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Inter-oceanic differences in macrozooplankton biomass and community structure in four regions around Hokkaido Island, Japan : consequences for marine ecosystem structure

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Abstract

Inter-oceanic differences in macrozooplankton (euphausiids, amphipods, cnidarians and chaetognaths) biomass and community structure were studied in four regions (northern Japan Sea, southern Okhotsk Sea, Donan and Doto areas of North Pacific) around Hokkaido Island. Whole zooplankton biomass ranged between 25 and 315 g WM m^{-2} and was significantly higher in the southern Okhotsk Sea. Macrozooplankton composed 5-15% of the whole zooplankton biomass. Across all macrozooplankton taxa, the number of species varied with region : the fewest species (2-4 species) were in the southern Okhotsk Sea, followed by the northern Japan Sea (3-5 species), and the most species (4-9 species) were in the Donan and Doto areas of the North Pacific. Depth topography and thermal conditions are considered possible causes of the differences in species richness across regions. Through inter-oceanic comparison, marine ecosystem characteristics of each region were evaluated. The zooplankton community in the northern Japan Sea was characterized by a predominance of carnivorous macrozooplankton taxa (amphipods, cnidarians and chaetognaths) and fewer herbivorous taxa (euphausiids and mesozooplankton), and it was determined to be as a top-down controlled ecosystem. In contrast, in the southern Okhotsk Sea, the zooplankton community was predominated by herbivorous mesozooplankton and euphausiids, and the marine ecosystem was determined to be a bottom-up control region. In the North Pacific, zooplankton community in the Doto area was predominated by chaetognaths. The zooplankton community in the Donan area showed mixed characteristics of the Doto area and the northern Japan Sea because of the seasonal water mass exchange from these two regions.

Key words : Amphipod, Euphausiid, Chaetognath, Cnidarian, Top-down, Bottom-up

Introduction

In marine ecosystem, macrozooplankton feed on phytoplankton, which are micro- and small meso-sized zooplankton (Pakhomov et al., 1999 ; Froneman et al., 2002 ; Dapadado et al., 2008). Macrozooplankton are fed upon by fishes (Moku et al., 2000 ; Yamamura et al., 2002), marine birds (Sydeman et al., 2001) and whales (Murase et al., 2007 ; Watanabe et al., 2012). Thus, macrozooplankton are vital links that connect lower and upper trophic levels. Because large-body sized macrozooplankton perform large magnitude diel vertical migration (DVM) and egest large faecal pellets that quickly sink, macrozooplankton also have an important role in vertical material flux, termed the "biological pump" (Steinberg et al., 2002 ; Wilson et al., 2008).

Information on the life cycle of macrozooplankton species around Japan is mainly concentrated at two locations : Toyama Bay, southern Japan Sea and the Oyashio region, off Kushiro, Hokkaido Islands. In Toyama Bay, life cycles are reported for euphausiids (Iguchi et al., 1993 ; Iguchi and Ikeda, 1999), amphipods (Ikeda et al., 1992 ; Ikeda, 1995) and cnidarians (Ikeda and Imamura, 1996). In the Oyashio region, comparable information is available for euphausiids (Kim et al., 2009), amphipods (Yamada et al., 2004 ; Yamada and Ikeda, 2006), cnidarians (Takahashi and Ikeda, 2006) and chaetognaths (Kotori, 1999).

Hokkaido Island is surrounded by four different oceanic

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regions, including two marginal seas (e.g., the northern Japan Sea, the southern Okhotsk Sea, and the Donan and Doto areas of the North Pacific). Inter-oceanic differences in marine zooplankton, including differences in abundance, biomass and species composition of mesozooplanktonic copepods, are well documented (Shimada et al., 2012). However, little information is available for inter-oceanic differences in biomass and species composition of macrozooplankton taxa.

In the present study, we studied the biomass and species composition of four macrozooplanktonic taxa (euphausiids, amphipods, cnidarians and chaetognaths) in four regions, including two marginal seas around Hokkaido Island (the northern Japan Sea, the southern Okhotsk Sea, and the Donan and Doto areas of North Pacific). We collected zooplankton samples collected within two-month intervals over two years (February 2013-February 2015). From these data, we compared inter-oceanic differences in macrozooplanktonic biomass and species composition. After combining the mesozooplankton biomass in each region, inter-oceanic differences in lower marine trophic levels were evaluated.

