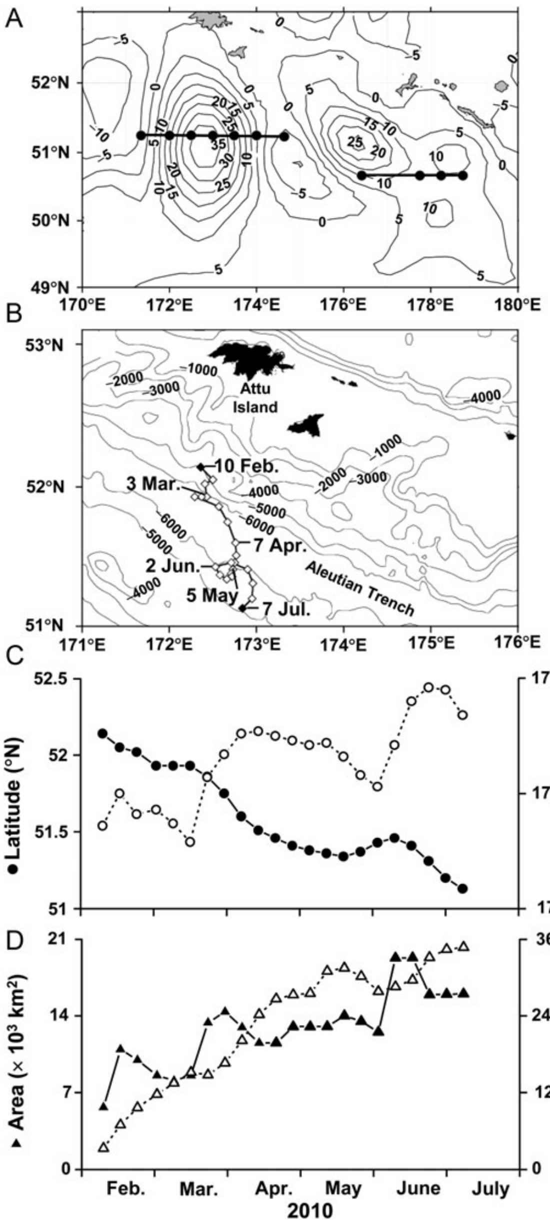

Fig. 2. Sea-level anomaly (cm) along the sampling lines on 7 July 2010 (**A**). Bathymetric contours are also shown every 1000 m in (A). A trajectory of mesoscale anticyclonic eddy from 10 February to 7 July 2010 in 7-day intervals (B). Diamond symbols in (**B**) indicate the centre of the eddy in each time period, and filled symbols show the eddy's origin and its position on 7 July 2010. Time series of position: latitude (filled circles) and longitude (open circles) (**C**), area (filled triangles) and sea-level anomaly (open triangles) (**D**) of the mesoscale anticyclonic eddy in 7-day intervals from 10 February to 7 July 2010.

masses were not observed along the Non-eddy line, and the water mass structure was mostly uniform along the section (Fig. 3A and B). Fluorescence was higher along the Eddy line than the Non-eddy line, particularly between 172.50 and 174.64°E at 25–50 m depth (Fig. 3C).

The range of integrated mean temperature at 0–150 m depth was 4.1–5.4°C along the Eddy line and 4.7–5.1°C along the Non-eddy line (Fig. 4). There was no significant difference in the integrated mean temperature (*U*-test, $P > 0.05$), but the eddy centre was colder. The range of fluorescence at 0–150 m was 57.9–79.4 mg m^{-2} along the Eddy line and 45.5–66.5 mg m^{-2} along the Non-eddy line (Fig. 4). There was no statistically significant difference in fluorescence between the lines ($P > 0.05$), but it was high near the eddy centre.

