

Variation in Zooplankton and Micro-Nekton Biomass in Response to Seawater Temperature Changes in the Central Bering Sea during Summer

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Abstract: We investigated biomass of zooplankton and micro-nekton using Norpac and bongo nets in the central Bering Sea in summer, 2007 to 2014 (except for 2010). We determined the biomass of zooplankton (including euphausiids, copepods, amphipods, decapods, chaetognaths, appendicularians, gastropods, hydrozoans, ostracods, and polychaetes) and micro-nekton (cephalopods, myctophids, and other fishes) in the central Bering Sea. The mean biomass of total zooplankton collected with the Norpac net increased from 2007 to 2009, but fluctuated from 2011 to 2014. Biomass of each prey category collected with bongo nets showed different tendencies among years. There were negative correlations between integrated mean seawater temperature and biomass of zooplankton collected with both Norpac and bongo nets. The biomass of copepods, amphipods, and hydrozoans was significantly lower in warm years. Other zooplankton categories (euphausiids, decapod larvae, ostracods, chaetognaths, and appendicularians) showed slightly negative or positive (polychaetes and gastropods) correlations with seawater temperature. These variations could not be explained by temperature changes alone. On the other hand, there was almost a constant correlation between integrated mean temperature and biomass of micro-nekton collected with bongo nets. The results of this study suggested that variation in zooplankton and micro-nekton biomass in the central Bering Sea may be affected by the seawater temperature.

Keywords: zooplankton, micro-nekton, biomass, annual variation, temperature, central Bering Sea

INTRODUCTION

Immature and maturing stages of Pacific salmon including chum (*Oncorhynchus keta*), pink (*O. gorbuscha*), sockeye (*O. nerka*), coho (*O. kisutch*), and Chinook salmon (*O. tshawytscha*) are widely distributed in the Bering Sea during summer and fall (e.g., Morita et al. 2007, 2008, 2009, 2011; Sato et al. 2009, 2012, 2014, 2015; Urawa et al. 2009). The Bering Sea is an important habitat for various chum salmon stocks originating from Asia and North America (Urawa et al. 2009).

Ishida et al. (1993) reported a significant negative correlation between abundance and growth of chum salmon, and they suggested that density dependence is one of the possible causes for the changes in the increase in mean return age and decrease in mean body weight of chum salmon in the North Pacific Ocean. If prey resources are limited, an increase in salmon abundance may lead to a decrease in available prey per individual (Tadokoro et al. 1996). As a result, decreased

growth of salmon will lead to a decline in body size, a delay in maturity, and possibly increased mortality.

Many studies of food habits of salmon have been conducted in the Bering Sea and adjacent areas (e.g., Percy et al. 1988; Brodeur 1990; Tadokoro et al. 1996; Davis et al. 2003; Volkov et al. 2007; Sakai et al. 2012). Zooplankton and micro-nekton are essential prey for many fish, including salmon. Salmon feed on crustacean and gelatinous zooplankton, squids, and fishes, although the composition of stomach contents differs by year (Percy et al. 1988; Tadokoro et al. 1996). Feeding habits of salmon vary in relation to climate events such as ENSO (Thayer et al. 2014); also dominant prey organisms differ between warm and cold years (Farley et al. 2007; Farley and Moss 2009). Long-term variation in zooplankton and micro-nekton biomass and composition is thought to be a key factor influencing growth and stock variation in pelagic fishes (e.g., Kotani and Odate 1991).

Previous studies in the Bering Sea have shown that the type and abundance of zooplankton differ between warm

and cold years (e.g., Coyle et al. 2008; Stabeno et al. 2012; Volkov 2012). Further, the distribution of zooplankton differs by region (Volkov et al. 2007). In contrast, Shimoto et al. (1997) reported that year-to-year variation (1985–1994) in pink salmon abundance plays an important role in controlling summer biomass of macrozooplankton and phytoplankton in the central subarctic North Pacific, with zooplankton biomass tending to be higher in even-numbered years compared with odd-numbered years. The variation in biomass of zooplankton and micro-nekton is thought to be both a “bottom-up” effect (e.g., temperature, salinity, nutrients) and a “top-down” effect (predation by a higher trophic level). Plankton are generally defined as passively floating, drifting, or slightly motile organisms (see Motoda 1944). They are short lived and respond quickly to changes in the physical environment (e.g., temperature and ocean currents; Hay et al. 2005). Thus, variations in the biomass of zooplankton and micro-nekton are thought to be strongly affected by “bottom-up” effects.

Although numerous investigations into the abundance and biomass of zooplankton in the central Bering Sea have been conducted to evaluate the prey environment of salmon (e.g., Tadokoro et al. 1996; Volkov et al. 2005), information about long-term variation in zooplankton and micro-nekton in the central Bering Sea is scarce compared to that available for the eastern and western Bering Sea. Variation in zooplankton and micro-nekton in the central Bering Sea provides useful information to evaluate the growth and stock assessment of salmon. This study reports on interannual variation in zooplankton and micro-nekton biomass in the south-central Bering Sea during summer, 2007–2014, except for 2010. Biomass data are compared to hydrographic data (especially seawater temperature) to clarify factors that result in these variations.