Materials and methods

Field sampling

Oceanographic observations were conducted at six stations (Sts. J15 and J36 in the northern Japan Sea, Sts. O26 and O36 in the southern Okhotsk Sea, St. P52 in the Donan areas of the North Pacific and St. P15 in the Doto-areas of the North Pacific) with three R/Vs (Hokushin-Maru, Hokuyo-Maru and Kinsei-Maru) belonging to the Hokkaido Research Organization. Observations were three to six times per year from February 2013 to February 2015 (Fig. 1).

Zooplankton samples were collected by vertically towing a flowmeter-mounted NORPAC net (mesh size : 335 µm, ring diameter : 45 cm) at a depth of 500 m. Because the water depth was shallow (350 m) at St. O26, the NOEPAC net was towed from 300 m at that station (water depths for the other stations were 560-4,000 m). At each sampling date, temperature and salinity were measured with CTD (Seabird Electronics Ltd., SBE-911Plus) casts.

Wet mass measurements and microscopic analysis

In a land laboratory, samples were half-divided with a Motoda splitter. The half aliquot was filtered through a preweighed plankton mesh (100 µm mesh) mounted on 90-mm diameter filter holder (ADVANTEC Ltd., KGS-90). Water between zooplankton was removed with dry filter paper, and wet mass (WM) was measured with a microbalance (A&D Ltd., HL-100) with precision of 0.1 g.

Zooplankton from one half aliquot of the samples were examined under a stereomicroscope (Nikon Ltd., C-BD115), and species were identified for four macrozooplanktonic taxa (euphausiids, amphipods, cnidarians and chaetognaths). For species identification, we mainly referred to Chihara and Murano (1997). Some additional references were also used for euphausiids (Endo and Komaki, 1979 ; Kim et al., 2009), amphipods (Yamada and Ikeda, 2000, 2001a, 2001b, 2004) and chaetognaths (Kitou, 1967). For euphausiid larvae, because of the difficulty in species identification, nauplii were treated as "euphausiid nauplii", and calyptopis were treated as "*Euphausia* spp. calyptopis" or "*Thysanoessa* spp. calyptopis". For cnidarians, because of the difficulty in species identification, *Abylopsis* species were treated as *Abylopsis* sp.

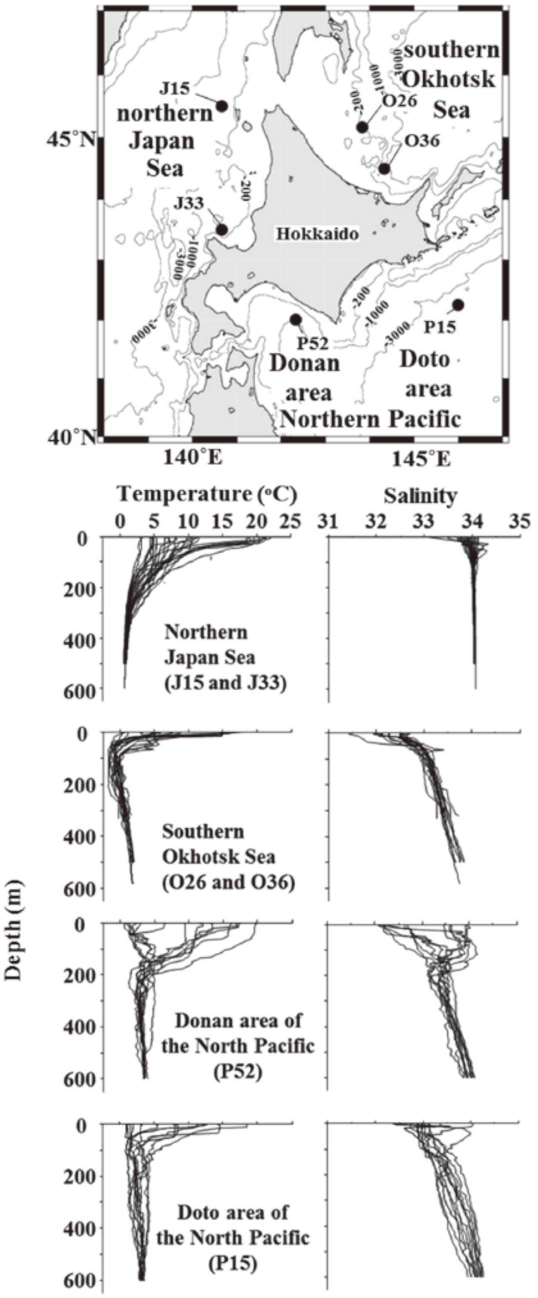

Fig. 1. Sampling stations in four areas around Hokkaido (upper panel). Temperature (left) and salinity (right) profiles for the four areas of this study.