Total zooplankton abundance and taxonomy

Total zooplankton abundance ranged from 1.0 to 2.7×10^5 ind. m^{-2} (mean: 1.7×10^5 ind. m^{-2}) along the Eddy line and 1.1–1.4×10^5 ind. m^{-2} (mean: 1.3×10^5 ind. m^{-2}) along the Non-eddy line (Fig. 5A), not statistically different (*U*-test, $P > 0.05$). Relative numerical abundances of some groups were different between the lines. Calanoid copepod nauplii (range: 3.3–29.3%, mean: 20.7%) and cyclopoid copepods (range: 20.5–60.4%, mean: 34.2%) were abundant along the Eddy line, and cyclopoid copepods (range: 20.3–41.4%, mean: 28.1%) and large oceanic calanoid copepods (*Neocalanus*, *Eucalanus* and *Metridia* spp.) (range: 13.3–38.9%, mean: 26.4%) were abundant along the Non-eddy line (Fig 5B). The numerical abundances of calanoid nauplii, cyclopoid copepods and poecilostomatoid copepods were 4.8, 0.7 and 2.9×10^4 ind. m^{-2}, respectively, along the Eddy line and 4.1, 0.8 and 2.3×10^4 ind. m^{-2}, respectively, along the Non-eddy line, and these were not statistically different between these lines (*U*-test, $P > 0.05$).

Calanoid copepods

In the zooplankton samples, 18 species of calanoid copepods belonging to 14 genera were observed (Table I). Six coastal species (*Acartia longiremis*, *Calanus marshallae* and four species of *Pseudocalanus*) and four large oceanic copepods were detected along both lines. Five deep-sea species (*Candacia columbiae*, *Microcalanus pygmaeus*, *Paraeuchaeta elongata*, *Pleuromamma scutullata* and *Scolecithricella minor*) were observed along both lines, but *Aetideopsis rostrata* and *Racovitzanus antarcticus* were found only along the Eddy line, and *Aetideus armatus* and *Heterorhabdus tanneri* were identified only along the Non-eddy line. Comparing these calanoid copepod abundances between the lines, the abundances of *A. longiremis*, *P. minutus* and *R. antarcticus* were significantly greater along the Eddy line than the Non-eddy line (*U*-test, $P < 0.05$, Table I).

Large oceanic calanoid copepods

Numerical abundance of the large oceanic calanoid copepod *N. cristatus* was significantly greater along the Eddy

