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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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22 **Abstract**

23 Mesoscale anticyclonic eddies have been observed south of the Aleutian Islands. Eddies
24 farther east, in the Gulf of Alaska, are known to transport coastal water and coastal zooplankton to
25 offshore open ocean. The impacts of mesoscale anticyclonic eddies formed south of the western
26 Aleutian Islands (Aleutian eddies) on the zooplankton community are not fully understood. In the
27 present study, we describe zooplankton population structures within an Aleutian eddy and outside
28 the eddy during July 2010. Based on the sea level anomaly, the Aleutian eddy was formed south
29 of Attu Island (172°54'E) in February 2010, and it moved southeastward in the next five months.
30 Large oceanic copepods, *Neocalanus cristatus*, *Eucalanus bungii* and *Metridia pacifica* were more
31 abundant inside the eddy than the outside. Inside the eddy, the life stage distribution of *N.*
32 *cristatus* was advanced than that outside, and *Neocalanus* spp. had accumulated more lipids.
33 These conditions probably reflect the greater primary production in the eddy, production enhanced
34 by nutrients advected into the eddy. The Aleutian eddy contained mostly oceanic copepods
35 because it was formed in the offshore water and/or eddy-eddy interaction occurred after its
36 formation. The sufficient food condition in the eddy presumably induced higher growth and
37 survival rates of these oceanic copepods, resulting in the greater abundance, advanced development
38 stages and greater lipid accumulation.

39 **Keywords:** mesoscale anticyclonic eddies; Aleutian eddies; zooplankton; calanoid copepods

40 **Introduction**

41 The Alaskan Stream is the northern boundary current of the North Pacific Subarctic Gyre,
42 flowing westward along the shelf break and the Aleutian Trench, south of the Alaska Peninsula and
43 the Aleutian Islands (Favorite, 1967; Ohtani *et al.*, 1997; Reed and Stabeno, 1999). The Alaskan
44 Stream connects the Alaskan Gyre, the Bering Sea Gyre and the Western Subarctic Gyre (Onishi,
45 2001).

46 Along the coasts of the Gulf of Alaska and the Aleutian Islands, several types of mesoscale
47 anticyclonic eddies are known to be formed (Fig. 1A). Haida eddies appear west of Haida Gwaii
48 (formerly called the Queen Charlotte Islands at 53°00'N, 132°00'W) and Alexander Archipelago
49 (56°40'N, 134°05'W), and propagate northwestward into the central Gulf of Alaska (Crawford *et al.*,
50 2000; Crawford, 2002, 2005). Sitka eddies form off Sitka, Alaska (57°03'N, 135°19'W), and
51 propagate northwestward (Crawford *et al.*, 2000; Rovegno *et al.*, 2009). Yakutat eddies appear in
52 the northern Gulf of Alaska, off Yakutat, Alaska (59°45'N, 140°42'W) and move westward along
53 the Alaskan Stream (Ladd *et al.*, 2005, 2007; Janout *et al.*, 2009). Kenai eddies form south of the
54 Kenai Peninsula between 143°W and 160°W, and propagate southwestward along the Alaskan
55 Stream (Rovegno *et al.*, 2009; Lippiatt *et al.*, 2011; Ueno *et al.*, 2012). These eddies do not cross
56 the 180° meridian (Ueno *et al.*, 2009). Anticyclonic eddies called Alaskan Stream eddies appear
57 in the Alaskan Stream region between 157°W and 169°W, south of the Alaska Peninsula and
58 Aleutian Islands (Ueno *et al.*, 2009). The Alaskan Stream eddies usually move westward for 1–5
59 years and sometimes cross the 180° meridian and reach the Western Subarctic Gyre. Mesoscale
60 anticyclonic eddies also form in the western Alaskan Stream region (Rogachev *et al.*, 2007;
61 Rogachev and Shlyk, 2009). These eddies form in the region between the 180° meridian and
62 Near Strait (about 170°E) and are called Aleutian eddies. Many of the Aleutian eddies move
63 southwestward, and reach the Western Subarctic Gyre.

64 Mesoscale anticyclonic eddies observed in the Alaskan Stream and the Alaska Current
65 regions (Fig. 1A) are thought transport significant mass of coastal water to the offshore open ocean.

66 For example, eddies in the Gulf of Alaska bring coastal water (which is warm, has a low-salinity
67 and is rich in nutrient and iron) to the offshore oceanic region (Crawford, 2005; Lippiatt *et al.*,
68 2011; Brown *et al.*, 2012). Satellite images show that these eddies are high in surface chlorophyll
69 and primary production from spring through summer (Crawford *et al.*, 2005, 2007). Alaskan
70 Stream eddies are also high in chlorophyll and hence primary production (Ueno *et al.*, 2010). A
71 recent study of a Haida eddy showed that the phytoplankton assemblage in the eddy was dominated
72 by diatoms, but as the eddy drifted away from the coast, the amount of diatoms significantly
73 decreased (Peterson and Harrison, 2012). Phytoplankton diversity inside that eddy greater than in
74 waters outside of it in autumn during the eddy's later evolution (Peterson *et al.*, 2011). These
75 mesoscale anticyclonic eddies are thought to influence strongly the density of phytoplankton in the
76 central subarctic North Pacific (Ueno *et al.*, 2010).

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

88 In the present study, we compared vertical profiles of hydrography and the zooplankton
89 communities between waters inside and outside of an Aleutian eddy for the first time. Analyses of
90 population structure and lipid accumulation of large oceanic calanoid copepods demonstrate the
91 possible impacts of that eddy on the growth and nutritive condition of the copepods.

