Plankton Biol. Ecol. 48 (1): 46–51, 2001

plankton
biology & ecology
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Winter zooplankton biomass and population structure of calanoid copepods in the Bering Sea basin

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Received 5 February 2000; accepted 3 July 2000

Abstract: The zooplankton biomass, species composition of calanoid copepods and population structure of dominant calanoid species were investigated using samples collected by vertical hauls from 500-m depth in the Bering Sea basin during winter 1993. Zooplankton biomass ranged from 13.9 to 57.9 g ww m^{-2} (mean=32.5 g ww m^{-2}) and was at the same level as summer biomass from 0–80-m depth. Calanoid copepods comprised 75% of the total biomass. Zooplanktonic and calanoid biomasses were lower at the eastern edge of the Bering Sea basin. A total of 34 calanoid species were identified. The dominant species in both numerical abundance and biomass were *Eucalanus bungii, Neocalanus cristatus, N. flemingeri* and *Metridia pacifica*. Developmental stages were mainly copepodite 4 (C4) to C6 (adult) for *E. bungii*, C1 and C5 for *N. cristatus*, C4 and adult for *N. flemingeri*, and C5 and adult for *M. pacifica*. Some of these stages are also known to be deep-dwelling, overwintering stages in the subarctic Pacific.

Key words: Bering Sea basin, biomass, zooplankton, calanoid copepods, population structure

Introduction

The Bering Sea is among the world's most important fisheries regions, and various studies have been carried out on the role of zooplankton as prey organisms sustaining the area's high fisheries production (e.g., Cooney 1981; Cooney & Coyle 1982; Vidal & Smith 1986; Springer et al. 1989; Coyle et al. 1996; Napp et al. 1996; Springer et al. 1996). However, most information on zooplankton in the Bering Sea is restricted to the period between spring and fall, because the severe climate during winter prevents zooplankton sampling (Pavlov & Pavlov 1996). Studies on the winter zooplankton population in this area remain limited (Coyle et al. 1996; Kitani & Komaki 1984).

To evaluate the complete dynamics of subarctic zooplankton, it is important to obtain information on the zooplankton populations during winter. In this paper, we describe the horizontal distribution of zooplankton biomass, species composition of calanoid copepods and the population structure of the dominant calanoid species by using samples from 500-m depth to the surface during the winter of 1993 in the Bering Sea basin.

Materials and Methods

Plankton samples were collected from 21 stations during a cruise of the R.V. *Kaiyo Maru*, Fisheries Agency of Japan, in the Bering Sea from 9 January to 14 March 1993 (Fig. 1). The bottom depths were greater than 3000 m except for 5 stations at the eastern part of the study area (Stns 310, 404, 406, 407, 408). A WP-2 net (mouth area 0.25 m^2, mesh size 0.2 mm; The Unesco Press 1968) was hauled vertically from 500-m depth to the surface for the collection of zooplankton samples, because the bulk of the zooplankton population lives below the surface layer during this season (Kitani & Komaki 1984). A vertical tow from 200 m to the surface was also carried out at Stn 201, to compare catches between 0–200 m and 0–500 m. All samples were preserved in 10% buffered formalin-seawater immediately after collection. The volume of water filtered by the net was determined using a flowmeter tied in the mouth ring. Hydrographic data were collected by CTD casts made with a

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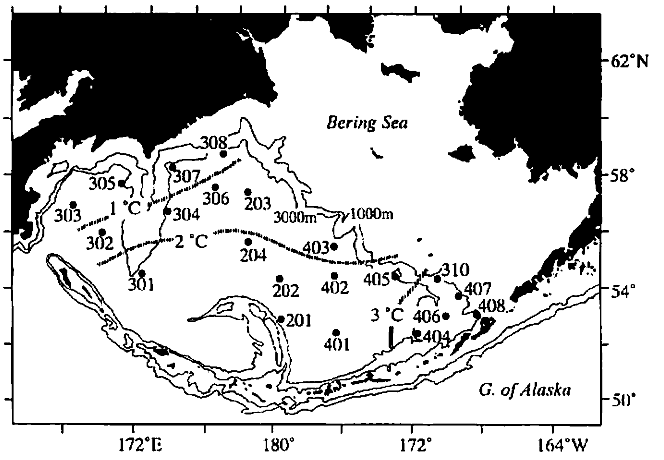

Fig. 1. The location of sampling stations and sea surface (at 10 m) temperature (°C) in winter of 1993. 1000- and 3000-m depth contours (solid lines) are shown.