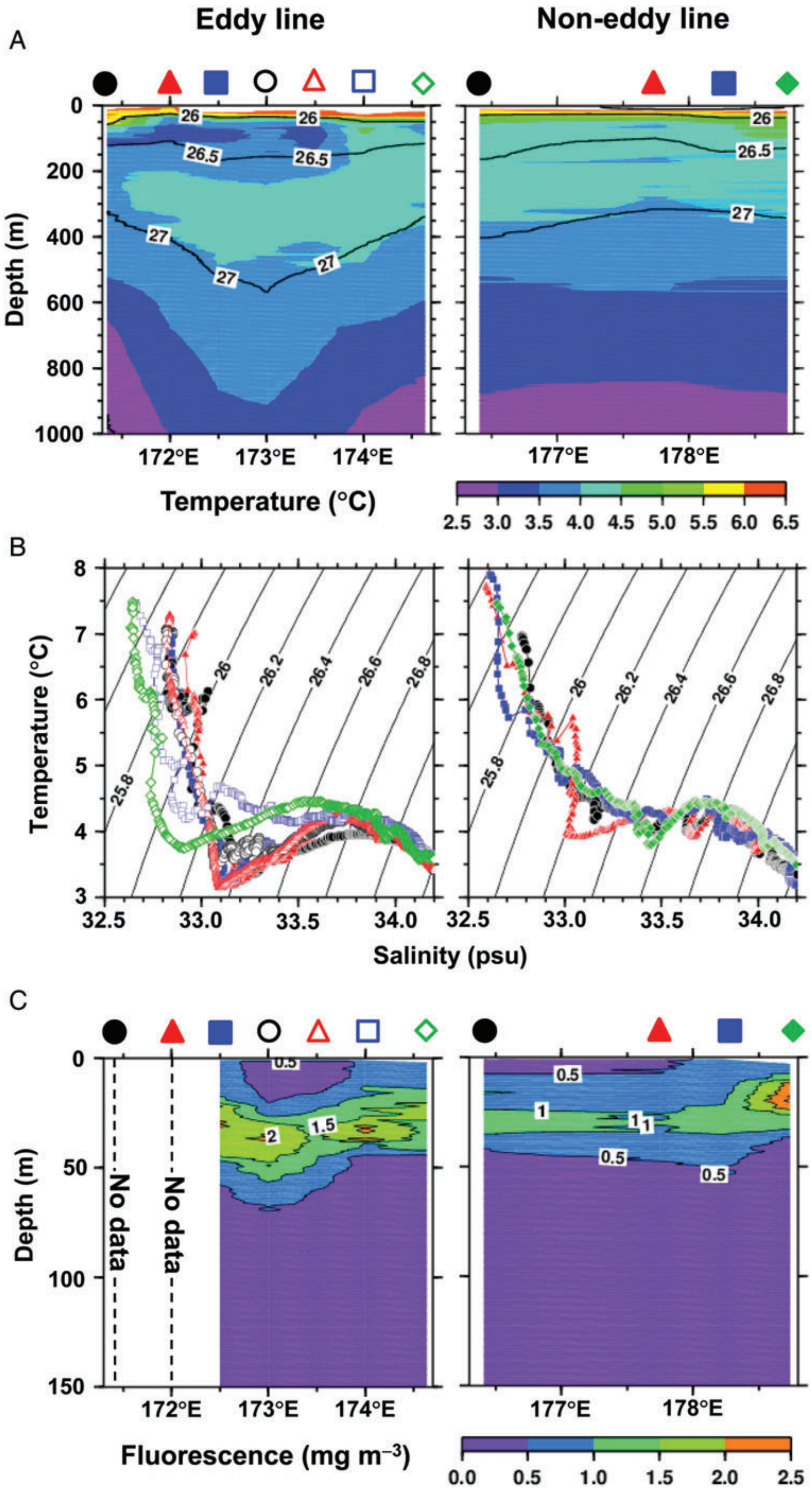

Fig. 3. (**A**) Temperature distribution (°C as colour scale) superimposed by the density distribution (σ_θ, contours) for 0–1000 m depth, (**B**) temperature–salinity relation and (**C**) fluorescence distributions for 0–150 m along the Eddy line and Non-eddy line. Symbols along at the tops of (A) and (C) represent the locations of profiles characterized by T–S relations in (B).

line (range: 0.8–5.2 × 10^3 ind. m^{-2}, mean: 2.7 × 10^3 ind. m^{-2}) than along the Non-eddy line (range: 0.9–1.7 × 10^3 ind. m^{-2}, mean: 1.2 × 10^3 ind. m^{-2}) (U-test, $P < 0.05$, Fig. 6A, Table I). Its mean stage was significantly higher along the Eddy line (mean: 3.2) than along the Non-eddy line (mean: 2.2) ($P < 0.05$, Table II), and C5 individuals were relatively more numerous along the Eddy line. In contrast, *N. plumchrus* abundance was significantly greater along the Non-eddy line (range: 2.0–10.0, 4.9 × 10^3 ind. m^{-2}) than along the Eddy line (range: 0.4–4.9, mean: 2.8 × 10^3 ind. m^{-2}) ($P < 0.05$, Fig. 6B, Table I). There was no significant difference between the lines in the mean stage. *Eucalanus bungii* abundance was also significantly higher along the Eddy line (range: 5.8–13.2, mean: 8.0 × 10^3 ind. m^{-2}) than along the Non-eddy line (range: 2.6–9.2, mean: 5.5 × 10^3 ind. m^{-2}) ($P < 0.05$, Fig. 6C, Table I), but there was no significant difference in its mean stage. The abundance of *M. pacifica* was significantly greater along the Eddy line (range: 8.0–40.6, mean: 24.1 × 10^3 ind. m^{-2}) than along the Non-eddy line (range: 6.7–39.3, mean: 17.1 × 10^3 ind. m^{-2}) ($P < 0.05$, Fig. 6D, Table I), but there was no difference in its mean stage.

The mean lipid scores of *N. cristatus* and *N. plumchrus* C5 individuals were significantly higher along the Eddy line (*N. cristatus*: 2.1 ± 0.4, *N. plumchrus*: 2.6 ± 0.2) than along the Non-eddy line (*N. cristatus*: 1.7 ± 0.2, *N. plumchrus*: 2.3 ± 0.1) (U-test, $P < 0.05$, Fig. 7, Table II). On the other hand, there was no difference in the mean lipid score of *E. bungii* C5 individuals.