For each macrozooplankton species, the sorted specimens were placed on pre-weighed plankton mesh (100 µm mesh). The specimens were dried with dry filter paper, and their WM was measured with a microbalance (Mettler Ltd, AE-100) with a precision of 0.1 mg. The WM data were divided by the water filter volume (m^3), multiplied by the net-tow depth (500 or 300 m), and expressed as standing stock of the water column (g or mg WM m^{-2} : 0-500 m or 0-300 m). We calculated the biomass of mesozooplankton from total WM by subtracting macrozooplankton WM (mesozooplankton WM = total WM – macrozooplankton WM). We compared inter-oceanic differences in WM using a one-way ANOVA and a Tukey-Kramer post-hoc test in Stat-View (Ver. 5.0).

Results

Hydrography

The water column temperature between 0 m and 500 m (0-300 m at St. O26) ranged from −1°C to 22°C, and the salinity ranged from 31.9 to 34.3 (Fig. 1). The surface layer of the northern Japan Sea (St. J15 and St. J36) varied seasonally (temperature ranged 4.2-22.0°C), but depths below 300 m were stable, cold (0-2°C) and saline (34) throughout the year. These cold deep water masses were considered "Japan Sea Proper Water" and compose the meso- and bathypelagic zones of the Japan Sea (Sudo, 1986). In the south Okhotsk Sea (St. O26 and St. O36), less saline (<32.5) water was observed at the surface layer, and a strong pycnocline was formed at approximately 30 m depth. In the south Okhotsk Sea, there was a sudden temperature decrease to approximately 0°C at 30 m depth, termed the dicothermal layer (Kitani, 1973), and high salinity water dominated below the dicothermal layer throughout the year.

The surface layer of the Doto area of the North Pacific (St. P15) was warm and saline (>13°C, >33.5) during summer and autumn, while the surface layer was cold and fresh (<8°C, <33.1) during winter and spring (Fig. 1). This seasonality in hydrography was caused by the dominance of warm-water masses that separated from Kuroshio water during summer and autumn, and the dominance of ice-melted cold Oyashio water during winter and spring (Kono, 1997). In the Donan area of the North Pacific (St. P15), the surface layer showed clear seasonality. The surface layer was warm and saline (>13°C, >33.5) during summer and autumn, and it was cold and fresh (<7°C, <32.5) during winter and spring. From these T-S data, the water mass during summer and autumn was considered the "Tsugaru Warm Current", and the water mass during winter and spring was the "Coastal Oyashio Water" (Ohtani, 1971).

Whole zooplankton biomass

The whole zooplankton biomass varied between 25 and 315 g WM m^{-2} throughout the study region (Fig. 2). In all regions, the whole zooplankton biomass was high during spring and summer. The whole zooplankton biomass in the southern Okhotsk Sea (Sts. O26 and O36) was significantly higher than the other regions (p<0.05, one-way ANOVA, Tukey-Kramer test). Macrozooplankton commonly composed 5-10% of the whole zooplankton biomass, and, at maximum, composed 15% of the total biomass (Fig. 2).

Macrozooplankton

Throughout the four regions around Hokkaido Island, there were seven euphausiid species belonging to four genera (Table 1). Within these seven species, *Euphausia pacifica*, *Thysanoessa inermis* and *T. longipes* occurred in all four regions. Inter-oceanic differences in biomass were seen in *E. pacifica* and *Euphausia* spp. calyptopis. The biomasses of these species were higher in the southern Okhotsk Sea and the North Pacific and lower in the northern Japan Sea (p<0.05, Table 1). *E. pacifica* was dominant in the Donan and Doto areas of the North Pacific and composed 77-84% of euphausiid biomass in these regions. Concerning *Thysanoessa* spp., *T. raschii* occurred only in the southern Okhotsk Sea, while *T. inspinata* occurred only in the North Pacific regions. The total euphausiid biomass was significantly higher in the southern Okhotsk Sea than in the other regions (p<0.05).

