

East-west differences in population structure and vertical distribution of copepods along 47°N in the subarctic Pacific in June 2009

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Abstract: Stratified zooplankton sampling was conducted in the subarctic Pacific in June 2009 at four stations along 47°N from 0 to 3,000 m depth to evaluate longitudinal changes in population structure and vertical distribution of the dominant copepod species. At the westernmost station (160°E), the population structure of *Eucalanus bungii* and *Metridia pacifica* was dominated by early copepodid stages. In *E. bungii*, nauplii were abundant and adult females had developed ovaries at 160°E, while at the three stations to the east (167°E, 174°E and 179°W), no *E. bungii* nauplii were collected, and the resting stages were dominant. This suggests the species was reproducing near 160°E and in diapause in the east. In all three *Neocalanus* species analyzed (*N. cristatus*, *N. flemingeri* and *N. plumchrus*), late copepodid stages were dominant at the eastern three stations. Lipid accumulation in the fifth copepodid stage of *Neocalanus* spp. was greater in the west than in the east. This probably resulted from better food conditions and lower temperatures in the west, where copepods could consume more food during development than in the east.

Key words: *Eucalanus*, lipid accumulation, *Metridia*, *Neocalanus*, ontogenetic vertical distribution

Introduction

The biomass of copepod assemblages in the subarctic Pacific is dominated by diapausing species that feed, grow and accumulate lipids near the surface during part of the year and then diapause at depth (Vinogradov 1968, Yamaguchi et al. 2002, 2005, Homma & Yamaguchi 2010), where they use stored lipids as an energy source and reproduce (Kobari et al. 2003a). As a result, their population structure and vertical distribution can vary greatly depending on location and season. For example, the vertical distribution of diapausing copepods varies greatly between the Bering Sea and subarctic Pacific during summer (Yamaguchi et al. 2002, Homma & Yamaguchi 2010).

The life cycles of the abundant calanoid copepods in the subarctic Pacific (*Neocalanus cristatus* (Krøyer, 1848), *N. plumchrus* (Marukawa, 1921), *N. flemingeri* Miller, 1988, *Eucalanus bungii* Giesbrecht, 1893 and *Metridia pacifica*

Brodsky, 1950) have been studied in both the east (Miller et al. 1984, Miller & Clemons 1988, Mackas et al. 1998) and the west regions (Kobari & Ikeda 1999, 2001a, b, Tsuda et al. 1999, 2004, Padmavati et al. 2004, Shoden et al. 2005). Regional differences in abundance, population structure, body size and lipid accumulation at epipelagic depths (0–200 m) have been examined (Dagg 1991, Tsuda et al. 2001, Batten et al. 2003, 2006, Kobari et al. 2003b). Few studies, however, have examined down to deep sea depths (>200 m). Since copepods diapause at depth (250–3,000 m, cf. Yamaguchi et al. 2002), to accurately evaluate their population structure, lipid stores and gonad maturation, deep samplings are needed. Moreover, east-west differences in the copepods have been evaluated at large scales (e.g., Oyashio region vs. Gulf of Alaska; Kobari & Ikeda 1999, 2001a, b), but little is known about small scale differences.

In the present study, stratified zooplankton samplings were conducted between 0 and 3,000 m depths at four stations along 47°N in the subarctic Pacific, and regional differences in population structure, lipid accumulation, gonad

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maturation and vertical distribution of large oceanic copepods (*E. bungii*, *M. pacifica*, *N. cristatus*, *N. flemingeri* and *N. plumchrus*) were evaluated. Based on these analyses, east-west differences in population structure, lipid accumulation and vertical distribution along 47°N are discussed.

Materials and Methods

Zooplankton samples were collected along 47°N at four stations (160°E, 167°E, 174°E and 179°W) during 6–11 June 2009 (Fig. 1). At each station, samples were collected from twelve discrete depth intervals (0–25, 25–50, 50–75, 75–100, 100–150, 150–250, 250–500, 500–750, 750–1,000, 1,000–1,500, 1,500–2,000 and 2,000–3,000 m) using a vertical multiple plankton sampler (VMPS, mouth opening 0.25 m², mesh size 60 μm, cf. Terazaki & Tomatsu 1997). The samples were collected between 19:27 and 22:15 local time from twilight to night (sunset occurred between 19:11 and 19:51). The volume of water filtered in each depth interval was estimated using a flowmeter mounted in the mouth of the net and ranged from 4.01 to 222.4 m³. The samples were split with a Motoda splitting device (Motoda 1959) on board, and microscopic examination in the laboratory was made on half of each sample, which was immediately preserved on board in 5% borax-buffered formalin-seawater. Profiles of water temperature, salinity and chlorophyll *a* (chl. *a*) were obtained with a Sea-Bird SBE911Plus CTD system at each station.