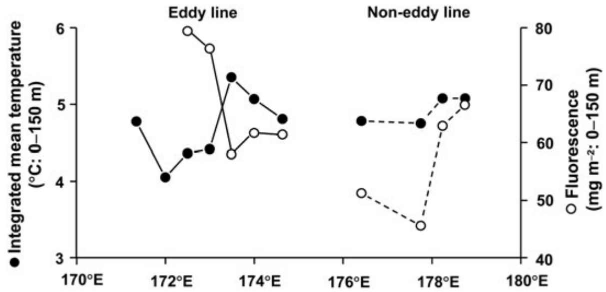

Fig. 4. 0–150 m integrated mean temperature (filled circles) and fluorescence (open circles) along the Eddy line and the Non-eddy line during 7–8 July 2010.

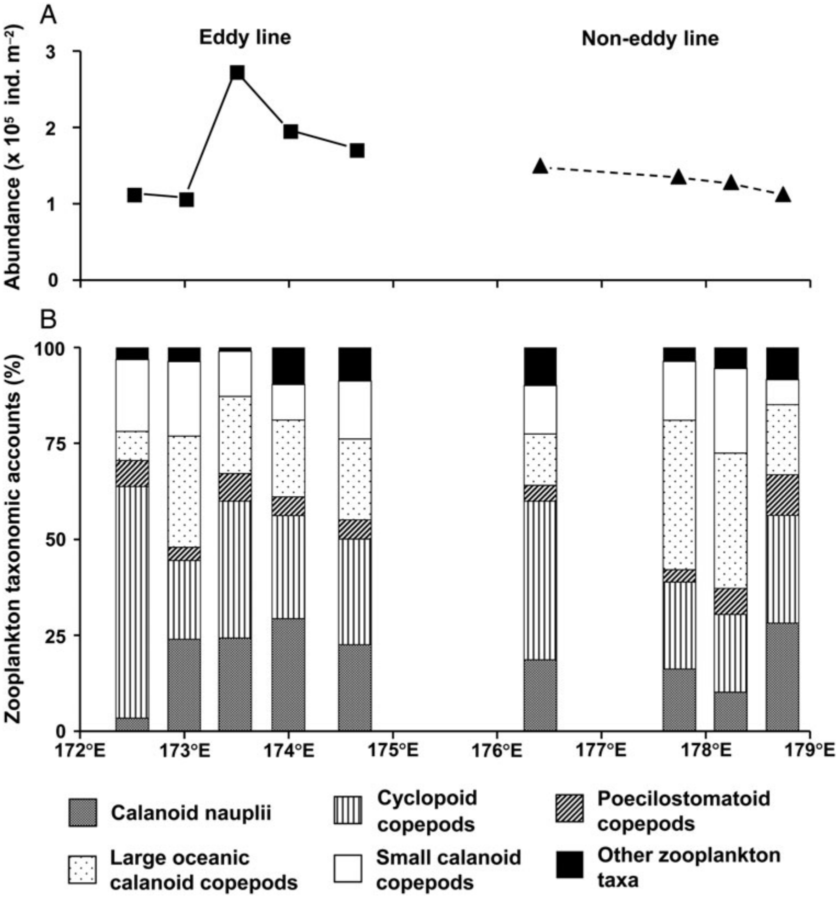

Fig. 5. Total zooplankton abundance (**A**) and its taxonomic composition (**B**) along the Eddy line and the Non-eddy line during 7–8 July 2010.