Throughout the four regions around Hokkaido Island, there were thirteen amphipod species belonging to twelve genera (Table 2). There were 2-4 species in the northern Japan Sea and southern Okhotsk Sea, and there were 6-9 species in the Doto and Donan areas of the North Pacific. Only two species, *Themisto japonica* and *Primno abyssalis*, commonly occurred in all four regions. There were significant inter-oceanic differences in *T. japonica* biomass (p<0.0001, one-way ANOVA), with higher biomasses in the northern Japan Sea and southern Okhotsk Sea than in the other regions (p<0.05, Tukey-Kramer test). Both *T. pacifica* and *Cyphocaris challengeri* occurred only in the North Pacific and composed 6.8-29% of the total amphipod biomass in that region. The total amphipod biomass was greatest in the northern Japan Sea and lowest in the North Pacific, especially in the Doto area (p<0.0001, one-way ANOVA).

Throughout the regions, there were six cnidarian species belonging to six genera (Table 3). The North Pacific had the highest number of species. In particular, *Obelia plana* and *Sarsia tubulosa* had high biomasses only in the Donan area of the North Pacific. For cnidarian species, *Aglantha digitale*, *Abylopsis* sp. and Difyidae spp. were the most common species throughout the regions. Interestingly, across all of these species, their biomasses were significantly higher in the northern Japan Sea than the other regions (p<0.05, one-way ANOVA). Consequently, the total cnidarian biomass was significantly higher in the northern Japan Sea than the other regions (p<0.0001, one-way ANOVA).

Throughout the four regions, there were ten chaetognath

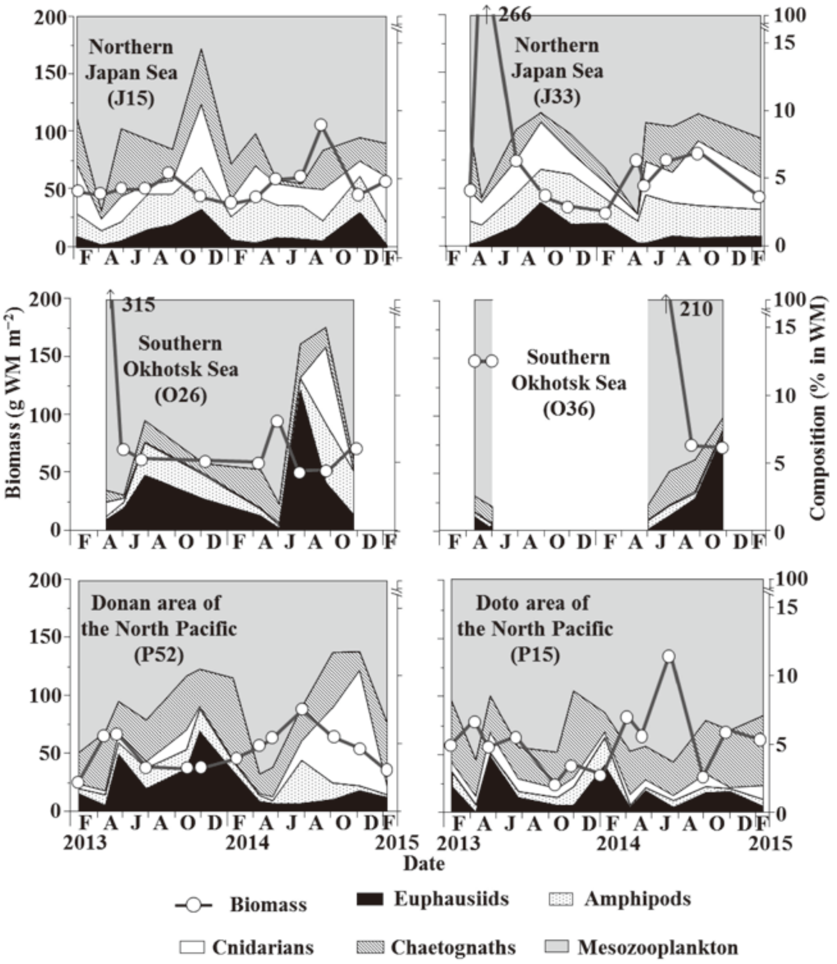

Fig. 2. Seasonal changes in zooplankton biomass (g wet mass [WM] m^{-2}) and composition of macrozooplankton taxa (euphausiids, amphipods, cnidarians and chaetognaths) in four areas around Hokkaido during February 2013 to February 2015. Note the break in the *Y*-axis (composition) approximately 15%.