In the land laboratory, a wide-bore pipette (1 cm diameter) was used to collect 1/10 to 1/2 subsamples to count copepodids and 1/223 to 1/2 subsamples to count *Eucalanus bungii* nauplii. Individuals of five large calanoid copepods (*E. bungii*, *Metridia pacifica*, *Neocalanus cristatus*, *N.*

flemingeri and *N. plumchrus*) were identified, and their developmental stages were determined and counted using a dissecting microscope. For late copepodid stages (copepodid stage 5 [C5] of *Neocalanus* spp. and adult females [C6F] of *E. bungii*), all the specimens were sorted from the whole preserved samples for analysis.

For *E. bungii*, gonad maturation in C6F was assessed, and naupliar stages were identified and counted based on the descriptions by Johnson (1937). Gonad maturation was classified into five stages: I (immature): the ovary is present, some granular oocytes or ova are visible in the posterior part of the oviduct; II (developing): one fully developed row of ova is observed at the ventral edge of the oviduct; III (mature): more than two full rows of ova are seen in the oviduct; IV (spawning): lower portion of oviduct does not contain ova, but is filled with lipid-like substances; V (spent): ovary and lipid droplets are not visible, and the body is transparent (Shoden et al. 2005).

For *N. cristatus*, *N. flemingeri* and *N. plumchrus*, lipid accumulation in stage C5 was classified into three types based on Ikeda et al. (1990): transparent (1): no lipid present; intermediate (2): lipids present to less than half of the prosome width; and solid (3): lipids present to more than half of the prosome width. The mean lipid score was defined as

$$\frac{\sum_{i=1}^3 iXi}{\sum_{i=1}^3 Xi}$$

where *i* is the score of lipid accumulation (1–3), and *Xi* is the abundance at each lipid accumulation (ind. m⁻²: standing stock of water column [0–3,000 m]).

To make quantitative comparisons, the depth where the 50th percentile of the population resided (*D*_{50%}) was calculated for each species (cf. Pennak 1943). Additional calculations were made to determine the depths at which the 25th (*D*_{25%}) and 75th (*D*_{75%}) percentiles of the population occurred.

Results

Hydrography

Sea surface temperature ranged from 4.8 to 8.6°C, and was highest at 179°W and lowest at 160°E (Fig. 2a). This east-west trend was observed from the surface to 150 m depth or a little more, and the temperature at 100 m depth was about 4°C at 179°W and below 4°C at the three western stations. Relatively strong temperature inversions were observed by 2.1°C from 120–170 m depth at 160°E, by 0.8°C from 110–150 m depth at 167°E, and by 0.5°C from 60–80 m depth at 174°E. Below 250 m depth, longitudinal differences were small, and water temperature decreased with increasing depth. Salinity ranged from 32.8 to 33.0, increased with increasing depth, and differed little between stations (Fig. 2b). Chlorophyll *a* in the surface layer

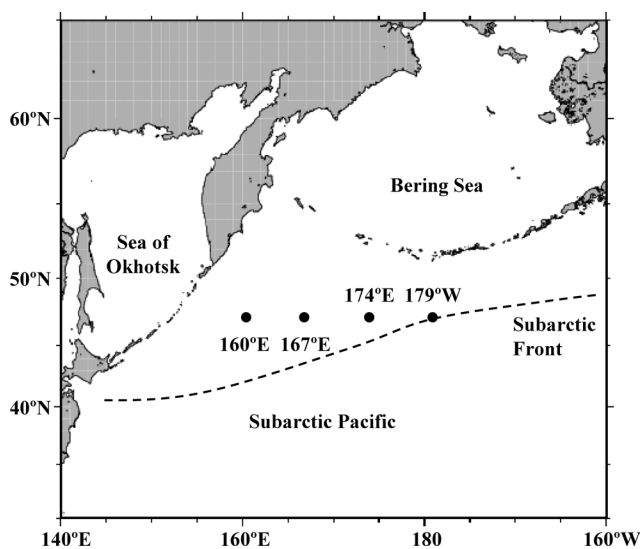


Fig. 1. Four stations along 47°N in the western subarctic Pacific during 6–11 June 2009. Dashed line indicates approximate position of the subarctic front.