92 **Method**

93 **Field study**

94 Our field study was conducted at seven stations along 51°15'N from 171°21'E to 174°38'E
95 and at four stations along 50°40'N from 176°24'E to 178°44'E on board T/S *Oshoro-Maru* of the
96 Faculty of Fisheries, Hokkaido University, during 7–8 July 2010 (Fig. 1B). At each station,
97 temperature, salinity and fluorescence were measured with a CTD (Sea-Bird Electronics, Inc., U. S.
98 A., CTD-SBE 9plus). At some stations, only temperature and salinity were measured by an
99 XCTD (Tsurumi Seiki Co., Ltd., Japan). These hydrographic data have been published
100 elsewhere (Hokkaido University, 2011).

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

107 **Data and sample analyses**

108 To evaluate the position of mesoscale anticyclonic eddies, delayed-time data of sea level
109 anomaly (SLA) in the period from the approximate date of eddy formation (6 January 2010) to the
110 date of field sampling (7 July 2010) were downloaded from AVISO (Collecte Localisation
111 Satellites, France; <http://www.aviso.oceanobs.com>; SSALTO/DUACS, 2012). The spatial
112 resolution was 1/4° × 1/4°. The SLA data at seven-day intervals was used to track eddies.
113 During summer, seawater expands due to the increase in water temperature, thus using raw SLA
114 data, the sea-level anomalies in the whole region tend to be positive in summer and negative in
115 winter (Ueno *et al.*, 2012). Accordingly, the weekly spatial mean state of the subarctic North

116 Pacific north of 45°N, except for the marginal seas, was removed from each weekly map of SLA to
117 compensate for seasonal steric effects (Ueno *et al.*, 2009, 2010, 2012). Eddies were tracked using
118 the Okubo-Weiss parameter: W (Okubo, 1970; Weiss, 1991) calculated from the SLA data
119 assuming geostrophy. In this analysis, we defined an area with $W < -2 \times 10^{-12} \text{ s}^{-2}$ as an eddy area
120 (Chelton *et al.*, 2007). The eddy area and the position of the eddy centre were analyzed, and the
121 eddies were tracked in the same manner as by Henson and Thomas (2008); Inatsu (2009) and Ueno
122 *et al.* (2012). The positions of eddy centres estimated from SLA data may have errors > 50 km
123 due to data resolution and eddy propagation (Ladd *et al.*, 2005, 2007).

124 In the land laboratory of Hokkaido University, each zooplankton sample was mixed well,
125 and a 1/10 subsample was taken using a large bore pipette. The subsample was observed under a
126 dissecting microscope, and calanoid nauplii, cyclopoid copepods, poecilostomatoid copepods, large
127 oceanic calanoid copepods, small calanoid copepods and other zooplankton taxa were sorted and
128 counted. Calanoid copepods were identified to species according to Brodskii (1967), Frost (1974,
129 1989) and Miller (1988). Among calanoid copepods, large oceanic species, *Neocalanus cristatus*,
130 *N. plumchrus*, *Eucalanus bungii* and *Metridia pacifica* are known to account for 70% of the
131 mesozooplankton biomass in the subarctic North Pacific (Ikeda *et al.*, 2008). For these species,
132 every copepodid stage (C1–C6) was counted. In addition, female and male identifications were
133 made for C4–C6 stages of *E. bungii* and *M. pacifica*. *Eucalanus bungii* nauplii, which
134 morphologically differ from other species and are easily identifiable (Johnson, 1937), were also
135 counted. *Metridia pacifica* performs diel vertical migration in the subarctic Pacific during summer
136 (Hattori, 1989; Padmavati *et al.*, 2004; Yamaguchi *et al.*, 2004; Takahashi *et al.*, 2009). The C6
137 females of *M. pacifica* are more abundant near the surface at night than during the day, which
138 affects its apparent population structure and the zooplankton community structure. Saito *et al.*
139 (2011) calculated the day: night ratio of *M. pacifica* C6F abundance in this region, and this ratio
140 was used to convert nighttime values to daytime values. For large copepods, the mean population
141 stage was calculated using the following equation,

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

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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 were observed and 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.

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Results

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Hydrography

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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 ca. 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 anticyclonic eddy “Eddy line” and the 50°40'N line “Non-eddy line”.

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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) (Figs. 2B, C). This eddy gradually increased in area (Fig. 2D) as it moved southeastward during the next five 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, continuously increased, and the area oscillated at one to two month periods overlain on

165 a general increase from $\sim 7,000$ to $\sim 18,000 \text{ km}^2$ (Fig. 2D). Fig. 3 (A) shows vertical profiles of
 166 temperature along the Eddy line and the Non-eddy line. Between 171.35°E (solid black circles)
 167 and 173.49°E (open red triangles) along the Eddy line, a subsurface cold water mass ($3.0\text{--}4.0^\circ\text{C}$ at
 168 $26.3\text{--}26.8\sigma_\theta$) was observed at 80–200 m. A somewhat warmer water mass ($4.0\text{--}4.5^\circ\text{C}$ at
 169 $26.5\text{--}27.5\sigma_\theta$) was also seen in this section at 200–500 m depth. In contrast, this warm water mass
 170 ($4.0\text{--}4.5^\circ\text{C}$) spreads from 50 m to 350 m between 174.00°E and 174.64°E . The
 171 temperature-salinity relation also separated the water mass into cold and warm volumes between
 172 26.2 and $26.6\sigma_\theta$ (Fig. 3B). Unlike the Eddy line, subsurface cold or warmer water masses were
 173 not observed along the Non-eddy line, and the water mass structure was mostly uniform along the
 174 section (Fig. 3A, B). Fluorescence was higher along the Eddy line than the Non-eddy line,
 175 particularly between 172.50°E and 174.64°E at 25–50 m depth (Fig. 3C).