Neil-Brown MARK II at each sampling station.

Calanoid copepods were first sorted from the samples. Calanoid specimens obtained from the center of the basin (Stns 201, 202, 203, 204, 301) were identified to developmental stages and species level under a binocular microscope. Wet weight of each individual was measured to the nearest 0.01 mg using a Mettler micro balance after blotting the specimens on filter paper. When the wet weight of a specimen was less than 0.1 mg, several specimens were measured together and an individual weight was calculated. Only the dominant calanoid species were sorted and counted for each developmental stage from the remaining 16 stations. Their biomasses were calculated by multiplying the individual wet weights by the individual numbers (Table 1). Wet weights of the non-dominant calanoid species and the rest of the zooplankton (excluding the calanoid copepods) were measured as a mass, after gently filtering through a fine mesh cloth and blotting on filter paper (Omori & Ikeda 1984). The term "zooplankton biomass" hence forth refers to the total zooplantkon biomass, including calanoids. Ovary maturation stages of the three dominant calanoid species (*Eucalanus bungii*, *Neocalanus cristatus* and *N. flemingeri*) were determined using the definitions of Miller et al. (1984) and Miller & Clemons (1988). Although zooplankton samplings were carried out both during the day ($n=7$) and night ($n=15$), both sample types were treated in parallel because no statistical difference was evident between them (unpaired t-test; $p=0.708$).

Results

Surface water temperature was quite low, ranging between 0.2 and 3.8°C (Figs 1, 2). High surface temperature was observed at the stations located in the eastern side of the study area (Stns 310, 404, 406, 407, 408), at which thermal stratification was weak, whereas a steep vertical gradient in temperature was observed at the western stations (Stns 302, 303, 304, 305, 307, 308). Salinity was low at the surface (ca. 32.5–33.2), and gradually increased to 34.0 at 500 m and 34.4 at 1000 m. Stations over the eastern slope

Table 1. Mean wet weight (mg) of each developmental stage of dominant calanoid species collected from the Bering Sea basin during winter. n=number of specimens measured.

Species	Stage	Mean±S.D.	n
Eucalanus bungii	C6♀	7.02±2.27	25
	C6♂	3.31±0.98	23
	C5	3.04±1.04	47
	C4	0.96±0.36	41
	C3	0.39±0.16	21
Neocalanus cristatus	C6♀	10.74±4.11	29
	C6♂	15.22±3.37	3
	C5	16.51±2.39	25
	C4	3.88±1.10	21
	C3	0.54±0.20	19
	C2	0.15±0.06	25
	C1	0.06±0.01	37
N. flemingeri	C6♀	3.00±1.19	56
	C6♂	3.11±0.64	10
	C5	1.07±0.35	10
	C4	0.70±0.12	28
	C3	0.22±0.05	29
	C2	0.07±0.03	32
	C1	0.03±0.01	11
Metridia pacifica	C6♀	0.81±0.15	31
	C6♂	0.28±0.08	30
	C5	0.28±0.08	30
	C4	0.13±0.04	33
	C3	0.06±0.01	29

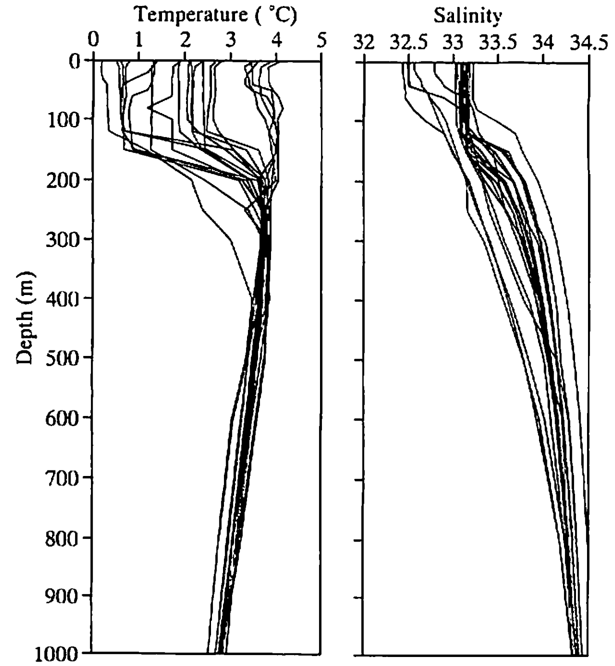

Fig. 2. Vertical profiles of temperature (°C) and salinity at each sampling station.