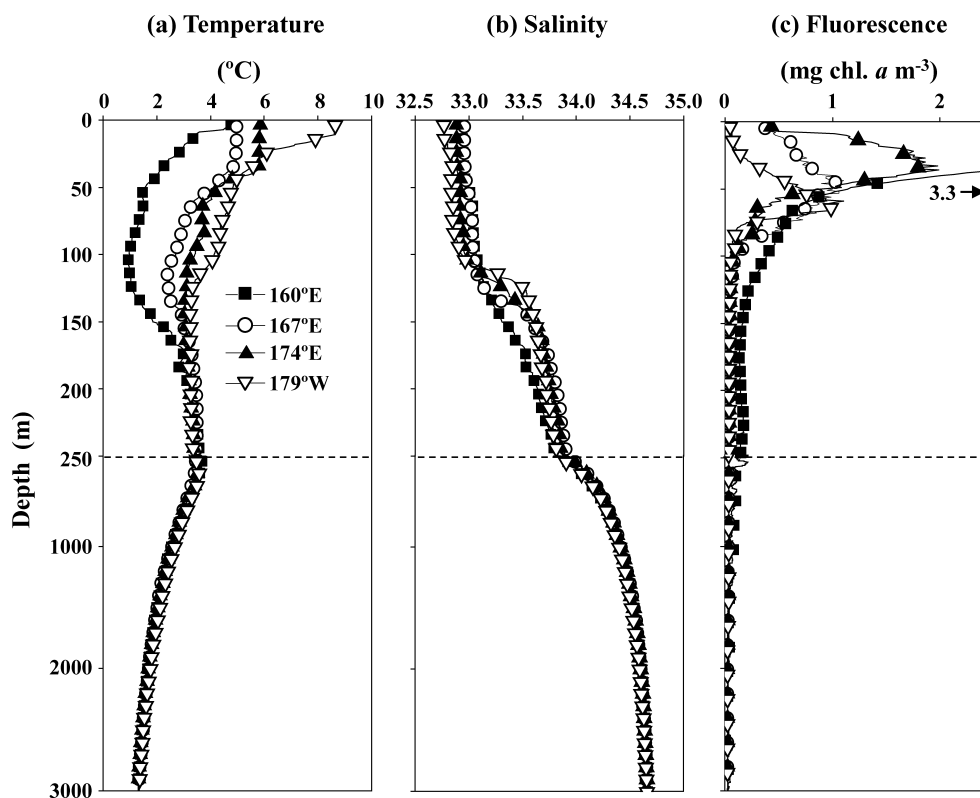


Fig. 2. Vertical profiles of temperature (a), salinity (b) and fluorescence (chlorophyll *a*) (c) from 0 to 3,000 m depth at four stations along 47°N in the western subarctic Pacific during 6–11 June 2009. Note that depth scale changes at 250 m (dashed lines).

ranged from 0.14 to 3.33 mg m⁻³, and was remarkably high at 160°E compared to the other stations and lowest at 179°W (Fig. 2c). The depth of the chl. *a* peak was shallower at 160°E (10 m) than at the three stations to the east (40–60 m). Thus east-west differences were observed for temperature and chl. *a*; stations in the west had lower temperature and higher chl. *a* than stations in the east.

Population structure

The abundance of *Eucalanus bungii* ranged between 3,400 and 20,000 ind. m⁻², and was highest at 160°E (Fig. 3a). At this station, the dominant copepodid stage was C1 (56%), and the mean stage number was 2.1. At the three stations to the east, no C1 or C2 occurred and C5–C6 dominated (66–89%). The mean copepodid stage numbers were 4.9–5.4.

The abundance of *Metridia pacifica* ranged between 1,200 and 34,000 ind. m⁻², and was also highest at 160°E (Fig. 3b). Similar to *E. bungii*, stage C1 was dominant (59%), and the mean stage number was low (1.8) at 160°E, while adults dominated and the mean copepodid stage number was higher (3.9–4.8) to the east (174°E–179°W).

The abundance of *Neocalanus cristatus* ranged between 1,500 and 3,500 ind. m⁻², and was highest at 160°E (Fig. 3c). The proportion of C5 and the mean copepodid stage number increased to the east (3.3–4.6).