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

182 **Total zooplankton abundance and taxonomic accounts**

183 Total zooplankton abundance ranged from 1.0×10^5 to $2.7 \times 10^5 \text{ ind. m}^{-2}$ (mean: 1.7×10^5
 184 ind. m^{-2}) along the Eddy line and $1.1\text{--}1.4 \times 10^5 \text{ ind. m}^{-2}$ (mean: $1.3 \times 10^5 \text{ ind. m}^{-2}$) along the
 185 Non-eddy line (Fig. 5A), not statistically different (U test, $p > 0.05$). Relative numerical
 186 abundances of some groups were different between the lines. Calanoid copepod nauplii (range:
 187 $3.3\text{--}29.3\%$, mean: 20.7%) and cyclopoid copepods (range: $20.5\text{--}60.4\%$, mean: 34.2%) were
 188 abundant along the Eddy line, and cyclopoid copepods (range: $20.3\text{--}41.4\%$, mean: 28.1%) and large
 189 oceanic calanoid copepods (*Neocalanus*, *Eucalanus* and *Metridia* spp.) (range: $13.3\text{--}38.9\%$, mean:

190 26.4%) were abundant along the Non-eddy line (Fig. 5B). The numerical abundance of calanoid
191 nauplii, cyclopoid copepods and poecilostomatoid copepods were 4.8×10^4 , 0.7×10^4 and 2.9×10^4
192 ind. m^{-2} respectively along the Eddy line and 4.1×10^4 , 0.8×10^4 and 2.3×10^4 ind. m^{-2}
193 respectively along the Non-eddy line, and these were not statistically different between these lines
194 (U test, $p > 0.05$).

195 Calanoid copepods

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

206 Large oceanic calanoid copepods

207 Numerical abundance of the large oceanic calanoid copepod *N. cristatus* was significantly
208 greater along the Eddy line (range: $0.8\text{--}5.2 \times 10^3$ ind. m^{-2} , mean: 2.7×10^3 ind. m^{-2}) than along the
209 Non-eddy line (range: $0.9\text{--}1.7 \times 10^3$ ind. m^{-2} , mean: 1.2×10^3 ind. m^{-2}) (U test, $p < 0.05$, Fig. 6A,
210 Table I). Its mean stage was significantly higher along the Eddy line (mean: 3.2) than along the
211 Non-eddy line (mean: 2.2) ($p < 0.05$, Table II), and C5 individuals were relatively more numerous
212 along the Eddy line. In contrast, *N. plumchrus* abundance was significantly greater along the
213 Non-eddy line (range: $2.0\text{--}10.0 \times 10^3$ ind. m^{-2} , 4.9×10^3 ind. m^{-2}) than along the Eddy line (range:

214 $0.4\text{--}4.9 \times 10^3 \text{ ind. m}^{-2}$, mean: $2.8 \times 10^3 \text{ ind. m}^{-2}$) ($p < 0.05$, Fig. 6B, Table I). There was no
 215 significant difference between the lines in its mean stage. *Eucalanus bungii* abundance was also
 216 significantly higher along the Eddy line (range: $5.8\text{--}13.2 \times 10^3 \text{ ind. m}^{-2}$, mean: $8.0 \times 10^3 \text{ ind. m}^{-2}$)
 217 than along the Non-eddy line (range: $2.6\text{--}9.2 \times 10^3 \text{ ind. m}^{-2}$, mean: $5.5 \times 10^3 \text{ ind. m}^{-2}$) ($p < 0.05$,
 218 Fig. 6C, Table I), but there was no significant difference in its mean stage. The abundance of *M.*
 219 *pacifica* was significantly greater along the Eddy line (range: $8.0\text{--}40.6 \times 10^3 \text{ ind. m}^{-2}$, mean: $24.1 \times$
 220 10^3 ind. m^{-2}) than along the Non-eddy line (range: $6.7\text{--}39.3 \times 10^3 \text{ ind. m}^{-2}$, mean: $17.1 \times 10^3 \text{ ind.}$
 221 m^{-2}) ($p < 0.05$, Fig. 6D, Table I), but there was no difference in its mean stage.

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

226 Discussion

227 Influences of the Aleutian eddy on zooplankton community

228 In the present study, the zooplankton community in and near a mesoscale anticyclonic
 229 Aleutian eddy (along the Eddy line) comprised more large oceanic copepods, particularly *N.*
 230 *cristatus* and *E. bungii* than coastal copepods (Table I, Fig. 6A, C). The eddy formation and
 231 modification processes may have influenced this result. For example, a Haida eddy that was
 232 formed on the continental shelf off British Columbia, Canada was reported to transport coastal
 233 water to offshore areas (e.g. Whitney and Robert, 2002), and three coastal copepods, *A. longiremis*,
 234 *Calanus marshallae* and *P. mimus* C4-C6 were abundant inside it (Mackas and Galbraith, 2002;
 235 Mackas *et al.*, 2005). In contrast, the Aleutian eddy that was sampled in the present study was
 236 formed and propagated in the offshore water south of the Aleutian Islands (bottom depth of ca.
 237 4000 m, cf. Fig. 2B). The water mass structure at time of the eddy's formation and throughout its
 238 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 less than 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 were significantly greater inside the eddy than outside (Table I). Inside the eddy, the mean lipid score of *N. cristatus* and *N. plumchurus* were 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 to 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 (HNLC) 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 biomasses (Fig 3C, Fig. 4). Mesoscale anticyclonic eddies are reported to increase the nutrient supply supporting productivity because eddy/wind interactions and submesoscale processes force upwelling to the surface of nutrient-rich