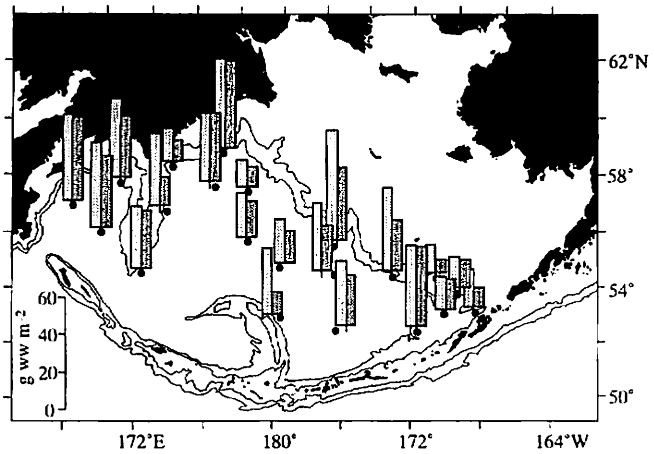

Fig. 3. The distribution of zooplankton (left bar) and calanoid copepod (right bar) biomass (g ww m^{-2}) collected from 0–500 m depth.

(Stns 310, 404, 406, 407, 408) were warmer (>3.0°C) and less saline (ca. 32.5) than the other stations, probably due to the inflow of the Alaskan Stream through the Aleutian Islands (Pavlov & Pavlov 1996).

The zooplankton biomass varied from 13.9 (Stn 203) to 57.9 g wet weight (ww) m^{-2} (Stn 403) and the mean±S.E. was 32.5±12.3 g ww m^{-2} (Fig. 3). Zooplankton and calanoid biomasses were low on the eastern slope and at a few stations in the center of the basin. Calanoid biomass varied from 6.7 (Stn 310) to 46.1 g ww m^{-2} (Stn 308) and the mean±S.E. was 24.8±12.2 g ww m^{-2}. They contributed 33 to 99% (mean=75%) of the total zooplankton biomass. Besides the calanoid copepods, the chaetognath *Sagitta elegans* was also one of the most numerous organisms in the zooplankton assemblages.

To compare the amount of zooplankton biomass from 0–500 m and 0–200 m depth, tentative sampling was carried out at Stn 201. Zooplankton and calanoid biomasses at 0–200 m were 11.4 and 5.8 g ww m^{-2}, respectively, contributing 36 and 22% of the total amounts from 0–500 m. This indicates the possibility that zooplankton biomass is distributed widely over the 0–500 m layer and is more concentrated at 200–500 m than at 0–200 m.

A total of 34 calanoid species were identified (Fig. 4). The most numerous species was *Eucalanus bungii* (mean=4580 indiv. m^{-2}), followed by *Metridia pacifica*, *Neocalanus flemingeri*, *Pseudocalanus* spp., *N. cristatus* and *Pleuromamma scutullata*. In terms of biomass, *E. bungii* was again most abundant (mean=7.6 g ww m^{-2}), followed by *N. cristatus*, *N. flemingeri*, *M. pacifica* and *Paraeuchaeta elongata*.

The horizontal distribution of the biomasses of these four dominant calanoid species showed some species-specific differences (Fig. 5). *E. bungii* and *N. cristatus* were most abundant at the western stations. Biomass ranged from 0.8 to 22.6 g ww m^{-2} (mean±S.E.=10.3±6.4 g ww m^{-2}) for *E. bungii* and 0.9 to 20.2 g ww m^{-2} (7.7±5.4 g ww m^{-2}) for *N. cristatus*. No apparent trend was detected for *N. flemingeri*, the biomass of which ranged from 0.5 to 3.6 g ww m^{-2} (2.0±0.9 g ww m^{-2}). *M. pacifica* was most abundant at the eastern stations; biomass ranged from 0.2 to 5.5 g ww m^{-2} (1.5±1.2 g ww m^{-2}). The biomass of *E. bungii*, *N. cristatus*, *N. flemingeri* and *M. pacifica* comprised 42, 31, 8 and 6% of the total calanoid copepod, and 32, 24, 6 and 5% of the total zooplankton fractions, respectively.