The abundance of *N. flemingeri* ranged between 1,600 and 12,000 ind. m⁻², and was highest at 179°W (Fig. 3d). C5 dominated at each station, and the mean copepodid stage was high (≥4.5) at all stations, but a little lower at the western two stations than at the eastern stations.

The abundance of *N. plumchrus* varied between 470 and 12,000 ind. m⁻², and was highest at 160°E and 179°W (Fig. 3e). C1–C3 stages dominated at 160°E, and C5 dominated at 179°W. The mean copepodid stage was lowest at 160°E (2.4) and highest at 179°W (4.6).

The gonad maturation stages of *E. bungii* adult females (stage C6F) were dominated by mature (stage III) and spawning (IV) stages, which together accounted for 70% of the total abundance of C6F at 160°E (Fig. 4a). At the three eastern stations, 54–97% of C6F were immature (stage I). At 160°E, all nauplii stages (N1–N6) were collected, and nauplii were much more abundant (450,000 ind. m⁻²) than copepodids (Fig. 4b). No nauplii were collected at the three stations to the east.

The mean lipid scores of *Neocalanus* spp. C5 were 1.8–2.5 for *N. cristatus*, 2.2–2.8 for *N. flemingeri* and 1.3–2.2 for *N. plumchrus* (Fig. 4c). The mean lipid scores were highest at 167°E for *N. cristatus* and at 160°E for *N. flemingeri* and *N. plumchrus*, and lowest for all species at 179°W.

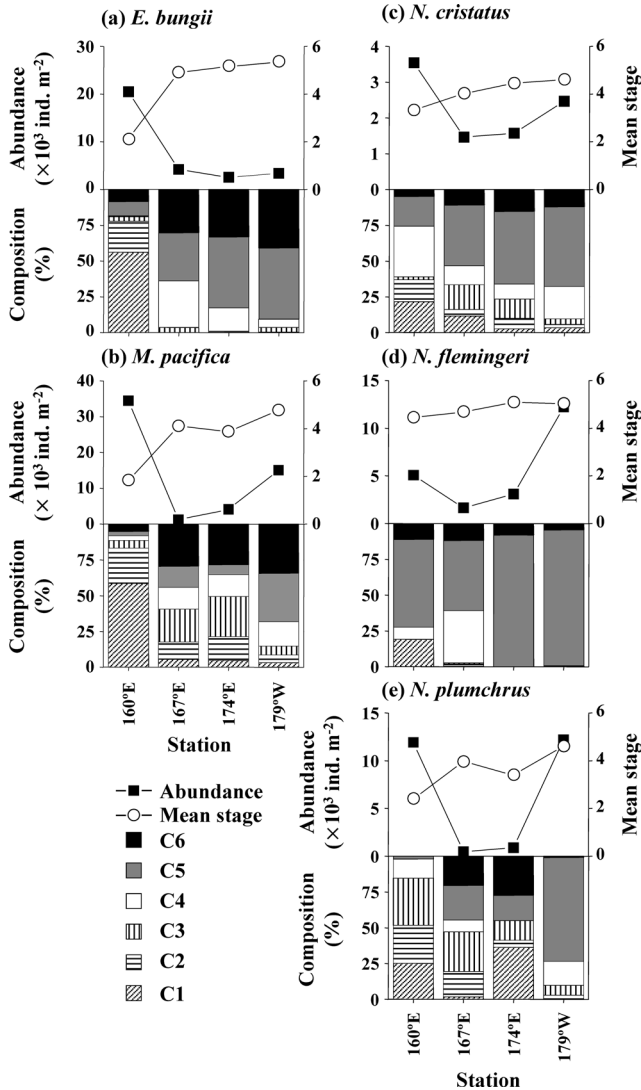


Fig. 3. Abundance, population structure and mean stage number of the copepods *Eucalanus bungii* (a), *Metridia pacifica* (b), *Neocalanus cristatus* (c), *N. flemingeri* (d) and *N. plumchrus* (e) at four stations along 47°N in the western subarctic Pacific during 6–11 June 2009.

Vertical distribution of the populations

Eucalanus bungii C1–C3 were collected mainly at 20–90 m, and C4–C6 were at 40–350 m, indicating the species underwent ontogenetic vertical descent (Fig. 5a). Although the depth distribution did not vary between stations, the range of the distribution center ($D_{50\%}$) of C4–C6 became broader at the eastern stations.