MATERIALS AND METHODS

Study Area and Schedule

Sampling was conducted at 17 stations (four stations at 175°E longitude, seven stations at 180° longitude, and six stations at 175°W longitude) in the south-central Bering Sea (Fig. 1). Sampling was conducted from late July to early August in 2007, 2009, and 2011–2014. Sampling in 2008 was conducted from late August to early September. No research cruise was conducted in 2010. All sampling was carried out by researchers aboard the R/V *Hokko maru*, Hokkaido National Fisheries Institute, Fisheries Research and Education Agency.

Zooplankton and Micro-nekton Sampling

Zooplankton and micro-nekton samples were collected by Norpac (0.45 m diameter, 335- μ m mesh) and bongo (0.7 m diameter, 335- μ m mesh) nets. The Norpac net was towed vertically from 150 m to the surface during daytime hours at all stations. The bongo net was towed in a dou-

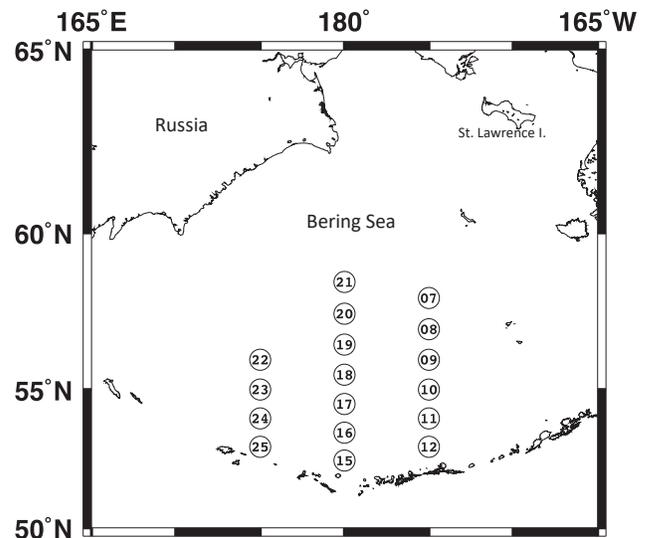


Fig. 1. Location of sampling stations in the south-central Bering Sea during the summers of 2007–2009 and 2011–2014.

ble oblique pattern from 100 m to the surface and deployed during evening hours (one hour after sunset) at seven to nine stations each year (Table 1). Both nets were equipped with a flow meter in the net opening to estimate the volume of water filtered. Samples were immediately preserved in 10% buffered formalin: seawater. Zooplankton were sorted into taxonomic categories including copepods, amphipods, euphausiids, decapod larvae, ostracods, hydrozoans, chaetognaths, appendicularians, polychaetes, and gastropods. Micro-nekton were sorted into taxonomic categories including myctophids, other fishes, and cephalopods. Wet weights were measured to the nearest mg for each category. Zooplankton and micro-nekton biomass estimates were calculated using the filtered volume from each net and expressed as mg wet weight (WW) \cdot m⁻³.

Environmental Conditions

Seawater temperature, salinity, and depth were recorded using STD (Alec Electronics Co., Ltd., Kobe, Japan) from approximately 500 m to the surface at intervals of 1 m at all stations. Temperatures from the surface to 100 m or 150 m depth at each station were used because the towed depth was 150 m for the Norpac net and 100 m for the bongo net.

Data Analysis

To compare seawater temperature with zooplankton and micro-nekton biomass, we calculated the integrated mean temperature (mean temperature from the surface to 150 m for the Norpac net and 100 m for the bongo net) at each station for each year. Zooplankton and micro-nekton biomass (X: mg WW \cdot m⁻³) were transformed to log (X+1) prior to

Table 1. Mean biomass (mg wet weight (WW) • m⁻³), SD, range, and number of samples of zooplankton and micro-nekton collected with Norpac and bongo nets each year in summer in the central Bering Sea. Parentheses indicate the annual range in biomass.