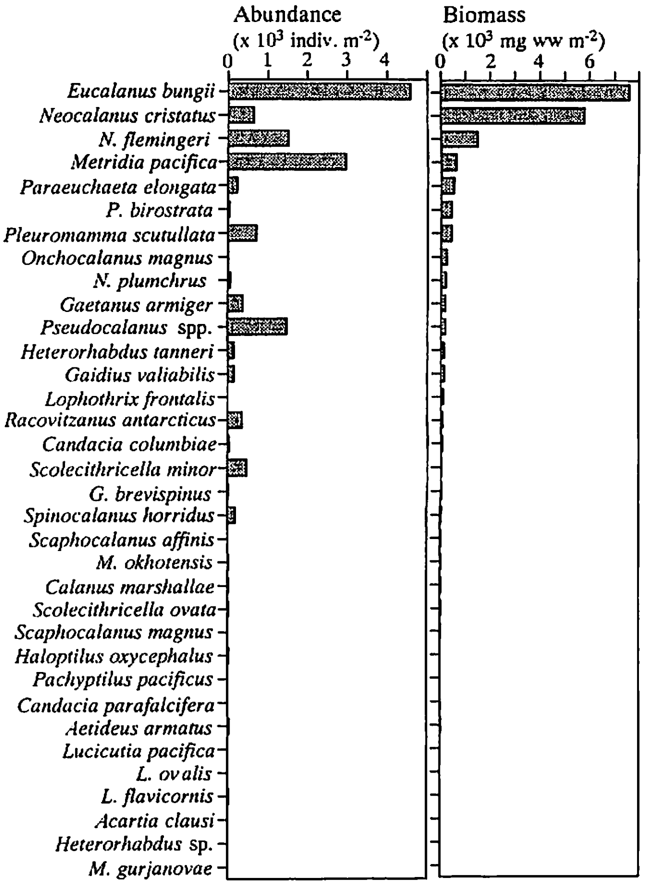

Fig. 4. Mean numerical abundance and biomass of all calanoid species collected from 0–500 m at the Stns 201, 202, 203, 204 and 301.

The developmental stage compositions of the four dominant calanoid species are shown in Fig. 6. Although wide variations in abundance (260–6901 indiv. m^{-2}) were observed, the developmental stage composition of *E. bungii* was relatively stable over the entire study area. Younger stages (C1–3) were few. Adult females occurred at all stations, and most of them were in a maturation condition (category 1), which is typical of females in diapause (Miller et al. 1984). For *N. cristatus*, the C5 and C1 stages were dominant at most stations. Females of this species were not abundant (0–82 indiv. m^{-2}) and most were in spent condition, bearing about 15 oocytes in their bodies. *N. flemingeri* occurred from C1 to adult stages, the dominat stages being C4 and adult females. Although spent females of this species were abundant (67.5%), actively spawning individuals (20.9%) were also collected. The population of *M. paci-*