Table 1. Regional comparison of euphausiid biomass (mg wet mass : WM m^{-2}), species composition in euphausiid biomass (%, numbers in the parentheses) and number of species in the northern Japan Sea (J15, J33), southern Okhotsk Sea (O26, O36), Donan (P52) and Doto (P15) areas of the North Pacific during February 2013 to February 2015. Regional differences were tested by one-way ANOVA and Tukey-Kramer test. －: no occurrence, * : $p<0.05$, ** : $p<0.01$, N.S. : not significant, N.D. : not detectable. For Tukey-Kramer test, any stations not connected by underlines are significantly different ($p<0.05$).

Species	Japan Sea		Okhotsk Sea		Donan	Doto	one-way ANOVA	Tukey-Kramer test
	J15	J33	O26	O36	P52	P15		
Euphausia pacifica	49.0 (9.2)	228.2 (47.3)	897.8 (51.9)	563.2 (25.2)	705.8 (77.4)	535.4 (84.6)	*	J15 J33 P15 O36 P52 O26
Euphausia spp. calyptopis	4.5 (0.8)	10.5 (2.2)	8.9 (0.5)	4.8 (0.2)	37.1 (4.1)	12.0 (1.9)	**	J15 O36 O26 J33 P15 P52
Nemotoscelis difficilis	－	－	－	－	－	6.1 (1.0)	N.S.	N.D.
Tessarabrachion oculatum	－	4.7 (1.0)	－	－	－	10.3 (1.6)	N.S.	
Thysanoessa inermis	4.3 (0.8)	16.9 (3.5)	44.3 (2.6)	33.7 (1.5)	46.7 (5.1)	53.3 (8.4)	N.S.	
Thysanoessa inspinata	－	－	－	－	65.0 (7.1)	9.8 (1.5)	N.S.	
Thysanoessa longipes	448.5 (84.0)	194.3 (40.3)	628.1 (36.3)	630.6 (28.2)	15.8 (1.7)	1.0 (0.2)	*	
Thysanoessa raschii	－	－	150.7 (8.7)	992.8 (44.5)	－	－	N.S.	
Thysanoessa spp. Calyptopis	20.8 (3.9)	20.9 (4.3)	0.6 (0.0)	7.3 (0.3)	23.8 (2.6)	4.1 (0.6)	N.S.	
Euphausiid nauplii	7.0 (1.3)	6.8 (1.4)	0.6 (0.0)	0.5 (0.02)	17.4 (1.9)	0.8 (0.1)	N.S.	
Total euphausiid biomass	534.2	482.4	1,731.0	2,232.9	911.6	632.8	*	N.D.
Number of species	3	4	4	4	4	6		

Table 2. Regional comparison of amphipod biomass (mg wet mass : WM m^{-2}), species composition in amphipod biomass (%, numbers in the parentheses) and number of species in the northern Japan Sea (J15, J33), southern Okhotsk Sea (O26, O36), Donan (P52) and Doto (P15) areas of the North Pacific during February 2013 to February 2015. Regional differences were tested by one-way ANOVA and Tukey-Kramer test. −: no occurrence, *** : $p<0.001$, **** : $p<0.0001$, N.S. : not significant, N.D. : not detectable. For Tukey-Kramer test, any stations not connected by underlines are significantly different ($p<0.05$).

Species	Japan Sea		Okhotsk Sea		Donan	Doto	one-way ANOVA	Tukey-Kramer test
	J15	J33	O26	O36	P52	P15		
Archaeoscina steenstrupi	1.0 (0.03)	−	−	−	−	−	N.S.	
Cyphocaris challengeri	−	−	−	−	328.8 (20.1)	166.3 (29.3)	****	N.D.
Hyperia golba	−	−	−	−	0.8 (0.05)	−	N.S.	
Lanceola serrata	−	−	−	−	−	4.0 (0.7)	N.S.	
Mimonecteola beebei	−	−	−	−	2.4 (0.1)	−	N.S.	
Mimonectes diomedeae	−	−	−	−	0.8 (0.05)	−	N.S.	
Platyscels serratulus	−	−	−	−	2.2 (0.1)	−	N.S.	
Parascelus typhoides	−	4.1 (0.08)	−	−	−	−	N.S.	
Primno abyssalis	88.3 (3.0)	574.0 (11.1)	4.6 (0.1)	73.6 (3.6)	373.2 (22.8)	16.2 (2.8)	N.S.	
Scina borealis	−	−	−	4.4 (0.2)	0.5 (0.03)	5.4 (1.0)	***	P52 O36 P15
Themisto pacifica	−	−	−	−	111.7 (6.8)	137.8 (24.2)	N.S.	
Themisto japonica	2,843.7 (96.8)	4,599.9 (88.8)	3,400.0 (99.9)	1,961.9 (96.2)	813.4 (49.8)	238.7 (42.0)	****	P15 P52 O36 J15 O26 J33
Vibilia australis	3.4 (0.1)	3.4 (0.07)	−	−	−	−	N.S.	
Total amphipod biomass	2,936.4	5,181.4	3,404.6	2,039.9	1,633.8	568.4	****	P15 P52 O36 J15 O26 J33
Number of species	3.44	4	2	3	9	6		