Category	2007		2008		2009		2011		2012		2013		2014	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Norpac samples														
Number of samples	17		17		17		17		17		17		17	
Total zooplankton	154.0	147.6	288.0	88.9	495.1	561.4	231.2	152.7	372.9	400.2	214.2	164.2	67.2	40.4
(Range)	(23.8–558.7)		(171.8–437.5)		(96.1–2097.5)		(47.6–590.1)		(121.7–1888.3)		(22.3–631.4)		(16.2–155.7)	
Bongo samples														
Number of samples	8		7		9		7		8		8		8	
Zooplankton														
Copepods	204.3	139.8	268.2	448.7	185.3	42.3	163.3	147.2	435.8	330.0	193.6	124.1	82.7	30.8
(Range)	(92.6–476.5)		(39.4–1273.0)		(117.9–264.6)		(53.4–481.6)		(115.7–1168.7)		(41.5–450.6)		(27.2–125.8)	
Amphipods	11.6	12.0	26.9	15.4	30.8	24.4	16.5	12.5	32.0	6.9	8.3	6.0	4.5	2.5
(Range)	(1.1–35.4)		(7.6–54.1)		(3.3–78.5)		(6.2–42.6)		(26.3–43.8)		(1.9–19.6)		(1.9–9.6)	
Euphausiids	3.8	3.3	61.3	85.0	27.8	30.3	14.7	19.7	53.2	37.0	14.3	15.3	15.6	16.7
(Range)	(0.4–9.2)		(10–250.4)		(5.5–87.2)		(0–56.6)		(16.2–120.4)		(5–50.8)		(5.3–55.2)	
Decapods	1.0	1.8	0.1	0.1	1.6	3.3	0.7	1.3	2.7	2.0	0.7	0.8	1.1	1.6
(Range)	(0–5.4)		(0–0.4)		(0–9.5)		(0–3.4)		(0.4–5.9)		(0–2.2)		(0–4.9)	
Ostracods	0.8	0.7	0.3	0.3	0.4	0.4	0.6	0.5	12.3	9.3	0.5	0.6	2.3	1.7
(Range)	(0.1–1.9)		(0.1–0.9)		(0–1.3)		(0–1.4)		(2.9–31.0)		(0–1.6)		(1.1–5.7)	
Hydrozoans	13.3	7.8	38.1	23.5	93.4	76.1	38.8	27.0	93.8	111.1	11.1	11.9	21.0	17.3
(Range)	(4.4–27.0)		(16.4–74.2)		(0–256.3)		(6.5–83.0)		(0–316.4)		(0–35.2)		(3.6–52.8)	
Chaetognaths	30.8	12.5	68.8	44.7	79.8	39.3	23.1	25.0	58.6	28.6	30.8	11.1	39.7	13.6
(Range)	(13.2–47.2)		(36.6–159.5)		(15.5–147.0)		(2.4–74.1)		(12.3–104.8)		(12.2–44.2)		(21.4–58.4)	
Appendicularians	17.3	37.4	6.1	4.7	9.0	8.6	15.9	24.4	0.7	2.0	7.3	13.3	2.1	5.4
(Range)	(0.2–109.8)		(0–12.1)		(2.9–29.4)		(1.6–68.7)		(0–5.7)		(0.4–40.0)		(0–15.3)	
Polychaetes	2.6	3.1	1.1	1.2	0.8	1.1	9.0	12.0	0.5	0.5	2.2	1.8	1.4	1.5
(Range)	(0.3–9.6)		(0–3.1)		(0–3.1)		(0–28.6)		(0–1.1)		(0.7–6.2)		(0.1–4.8)	
Gastropods	1.6	1.4	16.4	11.6	2.5	2.2	0.8	1.2	3.8	4.5	1.3	1.4	2.9	3.9
(Range)	(0–3.5)		(3.5–30.4)		(0–6.6)		(0–2.7)		(0–13.4)		(0–3.8)		(0.1–10.7)	
Others	0.1	0.1	0.0	0.0	0.0	0.1	11.2	13.9	5.3	4.7	0.5	1.1	0.0	0.0
(Range)	(0–0.2)		(0–0.1)		(0–0.3)		(0.8–35.3)		(1.8–16.0)		(0–3.2)		(0–0.1)	
Total zooplankton	287.4	167.0	487.5	536.0	431.4	124.5	294.5	230.6	698.9	296.3	270.6	126.8	173.4	45.0
(Range)	(146.4–566.6)		(118.7–1622.2)		(248.6–630.5)		(131–790.4)		(419.8–1339.9)		(139–522.5)		(75–225.4)	
Micro-nekton														
Myctophids	–	–	4.8	8.1	0.7	1.8	2.9	2.8	0.6	0.9	1.4	2.3	3.1	6.2
(Range)			(0–22.7)		(0–5.6)		(0–7.3)		(0–2.2)		(0–5.4)		(0–18.0)	
Other fishes	–	–	0.6	1.1	0.4	0.5	0.5	0.7	1.7	2.8	0.1	0.3	1.5	2.4
(Range)			(0–3.0)		(0–1.3)		(0–1.9)		(0–8.4)		(0–0.8)		(0–7.3)	
Cephalopods	–	–	0.4	0.5	1.8	1.6	2.3	1.5	2.0	2.4	0.7	0.5	1.0	1.0
(Range)			(0–1.4)		(0–4.4)		(1.1–5.6)		(0–6.2)		(0.1–1.5)		(0–2.8)	
Total nekton	–	–	5.8	7.8	3.0	3.5	5.7	3.6	4.3	3.7	2.3	2.2	5.6	8.3
(Range)			(0–23.0)		(0.3–11.2)		(2.3–12.9)		(0–11.6)		(0.6–6.3)		(0.1–25.4)	