264 water (e.g. McGillicuddy *et al.*, 2007; Mahadevan *et al.*, 2008). In the present study, the eddy area
265 was increasing (Fig. 2D), so the influence of eddy/wind interactions might be weak. The Aleutian
266 eddy in the present study seems to have been influenced by colder water from the offshore region
267 on the western side and by warmer water from the Alaskan Stream on the eastern side (Fig. 3A).
268 Alaskan Stream eddies south of the eastern Aleutian Islands have been reported to cause the
269 Alaskan Stream to meander to the south, and presumably carry nutrient/chlorophyll-rich water to
270 the south (Ueno *et al.*, 2010). The nutrient-rich/warm water presumably enters from the eastern
271 sides of those eddies, and colder water flows in to them from the western sides. These
272 advections and mixing are hypothesized to result in high phytoplankton concentration inside those
273 eddies. Although the phytoplankton concentration history in the Aleutian anticyclonic eddy before
274 our observations from the T/S *Oshoro-maru* is not known due to lack of satellite surface
275 chlorophyll data since the study areas was mostly covered by clouds, the high phytoplankton
276 concentration observed in the eddy presumably resulted in the greater lipid accumulations of large
277 oceanic copepods (Fig. 7).

278 The influence of phytoplankton concentration (the concentration of food) on the mass of
279 large oceanic copepods has been documented. For example, Dagg (1991) reported that in the
280 Bering Sea, where food was abundant, the carbon content in one *N. plumchrus* C5 individual was
281 $416 \mu\text{g C ind.}^{-1}$, whereas in an offshore region of the Gulf of Alaska, where food was scarce, the
282 carbon content was only $59\text{--}143 \mu\text{g C ind.}^{-1}$. In the present study, the relatively greater
283 abundance and lipid accumulations in *N. cristatus* and *N. plumchrus* within the mesoscale
284 anticyclonic Aleutian eddy are thought to have resulted from stronger survival and growth rates
285 supported by greater food availability. That, in turn would have been generated by high primary
286 production enhanced by the advection of nutrient-rich water and cold water into the eddy.

287

288 Conclusions

289 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 was presumed to include a substantial proportion of oceanic water. In addition, the high abundance and lipid accumulations 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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440 **Table and Figure legends**

441 **Table I.** The list of calanoid copepod species identified along the Eddy line (EL) and the
442 Non-eddy line (NEL) during 7–8 July 2010. Values are mean $\pm$ standard deviation of
443 abundance (ind. m⁻²). Differences between two lines were tested by Mann-Whitney *U* test.
444 *: $p < 0.05$, NS: not significant.

445 **Table II.** Comparison of mean stage and mean lipid score of large calanoid copepods between the
446 Eddy line (EL) and the Non-eddy line (NEL) during 7–8 July 2010. Differences between the
447 two lines were tested by Mann-Whitney *U* test. *: $p < 0.05$, NS: not significant.

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

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

460 **Fig. 3.** (A) Temperature distribution ($^{\circ}\text{C}$ as colour scale) superimposed by the density distribution
461 (σ_{θ} contours) for 0–1000 m depth, (B) temperature-salinity relation and (C) fluorescence
462 distributions for 0–150 m along the Eddy line and Non-eddy line. Symbols along at the tops
463 of (A) and (C) represent the locations of profiles characterized by T-S relations in (B).

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

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

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

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

Functional group/Species	Abundance (ind. m ⁻²)		<i>U</i> test
	Eddy line	Non-eddy line	
Coastal species			
<i>Acartia longiremis</i>	902 ± 180	367 ± 106	EL > NEL*
<i>Calanus marshallae</i>	163 ± 248	269 ± 185	NS
<i>Pseudocalanus mimus</i>	2,792 ± 1,227	2,288 ± 1,063	NS
<i>Pseudocalanus minutus</i>	3,177 ± 590	2,412 ± 1,571	EL > NEL*
<i>Pseudocalanus moultoni</i>	1,431 ± 408	1,463 ± 1,074	NS
<i>Pseudocalanus newmani</i>	625 ± 183	936 ± 728	NS
Deep sea species			
<i>Aetideopsis rostrata</i>	15 ± 34	0	NS
<i>Aetideus armatus</i>	0	92 ± 142	NS
<i>Candacia columbiae</i>	15 ± 34	451 ± 903	NS
<i>Microcalanus pygmaeus</i>	13,391 ± 4,166	6,773 ± 4,171	NS
<i>Paraeuchaeta elongata</i>	148 ± 113	69 ± 138	NS
<i>Pleuromamma scutullata</i>	30 ± 68	94 ± 188	NS
<i>Racovitzanus antarcticus</i>	89 ± 38	0	EL > NEL*
<i>Scolecithricella minor</i>	733 ± 339	794 ± 553	NS
Large oceanic species			
<i>Eucalanus bungii</i>	7,973 ± 3,010	5,492 ± 2,741	EL > NEL*
<i>Metridia pacifica</i>	24,076 ± 11,747	17,068 ± 15,296	EL > NEL*
<i>Neocalanus cristatus</i>	2,709 ± 1,645	1,175 ± 352	EL > NEL*
<i>Neocalanus plumchrus</i>	2,790 ± 1,874	4,930 ± 3,694	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.

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.