Table I: The list of calanoid copepod species identified along the eddy line (EL) and the Non-eddy line (NEL) during 7–8 July 2010

Functional group/ species	Abundance (ind. m^{-2}) Eddy line	Non-eddy line	*U*-test
Coastal species			
Acartia longiremis	902 ± 180	367 ± 106	EL > NEL*
Calanus marshallae	163 ± 248	269 ± 185	NS
Pseudocalanus mimus	2792 ± 1227	2288 ± 1063	NS
Pseudocalanus minutus	3177 ± 590	2412 ± 1571	EL > NEL*
Pseudocalanus moultoni	1431 ± 408	1463 ± 1074	NS
Pseudocalanus newmani	625 ± 183	936 ± 728	NS
Deep sea species			
Aetideopsis rostrata	15 ± 34	0	NS
Aetideus armatus	0	92 ± 142	NS
Candacia columbiae	15 ± 34	451 ± 903	NS
Microcalanus pygmaeus	13,391 ± 4166	6773 ± 4171	NS
Paraeuchaeta elongata	148 ± 113	69 ± 138	NS
Pleuromamma scutullata	30 ± 68	94 ± 188	NS
Racovitzanus antarcticus	89 ± 38	0	EL > NEL*
Scolecithricella minor	733 ± 339	794 ± 553	NS
Large oceanic species			
Eucalanus bungii	7973 ± 3010	5492 ± 2741	EL > NEL*
Metridia pacifica	24 076 ± 11 747	17 068 ± 15 296	EL > NEL*
Neocalanus cristatus	2709 ± 1645	1175 ± 352	EL > NEL*
Neocalanus plumchrus	2790 ± 1874	4930 ± 3694	NEL > EL*

Values are mean ± standard deviation of abundance (ind. m^{-2}) along the Eddy line (EL) and the Non-eddy line (NEL). Differences between the two lines were tested by Mann–Whitney *U*-test.
$^{*}P < 0.05$, NS, not significant.

DISCUSSION

Influences of the aleutian eddy on zooplankton community

In the present study, the zooplankton community in and near a mesoscale anticyclonic Aleutian eddy (along the Eddy line) comprised more large oceanic copepods, particularly *N. cristatus* and *E. bungii* than coastal copepods (Table I, Fig. 6A and C). The eddy formation and modification processes may have influenced this result. For example a Haida eddy that was formed on the continental shelf off British Columbia, Canada was reported to transport coastal water to offshore areas (e.g. Whitney and Robert, 2002), and three coastal copepods, *A. longiremis*, *Calanus marshallae* and *P. mimus* C4–C6 were abundant inside it (Mackas and Galbraith, 2002; Mackas *et al.*, 2005). In contrast, the Aleutian eddy that was sampled in the present study was formed and propagated in the