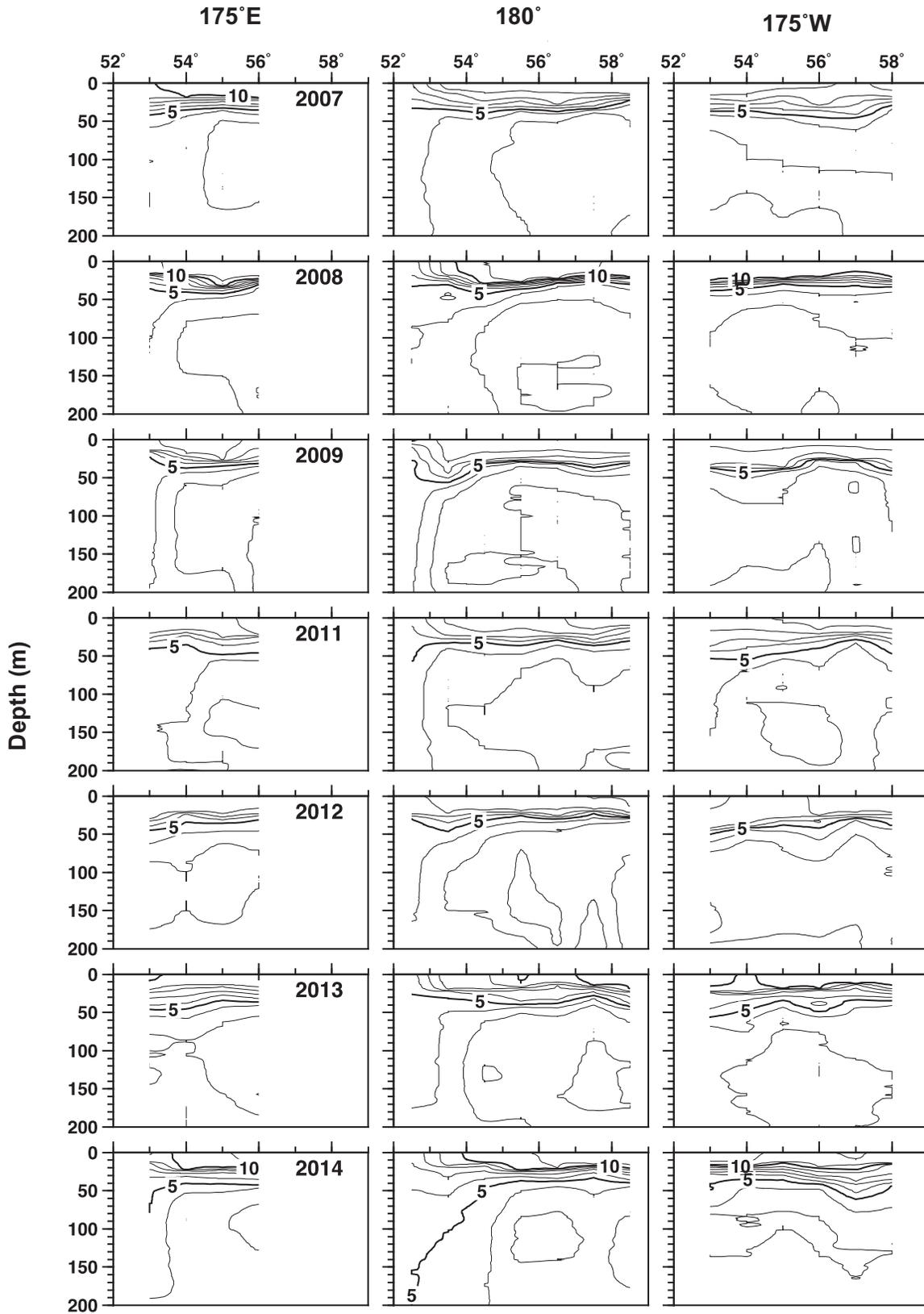


Fig. 2. Vertical temperature profiles (°C; 0–200 m depth) obtained from sampling stations located at 175°E, 180°, and 175°W in the south-central Bering Sea during the summers of 2007–2009 and 2011–2014.

analysis to reduce the bias. We used correlation analysis (Spearman’s correlation) to estimate the relationship between integrated mean temperature and zooplankton or micro-nekton biomass. Because the sample of micro-nekton in 2007 did not include a measurement of wet weight, it was excluded from the analysis.

RESULTS

Environmental Conditions

Vertical profiles of temperature from the surface to 150 m depth varied from 1.2°C to 12.7°C (Fig. 2). The thermocline was located at approximately 20–40 m depth. The temperature below 50 m was consistently < 4°C. Temperatures above 20 m depth in 2008 and 2014 were approximately 1–2°C higher than in other years.

Biomass and Interannual Variation in Zooplankton and Micro-nekton

Mean zooplankton biomass collected with the Norpac net at each station in each year ranged from 67.2 ± 40.4 to 495.1 ± 561.4 mg WW • m⁻³ among sampling years with the mean biomass during the sampling period at 260.4 ± 304.7 mg WW • m⁻³ (Fig. 3a, Table 1). Total zooplankton biomass increased from 2007 to 2009. It varied by year from 2011 to 2014, with lower values observed in odd-numbered years and higher values in even-numbered years.

Mean zooplankton biomass collected with the bongo net at each station in each year ranged from 173.4 ± 45.0 to 698.9 ± 296.3 mg WW • m⁻³ among sampling years with the mean biomass over the sampling period at 378.2 ± 291.2 mg WW • m⁻³ (Fig. 3b, Table 1). With the exception of 2014, total zooplankton biomass from 2007 to 2013 was higher in even-numbered years and lower in odd-numbered years.

Micro-nekton biomass collected with the bongo net at each station in each year ranged from 2.3 ± 2.2 to 5.8 ± 7.8 mg WW • m⁻³ among sampling years. The mean biomass during 2007 to 2014 was 3.7 ± 5.0 mg WW • m⁻³ (Fig. 3c, Table 1). The variation in total micro-nekton biomass showed no consistent pattern.