Parameter/Species	Mean $\pm$ sd.		<i>U</i> test
	Eddy line	Non-eddy line	
Mean stage			
<i>Eucalanus bungii</i>	3.9 $\pm$ 0.2	3.8 $\pm$ 0.4	NS
<i>Metridia pacifica</i>	2.5 $\pm$ 0.4	2.6 $\pm$ 1.2	NS
<i>Neocalanus cristatus</i>	3.2 $\pm$ 0.7	2.3 $\pm$ 0.3	EL > NEL*
<i>Neocalanus plumchrus</i>	4.3 $\pm$ 0.2	4.3 $\pm$ 0.6	NS
Mean lipid score			
<i>Eucalanus bungii</i> C5	2.2 $\pm$ 0.2	2.1 $\pm$ 0.2	NS
<i>Neocalanus cristatus</i> C5	2.1 $\pm$ 0.4	1.7 $\pm$ 0.2	EL > NEL*
<i>Neocalanus plumchrus</i> C5	2.6 $\pm$ 0.2	2.3 $\pm$ 0.1	EL > NEL*

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

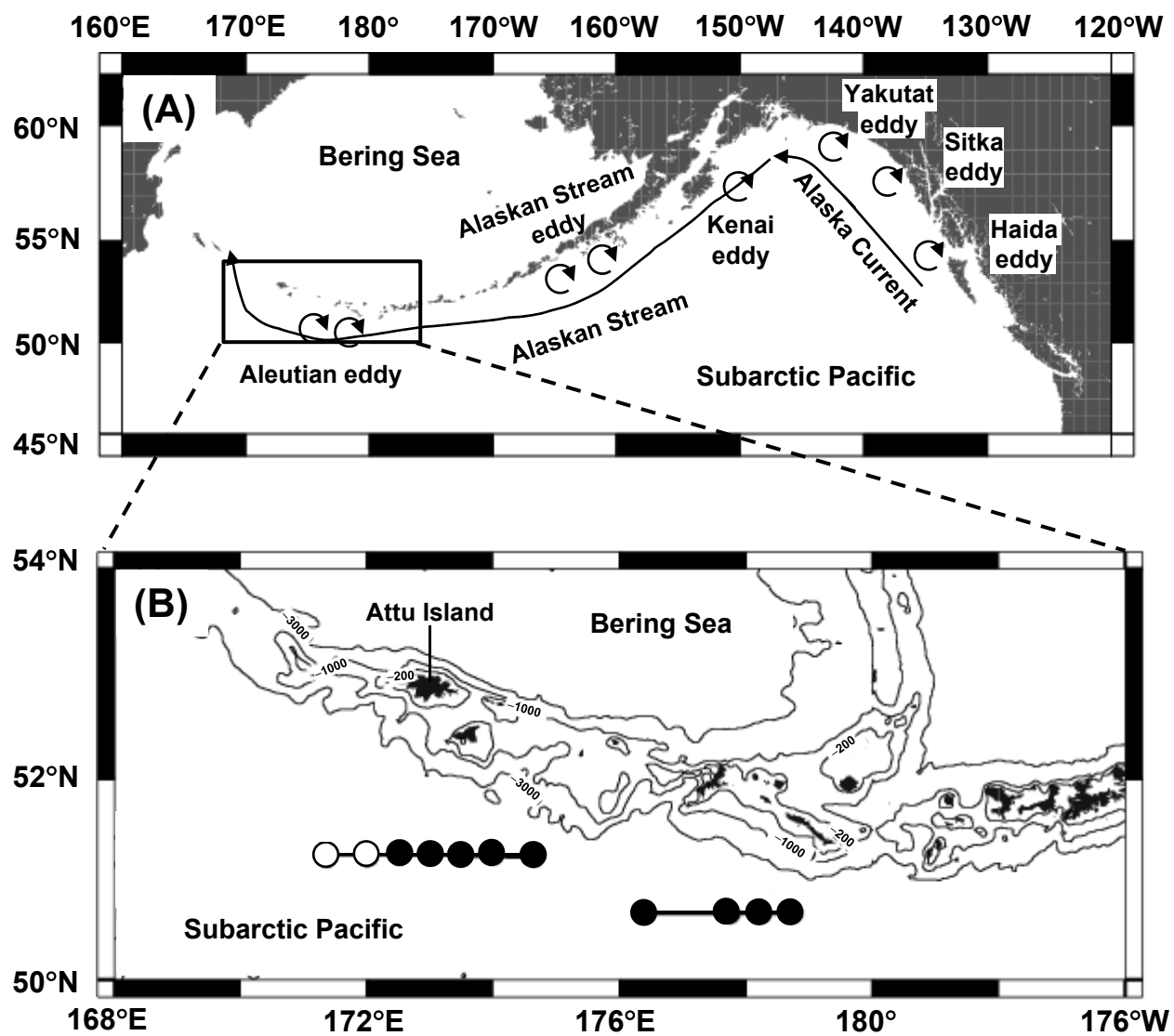


Fig. 1. (Saito *et al.*)