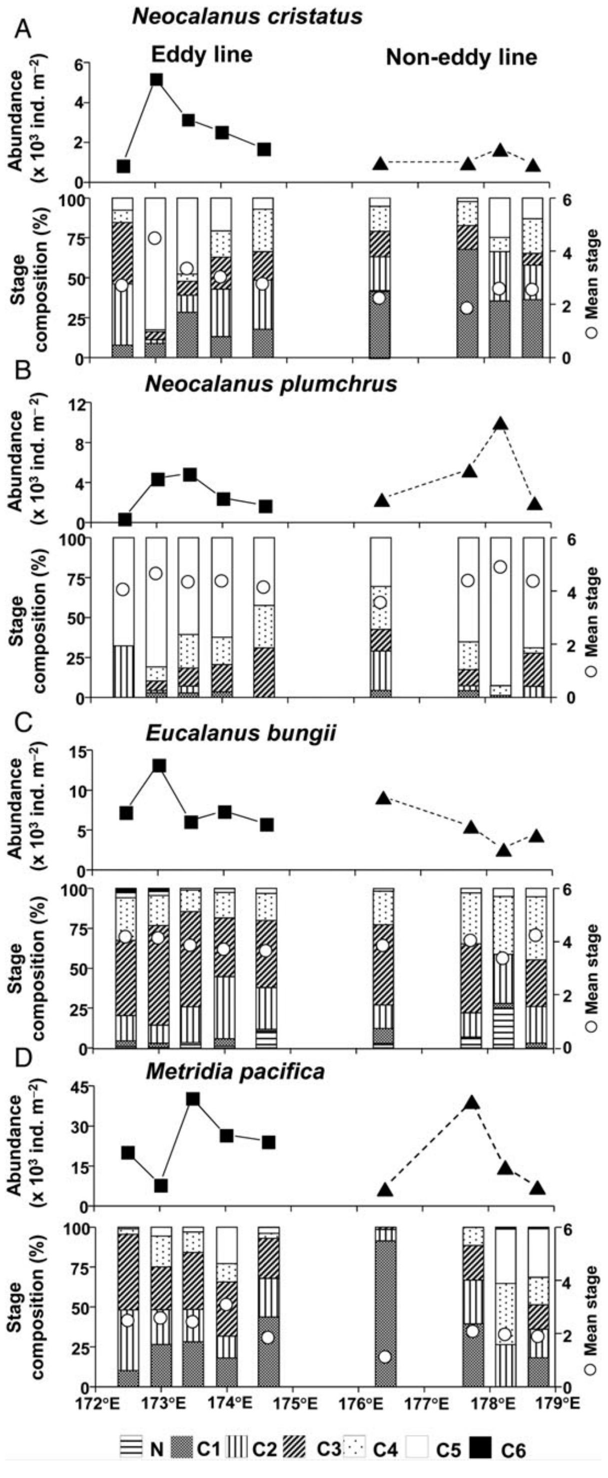

Fig. 6. Abundance, stage composition and mean population stage of *Neocalanus cristatus* (**A**), *N. plumchrus* (**B**), *Eucalanus bungii* (**C**) and *Metridia pacifica* (**D**) along the Eddy line and the Non-eddy line during 7–8 July 2010.

Table II: Comparison of mean stage and mean lipid score of large calanoid copepods between the eddy line (EL) and the Non-eddy line (NEL) during 7–8 July 2010

	Mean ± SD		
Parameter/species	Eddy line	Non-eddy line	*U*-test
Mean stage			
Eucalanus bungii	3.9 ± 0.2	3.8 ± 0.4	NS
Metridia pacifica	2.5 ± 0.4	2.6 ± 1.2	NS
Neocalanus cristatus	3.2 ± 0.7	2.3 ± 0.3	EL > NEL*
Neocalanus plumchrus	4.3 ± 0.2	4.3 ± 0.6	NS
Mean lipid score			
Eucalanus bungii C5	2.2 ± 0.2	2.1 ± 0.2	NS
Neocalanus cristatus C5	2.1 ± 0.4	1.7 ± 0.2	EL > NEL*
Neocalanus plumchrus C5	2.6 ± 0.2	2.3 ± 0.1	EL > NEL*

Differences between the two lines were tested by Mann–Whitney *U*-test. *$P < 0.05$, NS, not significant.

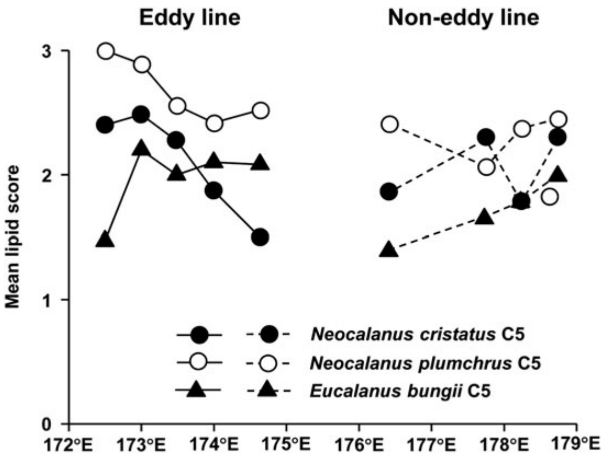

Fig. 7. Mean lipid scores of C5 individuals of *Neocalanus cristatus*, *N. plumchrus* and *Eucalanus bungii* along the Eddy line and the Non-eddy line during 7–8 July 2010.

offshore water south of the Aleutian Islands (bottom depth of ~4000 m, cf. Fig. 2B). The water mass structure at time of the eddy's formation and throughout its transit and growth is not fully understood. Furthermore, another anticyclonic eddy was observed adjacent to this eddy, and eddy–eddy interaction between the two might have occurred. Eddy–eddy interaction can cause a sudden increase in SLA, and water inside an eddy can exchange with other water masses (Ueno *et al.*, 2012). Thus, it is uncertain whether the water mass injected at the formation remained in the eddy during the sampling period. We found that the large oceanic copepods *N. cristatus* and *E. bungii* were abundant within the eddy, suggesting that the eddy may have been composed of offshore water during the sampling period rather than coastal water. Unlike in the Gulf of Alaska and the eastern Bering Sea shelf, in the western Aleutian Islands, coastal area (the depth <200 m) is much smaller and strictly limited around the islands (Fig. 1B). The Aleutian eddy could draw coastal water into it; however, its mass compared with offshore water is presumably much smaller. Therefore, more oceanic copepods could be drawn into the Aleutian eddy rather than coastal copepods.