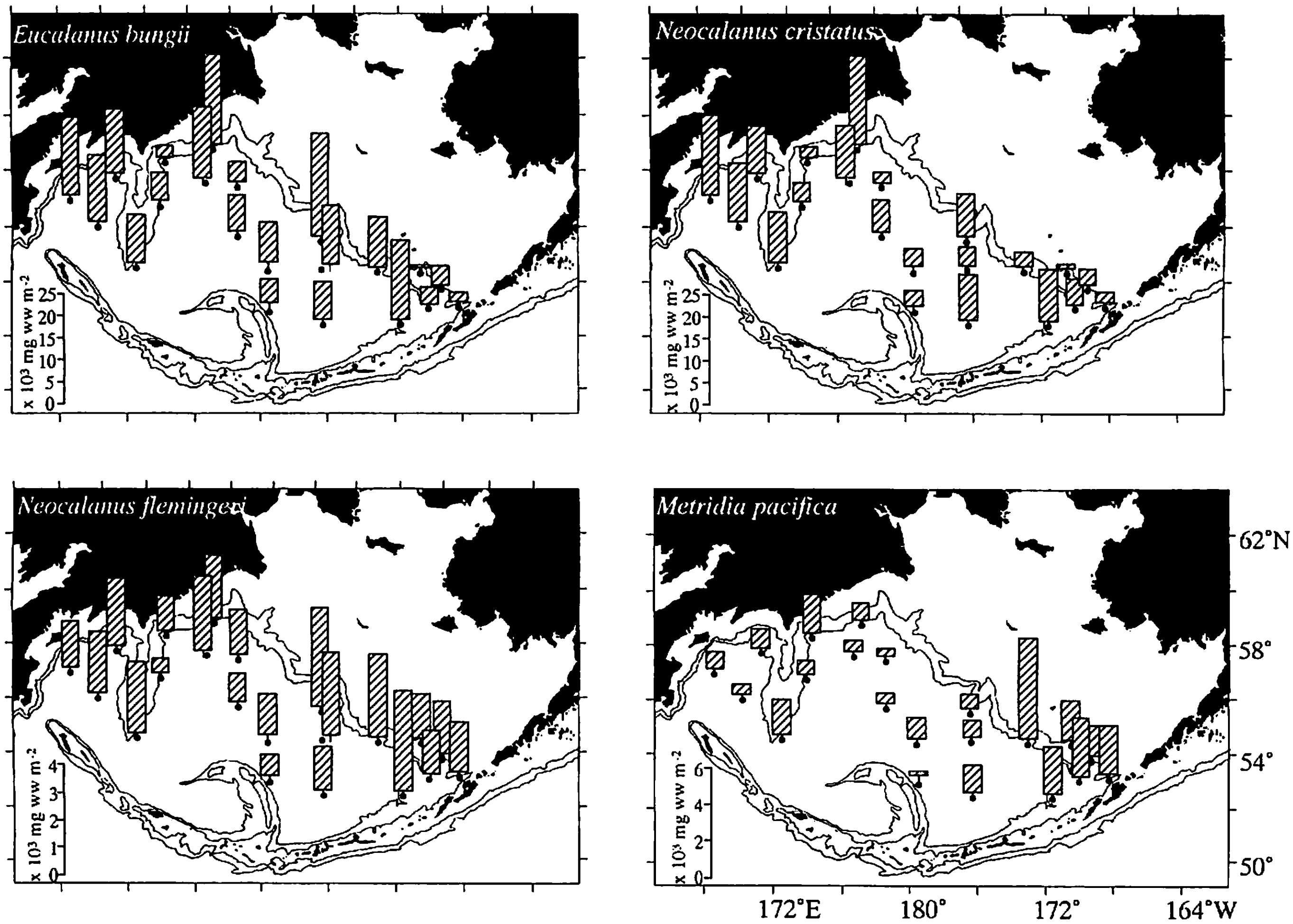

Fig. 5. Horizontal distribution of biomass ($\times 10^3$ mg ww m^{-2}) of the four dominant calanoid species. Note biomass scale differs for each species.

fica was mainly composed of C5 and adult females.

Discussion

Several studies on zooplankton biomass in the Bering Sea basin have been conducted during summer. Motoda & Minoda (1974) analyzed the zooplankton biomass collected by vertical hauls from 80-m depth with a Norpac net (0.33–0.35 mm mesh) and reported that the summer zooplankton biomass ranged from 22.8–45.9 g ww m^{-2} in the basin. Although the collections by the present study were made by a WP-2 net that has a slightly smaller mesh size than the Norpac net, mean zooplankton biomass was 32.5 g ww m^{-2} between 0- and 500-m depth. Thus, the winter zooplankton biomass between 0–500 m depth is of the same order as that during summer between 0–80 m depth.

Motoda & Minoda (1974) showed that zooplankton biomass is low at the center and southern parts of the Bering Sea basin, and high at the western and eastern edges during winter. In the present study, although we can not describe geographical trends in detail because of the coarse sampling strategy over a broad area, zooplankton biomass tended to be low at the eastern stations of the basin. Thus, horizontal trends in zooplankton biomass in the Bering Sea basin appear to vary seasonally.

The dominant species both by number and biomass, i.e. *E. bungii*, *N. cristatus*, *N. flemingeri* and *M. pacifica*, are considered typical oceanic species in the subarctic North Pacific and adjacent seas (Zenkevitch 1963; Vinogradov 1968; Motoda & Minoda 1974; Miller & Clemons 1988). Table 2 shows brief information on the life cycles of each species. The expected developmental stages and reproductive condition of adult females from our sampling period and depth are superimposed on this table. Results for *E. bungii*, *N. cristatus* and *N. flemingeri* were mostly in agreement with the expected results, and most of the dominant stages are deep living, overwintering stages (see reference in Table 2). However, the developmental stage composition of *M. pacifica* differed from our expectations. The life cycle of *N. flemingeri* is conjectured to take 1 or 2 years (Miller & Terazaki 1989; Tsuda et al. 1999). The apparent occurrence of the C4 stage of this species during winter may support the 2-year life cycle conjecture for the Bering Sea basin.