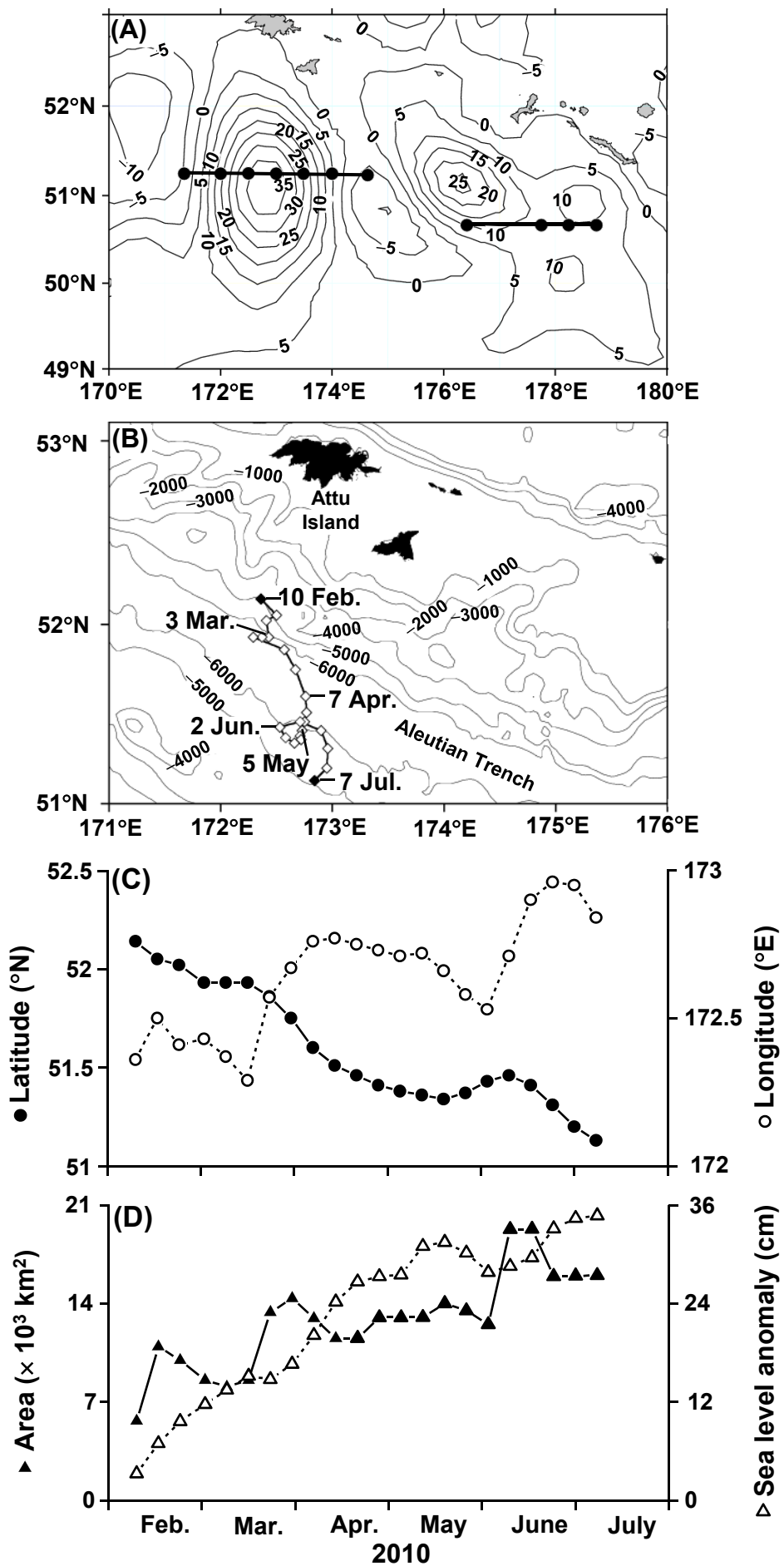


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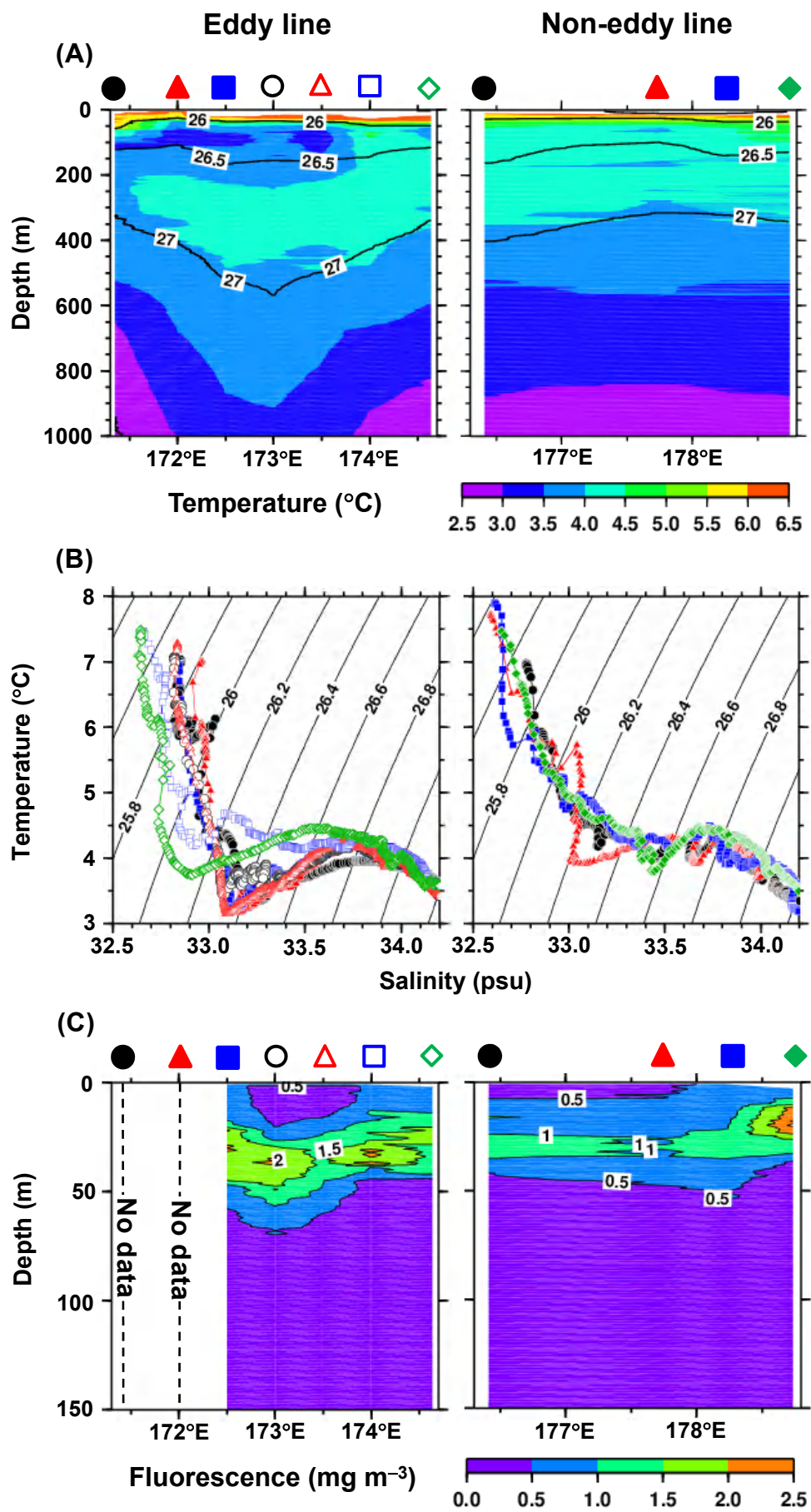