The trends in interannual variation in zooplankton and micro-nekton biomass collected with the bongo net differed among taxonomic categories (Fig. 4). The biomass of copepods and euphausiids varied from 2007 to 2013, with lower values observed in odd years and higher values in even years, but was different from the trend in 2014. The biomass of decapod larvae varied from 2007 to 2009, with higher values observed in odd years and lower values in even years, opposite to the tendency in 2011 to 2014, which showed higher values in even years and lower values in odd years. Amphipod biomass increased from 2007 to 2009; the biomass after 2011 showed the same patterns as those for copepods and euphausiids. The biomass of ostracods was

almost constant across sampling years, except for 2012. The biomass of appendicularians varied over the sampling period, with lower values observed in even-numbered years and higher values in odd-numbered years. In contrast, variation in gastropod biomass was lower in odd-numbered years and higher in even-numbered years. Hydrozoan and chaetognath biomass increased from 2007 to 2009 and varied from 2011 to 2014, with lower values observed in odd-numbered years compared to even-numbered years. The biomass of

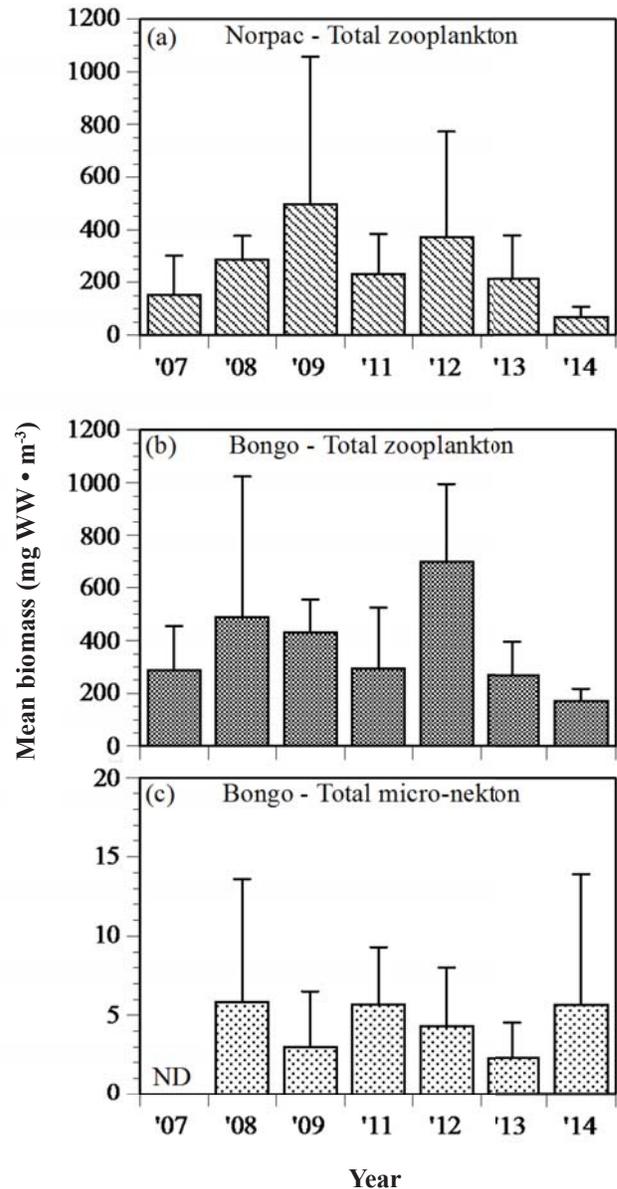


Fig. 3. Interannual variation of mean total zooplankton biomass collected with a Norpac net (a) and a bongo net (b), and mean total micro-nekton biomass collected with a bongo net (c) at stations located in the south-central Bering Sea during the summers of 2007–2009 and 2011–2014. Error bars show standard deviation. ND indicates no data.