For *Metridia pacifica*, the distribution depth increased with development except for C6F. C1 occurred at 30–140 m, and C6M was at 430–620 m (Fig. 5a). C6F occurred shallower (70–310 m) than C5 and C6M. Late copepodid stages occurred deeper at 179°W than they did at the three stations to the west.

Neocalanus cristatus showed evidence of ontogenetic

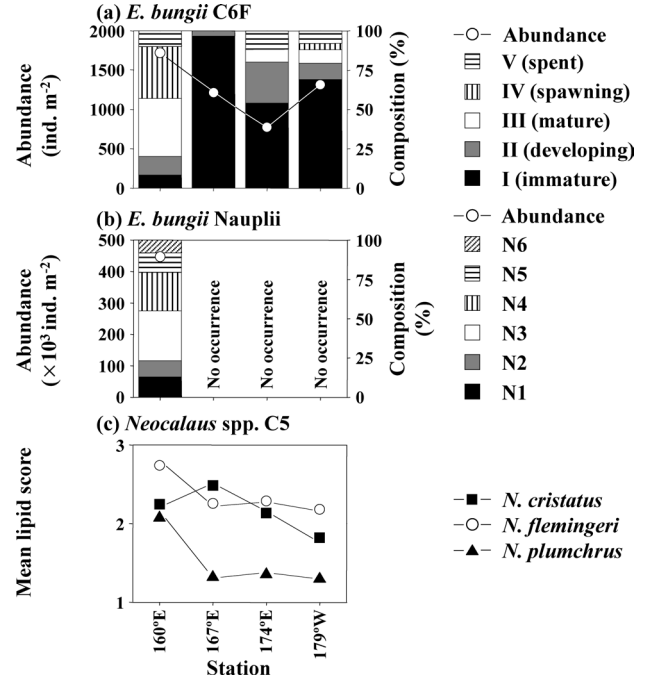


Fig. 4. Longitudinal comparison of several parameters of the copepod population along 47°N in the western subarctic Pacific during 6–11 June 2009: (a) abundance and gonad maturation of *Eucalanus bungii* C6F, (b) abundance and stage structure of *E. bungii* nauplii, and (c) mean lipid score of *Neocalanus* spp. C5.

vertical descent; C1–C4, C5 and C6 occurred at 40–140 m, 180–380 m and 870–2,140 m, respectively (Fig. 5b). C5 occurred deepest (374 m) at 160°E and shallower (179–222 m) at the three eastern stations. C1–C5 of *N. cristatus* occurred deeper than those of the other two *Neocalanus* species.

For *N. flemingeri*, C1–C5 occurred shallower (10–60 m) than C6 (200–1,410 m) (Fig. 5b), and the depth distribution varied little between stations.

The vertical distribution of *N. plumchrus* was similar to that of *N. flemingeri*, and C1–C5 occurred shallower (10–340 m) than C6 (710–930 m) (Fig. 5b). The depth distribution did not show clear east-west differences.

Figure 6 shows the abundance of stage C5 of the three *Neocalanus* spp. and their lipid accumulation at 0 to 3,000 m at each station. For *N. cristatus*, lipid-rich individuals (solid) generally outnumbered (12–100%) others at 160°E, while lipid-less individuals (transparent) were distributed throughout the water column at the three stations to the east (Fig. 6a). For *N. flemingeri*, lipid-rich individuals outnumbered (57–100%) others above 750 m at 160°E, and individuals with intermediate or no lipid increased at 174°E and 179°W (Fig. 6b). For *N. plumchrus*, the abundance of C5 was high (199 ind. m⁻³) at the surface at 179°W and low (<5 ind. m⁻³) at the three stations to the west. At all stations, most individuals of *N. plumchrus* contained intermediate or no lipids (Fig. 6c).