Table 2. The life cycle parameters of the dominant calanoid species previously reported in the subarctic Pacific. The expected developmental stages and female maturation conditions during winter are also shown.

Species	Life cycle	Reproductive peak	Spawning depth (m)	Expected stages	Reference*
Eucalanus bungii	1 or 2 years	May–July	Surface	C4–5 and diapausing female	1, 2
Neocalanus cristatus	1 year	October–December	500–2000	C1–2 and spawning-spent female	2, 7
N. flemingeri	1 or 2 years	December–February	250–500	C4 and spawning-spent female	4, 8, 6
Metridia pacifica	3–4 months	March–October	Surface	All stages	3, 5

* 1, Krause & Lewis 1979; 2, Miller et al. 1984; 3, Batchelder 1985; 4, Miller & Clemons 1988; 5, Batchelder & Miller 1989; 6, Miller & Terazaki 1989; 7, Kobari & Ikeda 1999; 8, Tsuda et al. 1999.

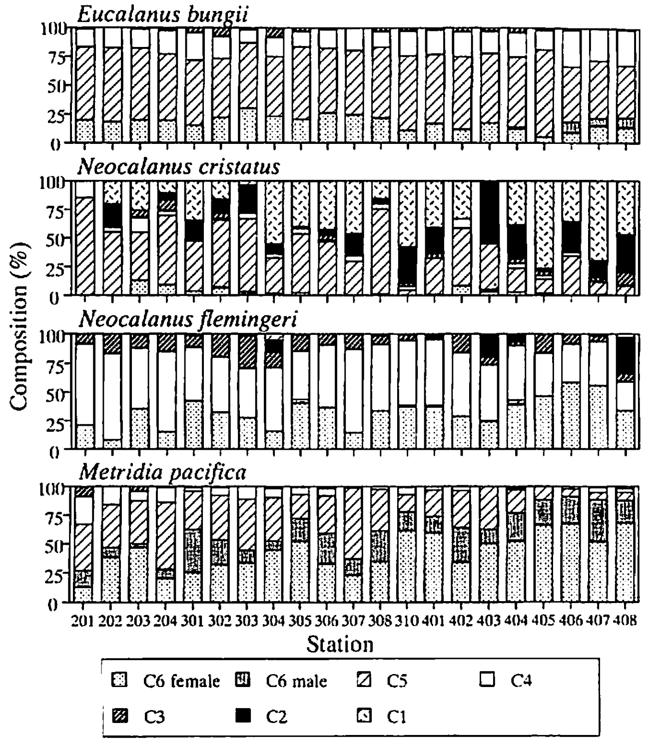

Fig. 6. Developmental-stage compositions of the four dominant calanoid species.

In the present study, calanoid copepods contributed 75% on average to the total zooplankton biomass. Coyle et al. (1996) reported that *Calanus cristatus* (=*Neocalanus cristatus*), *C. plumchrus* (=*N. flemingeri*+*N. plumchrus*) and *E. bungii* contributed more than 90% of the total zooplankton biomass at an oceanic area of the Bering Sea during spring–summer. Thus, the contribution of calanoid copepod biomass to the total zooplankton biomass during winter in the Bering Sea basin is less than that during spring–summer. One possible reason for this is that *N. plumchrus*, which is a major component of the zooplankton population during spring–summer in this subarctic area, was only collected in small numbers during this study. The most persuasive explanation for this result is that their overwintering depth in the Bering Sea basin is deeper than our maximum sampling depth (=500 m).

Many features of the calanoid population during winter in the Bering Sea basin were similar to those in the subarctic Pacific. However, there is some possibility that different population dynamics exist between the two sites, as exemplified by the low number or lack of occurrence of *N. plumchrus* and the younger stages of *M. pacifica* in the Bering Sea basin. To confirm these features and elucidate their causes, samples that can determine the seasonal change in population structure and assess vertical distribution throughout a greater depth range need to be collected.

Acknowledgment

Plankton collections and oceanographic data used in this study were supplied by the National Research Institute of Far Seas Fisheries.

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