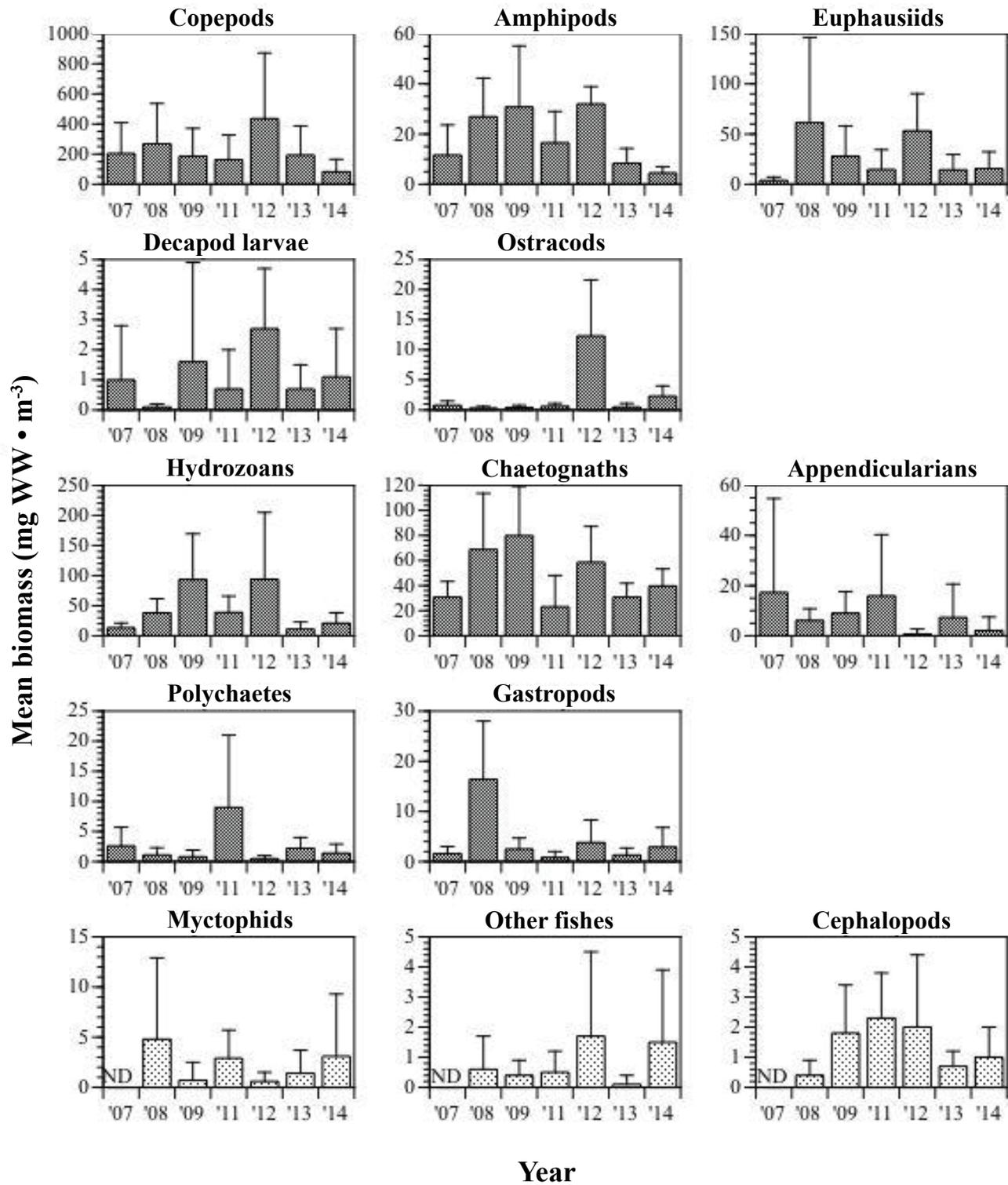


Fig. 4. Mean biomass (mg WW • m⁻³) of zooplankton and micro-nekton collected by bongo net in the south-central Bering Sea during the summers of 2007–2009 and 2011–2014. Error bars show standard deviation. ND indicates no data.

micro-nekton (myctophids, other fishes, and cephalopods) did not show a consistent pattern among years.

Relationship between Temperature and Zooplankton and Micro-nekton Biomass

There was a significant negative correlation ($P < 0.01$) between total zooplankton biomass collected with the Norpac net and integrated (surface to 150 m) mean temperature (Fig. 5a). There was also a significant negative correlation ($P < 0.05$) between total zooplankton biomass collected with the bongo net and integrated (surface to 100 m) mean temperature (Fig. 5b). On the other hand, there was no correlation ($P > 0.50$) between total micro-nekton collected with the bongo net and integrated (surface to 100 m) mean temperature (Fig. 5c).

In the each taxonomic category, there was a significant negative correlation between integrated mean temperature (surface to 100 m) and biomass of copepods, amphipods and hydrozoans collected with the bongo net (copepods, $P < 0.01$; amphipods and hydrozoans, $P < 0.05$; Fig. 6). The biomass of euphausiids, decapod larvae, ostracods, chaetognaths, and appendicularians collected by the bongo net was negatively correlated with temperature, and that of polychaetes and gastropods was slightly positively correlated with temperature, but these relationships were not significant (Fig. 6). The biomass of myctophids and other fishes collected in the bongo net were positively correlated with temperature, and that of cephalopods was negatively correlated with temperature, but these relationships were not significant (Fig. 6).

DISCUSSION

The Norpac and bongo nets used in this study collected a variety of categories of zooplankton and micro-nekton. These results are roughly consistent with earlier zooplankton studies in the southeastern Bering Sea (e.g., Coyle et al. 2011; Volkov 2012; Ohashi et al. 2013). There were negative correlations between integrated mean temperatures and biomass of zooplankton collected with both the Norpac and bongo nets in this study. In contrast, there was almost a constant correlation between integrated mean temperature and biomass of micro-nekton collected with bongo nets. Coyle et al. (2008) reported that in cold years the biomass of large species such as scyphozoans (*Chrysaora melanaster*), large copepods (*Calanus marshallae*), arrow worms (*Sagitta elegans*) and euphausiids (*Thysanoessa rashii*, *T. inermis*) was higher than in samples collected in a warm year. In a warm year, they showed significantly higher densities of small copepods (*Pseudocalanus* spp., *Oithona similis*) and small hydromedusae (*Euphysa flammea*). Ohashi et al. (2013) reported that large and small copepods collected over a 16-year period in the southeastern Bering Sea shelf showed a clear negative correlation with habitat temperature. Volkov