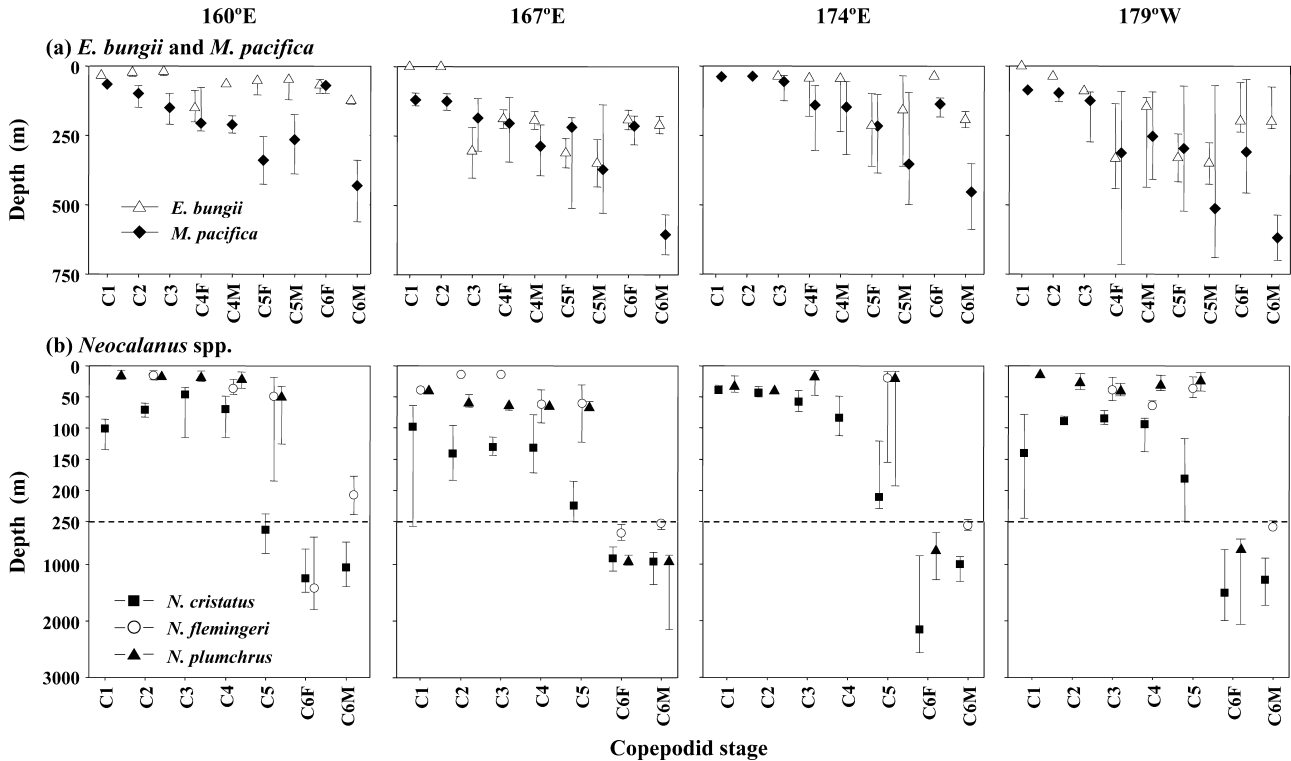


Fig. 5. Vertical distribution of stages of *Eucalanus bungii* and *Metridia pacifica* (a), and *Neocalanus* spp. (b) at four stations along 47°N in the western subarctic Pacific. Symbols and bars indicate depths where the 50% of the population resided ($D_{50\%}$) and ranges between $D_{25\%}$ and $D_{75\%}$, respectively. Note that the depth scale in (b) changes at 250 m (dashed lines).

Discussion

During the present study, the temperature at 100 m depth was below 4°C between 160°E and 174°E and about 4°C at 179°W. This indicates that stations between 160°E and 174°E were located in the subarctic region, and the station at 179°W was located around the subarctic front between the subarctic region and transition domain (e.g., Favorite et al. 1976, Yasuda 2003). In addition, relatively strong temperature inversions (>0.5°C) were observed between 160°E and 174°E. Temperature inversions are often apparent in the subarctic North Pacific (Ueno & Yasuda 2000, 2005), supporting the conclusion that the stations between 160°E and 174°E were located in the subarctic region. The present results revealed that in the surface layer, temperature was higher and chl. *a* was lower in the east than in the west. Satellite images of monthly mean chl. *a* and sea surface temperature along 47°N (46.5–47.5°N) during the present study year 2009 (NASA 2008), indicate that these east-west gradients in sea surface temperature and chl. *a* continued throughout the year (Fig. 7).

In *Eucalanus bungii*, early copepodid and gonad-mature C6F stages were abundant at 160°E, and nauplii occurred only at this station. For *Metridia pacifica*, C1 were abundant and the mean copepodid stage number was low (1.8) at 160°E. These results indicate that these species were reproducing at 160°E during the study period. This is

supported by the results that chl. *a* concentration was remarkably high (3.3 mg m⁻³) at this station. At the three stations to the east, in *E. bungii* only C3–C6, which are known to be able to diapause (Miller et al. 1984, Shoden et al. 2005) were collected. C6F stages had immature gonads, and no nauplii were collected, suggesting that they were in diapause. This is also suggested by the deeper distributions of stages C4–C6 at these stations.