Biological productivity of the Aleutian eddy

In the present study, the abundance of most species of large calanoid copepods was significantly greater inside the eddy than outside (Table I). Inside the eddy, the mean lipid score of *N. cristatus* and *N. plumchurus* was significantly greater, and the mean stage of *N. cristatus* was more advanced (Table II). The high abundances, lipid accumulations and advanced life stages of large oceanic copepods suggest better survival and growth conditions for large copepods inside the eddy than outside.

The eastern subarctic North Pacific around the study area is known to be a high nutrient and low chlorophyll region (Reid, 1962; Anderson *et al.*, 1969), and iron is thought to be a major limiting factor for phytoplankton growth there (Boyd *et al.*, 2004). Nevertheless, the mesoscale Aleutian anticyclonic eddy observed in the present study had higher fluorescence than outside the eddy, and thus substantial phytoplankton biomass (Figs. 3C and 4). Mesoscale anticyclonic eddies have been reported to increase the nutrient supply supporting productivity because eddy/wind interactions and submesoscale processes force upwelling to the surface of nutrient-rich water (e.g. McGillicuddy *et al.*, 2007; Mahadevan *et al.*, 2008). In the present study, the eddy area was increasing (Fig. 2D), so the influence of eddy/wind interactions might be weak. The Aleutian eddy in the present study seems to have been influenced by colder water from the offshore region on the western side and by warmer water from the Alaskan Stream on the eastern side (Fig. 3A). Alaskan Stream eddies south of the eastern Aleutian Islands have been reported to cause the Alaskan Stream to meander to the south, and presumably carry nutrient/chlorophyll-rich water to the south (Ueno *et al.*, 2010). The nutrient-rich/warm water presumably enters from the eastern sides of those eddies, and colder water flows in to them from the western sides. This advection and mixing are hypothesized to result in high phytoplankton concentration inside these eddies. The phytoplankton concentration history in the Aleutian anticyclonic eddy before our observations from the T/S *Oshoro-maru* is not known due to lack of satellite surface chlorophyll data since the study areas was mostly covered by clouds. However, the high phytoplankton concentration observed in the eddy presumably resulted in the greater lipid accumulations of the large oceanic copepods (Fig. 7).

The influence of phytoplankton concentration (the concentration of food) on the mass of large oceanic copepods has been documented. For example Dagg (Dagg, 1991) reported that in the Bering Sea, where food was abundant, the carbon content in one *N. plumchrus* C5 individual was 416 μg C ind. $^{-1}$, whereas in an offshore region of the Gulf of Alaska, where food was scarce, the carbon content was only 59–143 μg C ind. $^{-1}$. In the present study, the relatively greater abundance and lipid accumulation in *N. cristatus* and *N. plumchrus* within the mesoscale anticyclonic Aleutian eddy are thought to have resulted from stronger survival and growth rates supported by greater food availability. This, in turn, would have been generated by high primary production enhanced by the advection of nutrient-rich water and cold water into the eddy.

CONCLUSIONS

The Aleutian eddy we studied was formed south of the Aleutian Islands, and some water exchange due to eddy–eddy interaction might have occurred after the initial formation. Since large oceanic copepods were abundant during the sampling, the eddy is presumed to include a substantial proportion of oceanic water. In addition, the high abundance and lipid accumulation of oceanic copepods and the advanced life stages in some species probably reflect high primary production caused by the advective transfer into the eddy of colder nutrient-rich waters. In the future, time-series analyses of the eddy modification process, primary production, phytoplankton community and zooplankton community are required to more fully understand the effects of Aleutian eddies on their entrained zooplankton communities.

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