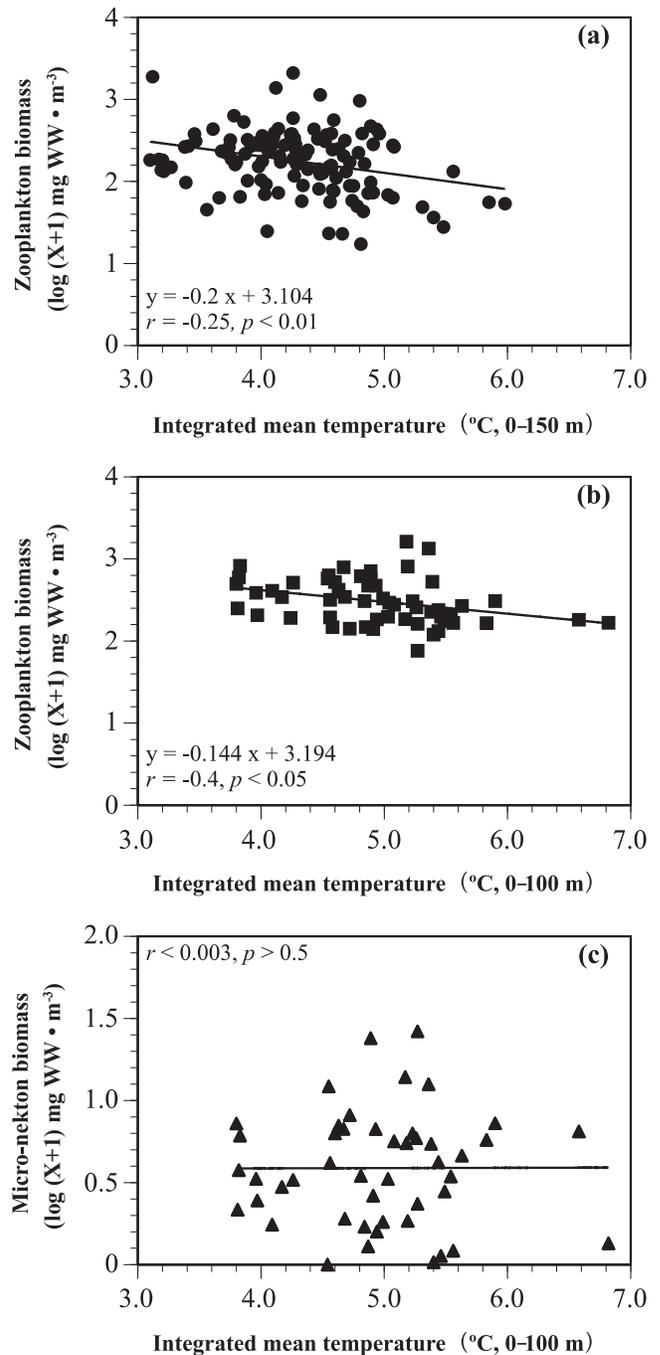


Fig. 5. Relationship between integrated mean temperature (°C) and zooplankton and micro-nekton biomass (log (X+1) mg WW · m³) in the south-central Bering Sea. (a) integrated mean temperature (°C; 0–150 m) and zooplankton biomass collected with Norpac net; (b) integrated mean temperature (°C; 0–100 m) and zooplankton biomass collected with bongo net; (c) integrated mean temperature (°C; 0–100 m) and micro-nekton biomass collected with bongo net.