In *M. pacifica*, the dominance of C4–C6 stages at the three eastern stations, as in *E. bungii*, suggests that reproductive activity was low at these stations. However, the occurrence of C1 stages at these stations indicates that *M. pacifica* was not in dormancy. *Metridia pacifica* has been reported to be dormant in the Sea of Japan (Hirakawa & Imamura 1993) and the Oyashio region (Padmavati et al. 2004). Contrary to these reports, active diel vertical migration during summer in the present region (Kobari et al. 2008) suggests that there is no dormancy during summer in this region.

The population structure of *Neocalanus flemingeri* was dominated by C5 at all stations, while that of *N. plumchrus* was dominated by early copepodid stages, especially at the westernmost station. The C1–C5 stages of *Neocalanus* species are known to suspension feed near the surface and then to descend to diapause (Miller et al. 1984, Miller & Clemons 1988, Kobari & Ikeda 1999, 2001a, b, Tsuda et al. 1999, 2004). *Neocalanus flemingeri* occurs in surface wa-

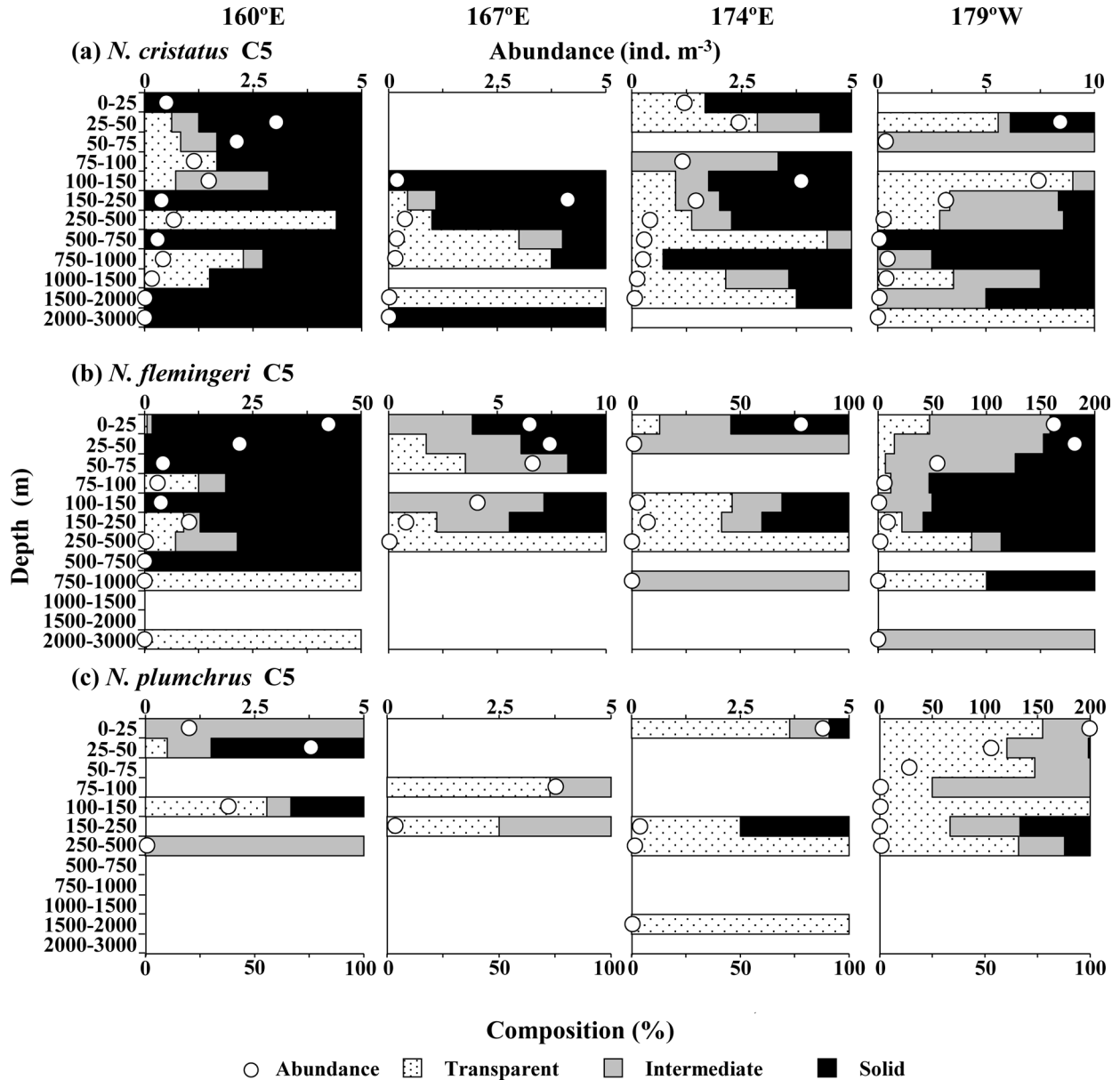


Fig. 6. Vertical changes in abundance and lipid content of C5s of *Neocalanus cristatus* (a), *N. flemingeri* (b) and *N. plumchrus* (c) at four stations in the western subarctic Pacific during 6–11 June 2009. Lipid contents were classified into three categories: transparent, intermediate and solid (Ikeda et al. 1990). Blank columns indicate no C5 individuals occurred in the layer.