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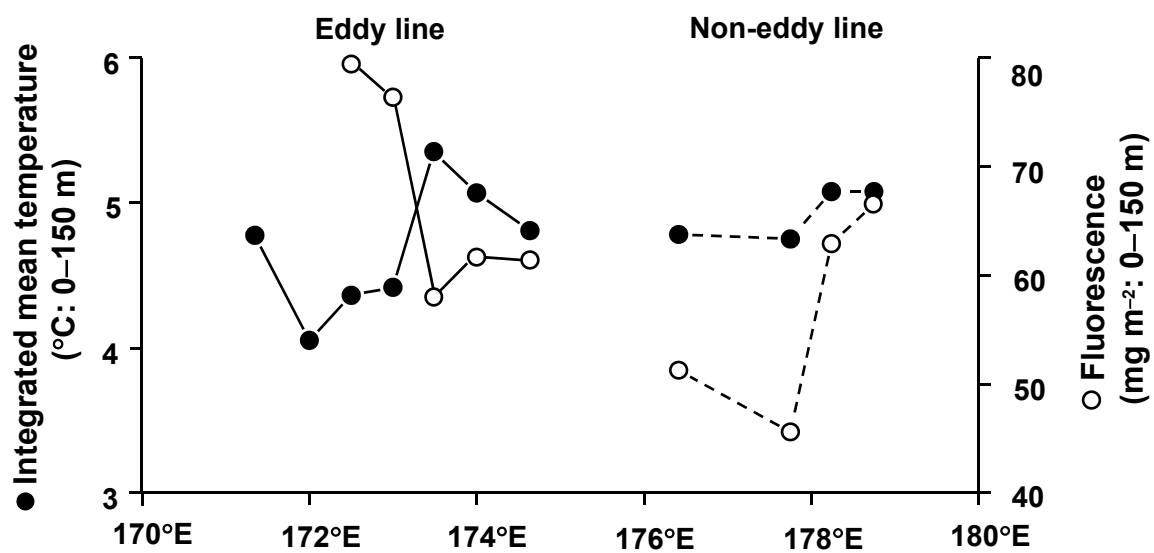


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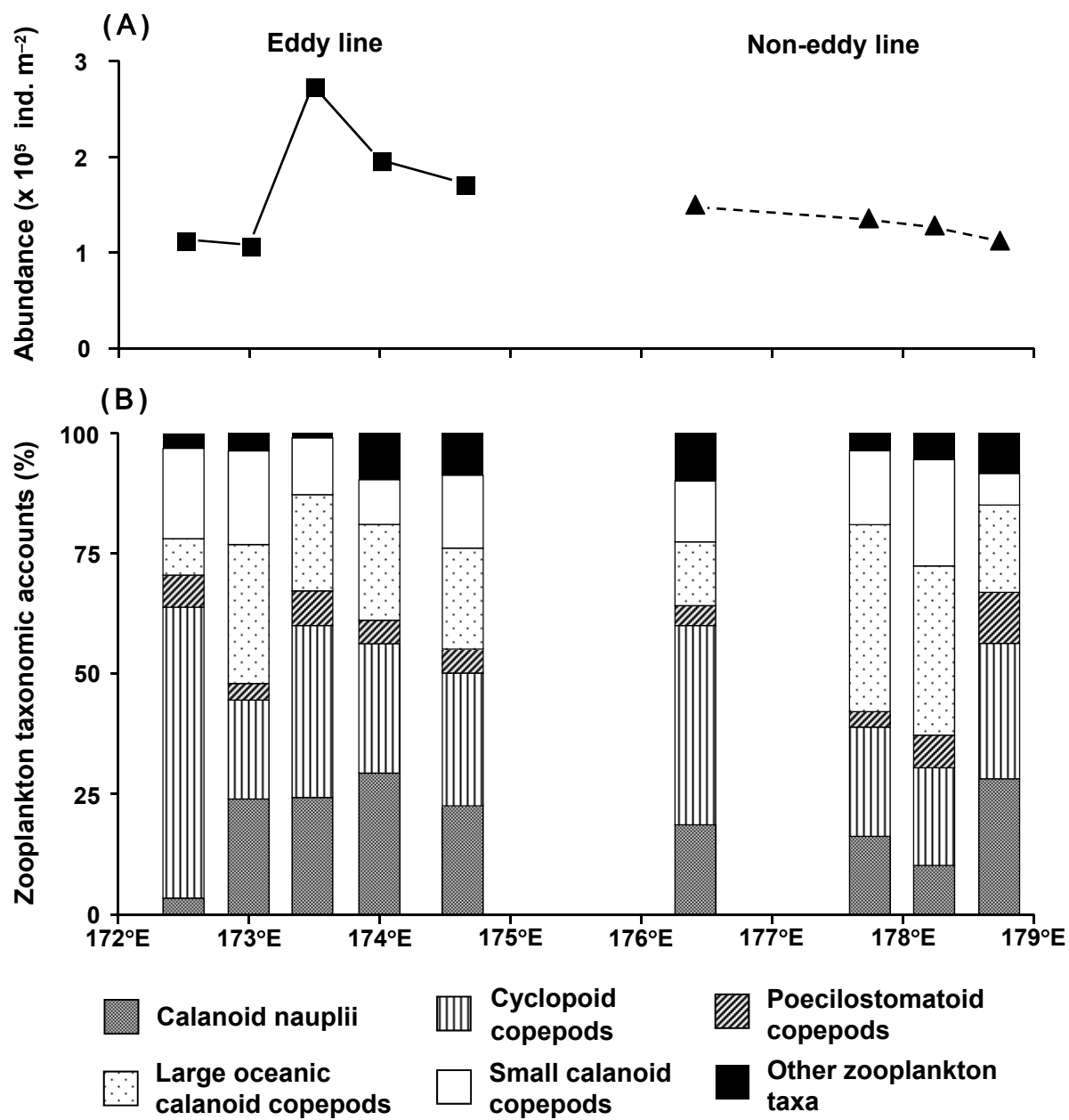