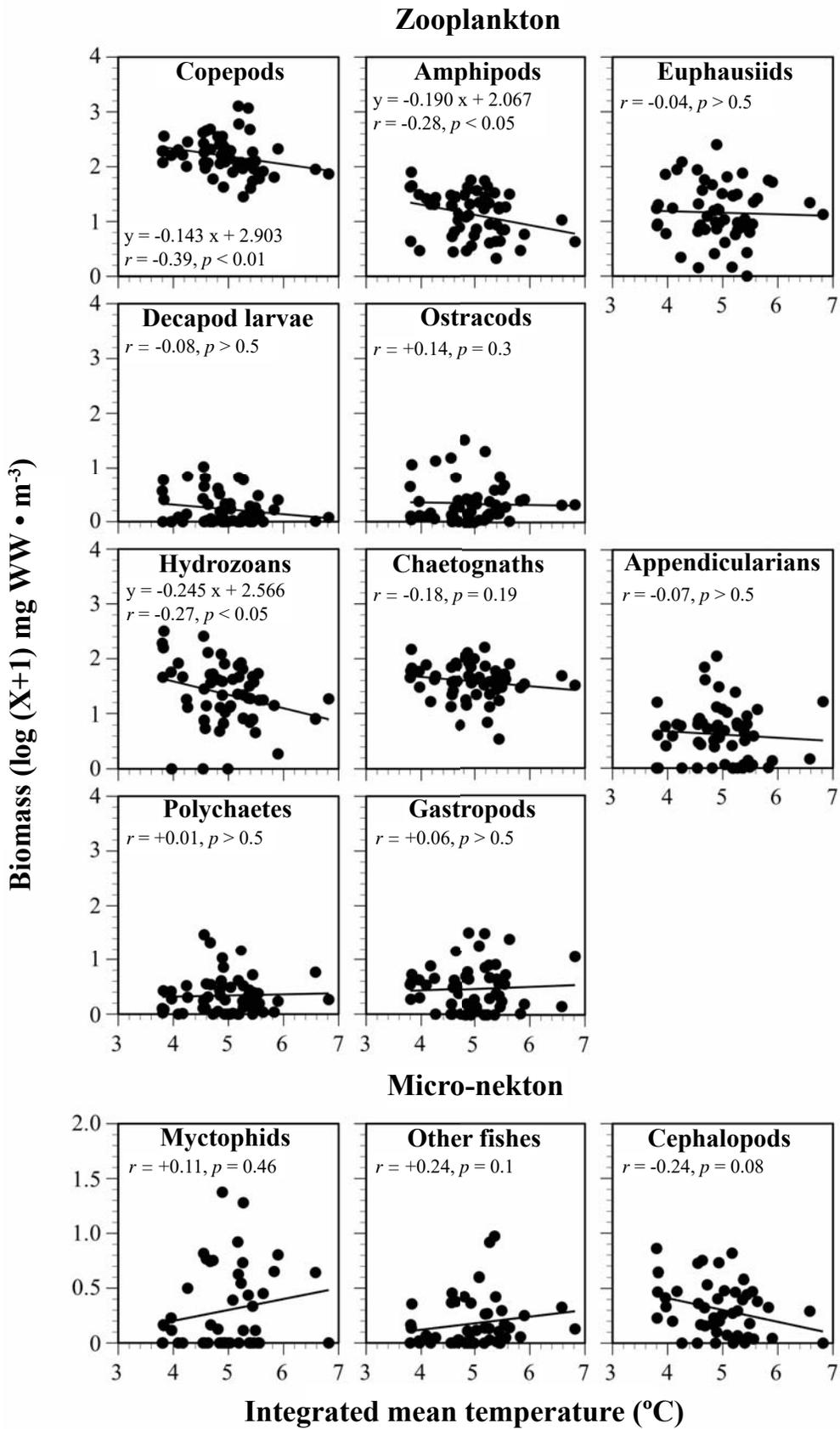


Fig. 6. Relationship between integrated mean temperature (°C; 0–100 m) and each category of zooplankton biomass and micro-nekton ($\log(X+1)$ mg WW · m⁻³) collected with a bongo net in the central Bering Sea during the summers of 2007–2009 and 2011–2014.

(2012) reported that the emergence of the hyperiid *Themisto libellula* coincides with the beginning of a series of cold years. Biomass of copepods, amphipods, and hydrozoans in this study was significantly lower in the summer of warm years. Relationships between temperature and biomass of the above three taxonomic categories in this study coincided with results of previous studies in the eastern and western Bering Sea. Biomass of copepods, amphipods and hydrozoans in the central Bering Sea may have been influenced by temperature, similar to that seen in the eastern Bering Sea (Coyle et al. 2008, 2011). Correlations of other zooplankton categories were either slightly negative (euphausiids, decapod larvae, ostracods chaetognaths and appendicularians), or positive (polychaetes and gastropods) and cannot be explained by temperature alone.

Abundance of myctophids (*Symbolophorus evermanni*, *Hygophum reinhardtii*, and *Myctophum orientale*) in the Kuroshio region showed a positive correlation with average SST (Watanabe and Kawaguchi 2003). Myctophids and other fish biomass in the micro-nekton in this study indicated, similarly, a positive correlation with temperature, contrary to that of zooplankton. The results of Watanabe and Kawaguchi (2003) show variation over a long-term period (1957–1994) in the Kuroshio region, which reflects variation in myctophid abundance. Positive correlation of myctophids and other fish biomass with temperature may suggest that a similar phenomenon had occurred in the central Bering Sea.

The biomass of zooplankton and micro-nekton are influenced not only by physical parameters but also by animals at higher trophic levels such as anadromous salmon, non-salmonid fishes, and birds (Baduini et al. 2001; Davis et al. 2009; Coyle et al. 2011). Shiimoto et al. (1997) reported that year-to-year variation in pink salmon abundance plays a large part in controlling the summer biomass of macrozooplankton and phytoplankton in the central subarctic North Pacific. Kaga et al. (2013) reported that analysis of stomach contents of chum salmon indicated non-crustacean zooplankton (appendicularians, chaetognaths, hydrozoans, polychaetes and pteropods) were consumed at a higher frequency when pink salmon were more abundant. Tadokoro et al. (1996) reported that chum salmon changed their dominant diet from gelatinous zooplankton in 1991, when pink salmon were abundant, to a diet of crustaceans in 1992, when pink salmon were less abundant. Although pink salmon abundance during summer in this area might be expected to control zooplankton biomass, we did not catch many pink salmon in the survey area because they had already moved to coastal areas for spawning (e.g., Morita et al. 2011; Sato et al. 2012, 2014, 2015). However, regular variation in zooplankton such as that reported by Shiimoto et al. (1997) was not seen in this study. Based on our data, the “top-down” effects of zooplankton and micro-nekton biomass cannot be discussed.

Although the precise mechanisms behind the variation in zooplankton and micro-nekton biomass are still unclear, we think that temperature is one of many important factors

influencing the quality and quantity of zooplankton and micro-nekton biomass in the central Bering Sea. Variation in the many categories of zooplankton and cephalopods indicate a trend toward negative correlations with temperature, whereas micro-nekton (except for cephalopods) indicate a trend toward positive correlations with temperature. We believe that these results will be helpful in understanding the growth and survival of Pacific salmon as well as other fishes. Therefore, it is necessary to continue to study the abundance of zooplankton, micro-nekton, and salmon in the central Bering Sea.

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