ters earlier in the year than *N. plumchrus* does (Kobari & Ikeda 2001a, b). In the present study, the dominance of C5 in *N. flemingeri* in contrast to that of early stages of *N. plumchrus* in June 2009 is explainable by the difference in their life cycle schema, that is, earlier development in *N. flemingeri* than in *N. plumchrus*. Kobari et al. (2008) revealed that during 31 July–16 August 2005, which was a season more than a month later than in the present study, *N. flemingeri* was distributed at 200–500 m during both day and night while *N. plumchrus* was distributed mostly at 0–50 m during both day and night. These vertical distributions may also be explained by the above life cycle schema.

Given that lipid accumulation is affected by the amount of food consumed (Dagg 1991), higher lipid accumulation by *Neocalanus* spp. in the west can be attributed to higher chl. a concentrations, i.e. better food conditions, and lower temperature conditions, at which copepods generally grow slower and therefore can consume more food during development, in the west.

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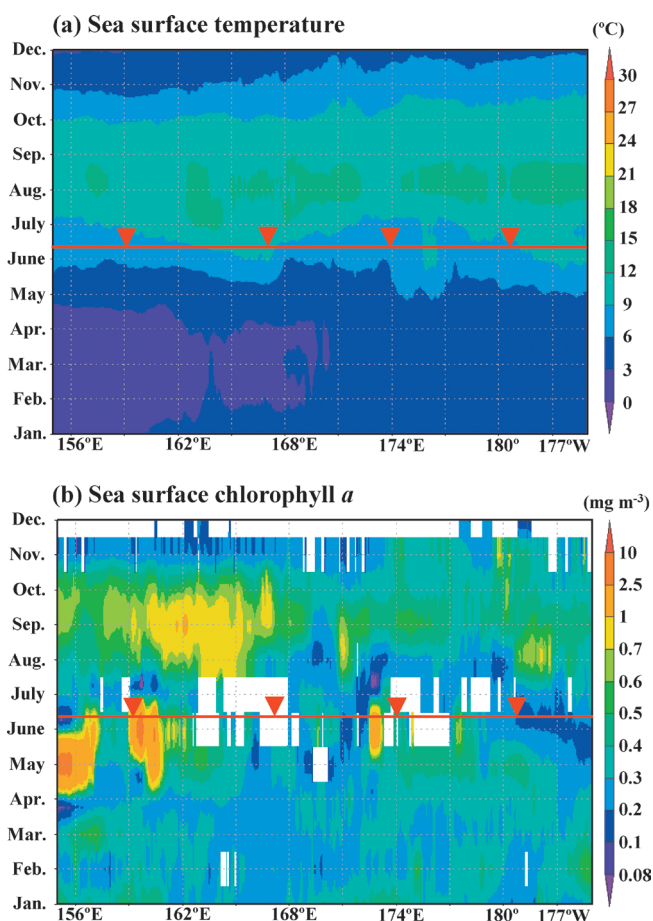


Fig. 7. Temporal changes in sea surface temperature (a) and chlorophyll *a* (b) along 46°30'–47°30'N between 155°00'E–175°00'W evaluated from monthly mean satellite (MODIS) data during 2009. Horizontal lines and triangles indicate sampling periods and stations, respectively.

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