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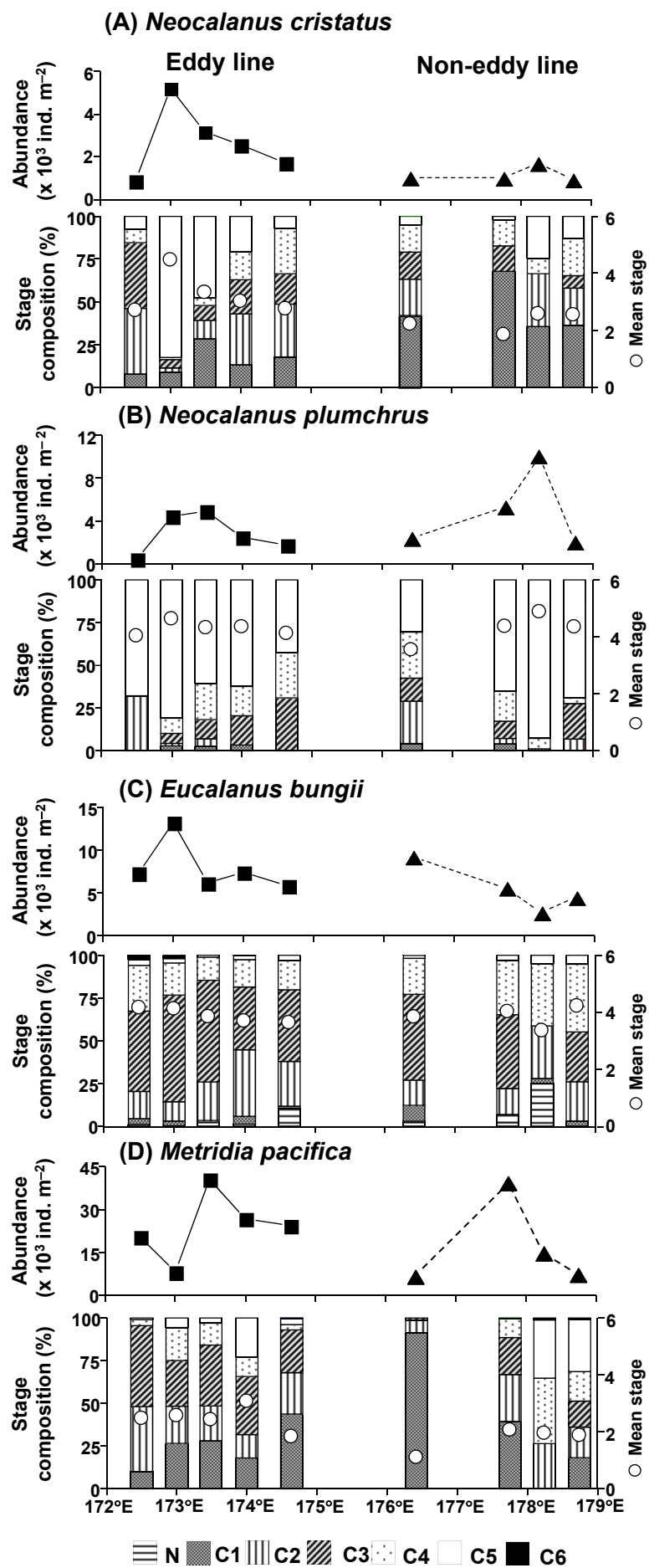


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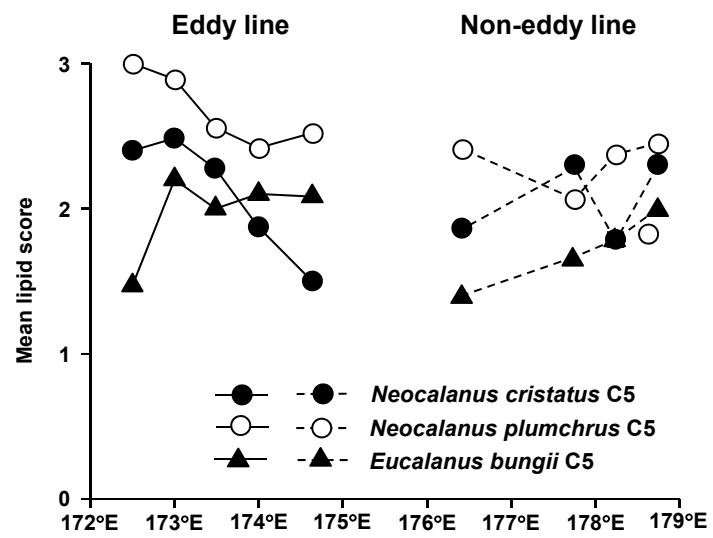


Fig. 7. (Saito *et al.*)