Table 3. Regional comparison of cnidarian biomass (mg wet mass : WM m^{-2}), species composition in cnidarian biomass (%, numbers in the parentheses) and number of species in the northern Japan Sea (J15, J33), southern Okhotsk Sea (O26, O36), Donan (P52) and Doto (P15) areas of the North Pacific during February 2013 to February 2015. Regional differences were tested by one-way ANOVA and Tukey-Kramer test. −: no occurrence, * : $p<0.05$, ** : $p<0.001$, **** : $p<0.0001$, N.S. : not significant, N.D. : not detectable. For Tukey-Kramer test, any stations not connected by underlines are significantly different ($p<0.05$).

Species	Japan Sea		Okhotsk Sea		Donan	Doto	one-way ANOVA	Tukey-Kramer test
	J15	J33	O26	O36	P52	P15		
Abylopsis sp.	62.1 (6.1)	61.2 (6.3)	19.3 (6.2)	43.1 (56.5)	38.5 (7.6)	27.7 (10.2)	*	O26 P15 P52 O36 J33 J15
Aglantha digitale	501.3 (49.6)	596.5 (61.6)	280.8 (90.4)	16.8 (22.0)	233.8 (46.0)	149.3 (55.2)	**	O36 P15 P52 O26 J15 J33
Eutonina indicans	−	−	−	−	−	2.5 (0.9)	N.S.	
Liriope tetraphylla	−	−	−	−	−	1.6 (0.6)	N.S.	
Obelia plana	−	−	−	−	75.6 (14.9)	−	N.S.	
Sarsia tubulosa	−	−	−	−	95.2 (18.7)	7.2 (2.7)	N.S.	
Anthomedusae spp.	−	−	−	−	−	10.5 (3.9)	N.S.	
Difyidae spp.	447.3 (44.3)	311.1 (32.1)	10.6 (3.4)	16.4 (21.5)	65.1 (12.8)	71.9 (26.6)	****	O26 O36 P52 P15 J33 J15
Total cnidarian biomass	1,010.7	968.8	310.7	76.3	508.2	270.7	****	O36 P15 O26 P52 J33 J15
Number of species	3	3	3	3	5	7		

species belonging to nine genera (Table 4). There were 2–3 species in the southern Okhotsk Sea, 5 species in the northern Japan Sea and 8–9 species in the Donan and Doto areas of the North Pacific. *Parasagitta elegans* was the only chaetognath species that occurred in all four regions, and its biomass was significantly higher in the northern Japan Sea ($p<0.01$, one-way ANOVA). *Eukrohnia hamata* composed a high proportion of the biomass (37–75%) in the southern Okhotsk Sea and Donan and Doto areas of the North Pacific, but it did not occur in the northern Japan Sea.

Discussion

Sampling methodology

When sampling macrozooplankton, underestimating biomass due to net avoidance should be considered. For macrozooplankton taxa, large net avoidances were reported especially for euphausiids and amphipods (Laval, 1974 ; Hovekamp, 1989 ; Ianson, 2004). To reduce the effect of net avoidance, sampling with an oblique tow of a large-sized mouth net (e.g., Bongo net and MOCNESS) is sufficient (Sameoto et al., 2000). Because a NORPAC net was vertically towed in this study, the biomass values of euphausiids and amphipods may be underestimated.

Table 4. Regional comparison of chaetognath biomass (mg wet mass : WM m^{-2}), species composition in chaetognath biomass (%, numbers in the parentheses) and number of species in the northern Japan Sea (J15, J33), southern Okhotsk Sea (O26, O36), Donan (P52) and Doto (P15) areas of the North Pacific during February 2013 to February 2015. Regional differences were tested by one-way ANOVA and Tukey-Kramer test. －: no occurrence, ** : $p<0.001$, **** : $p<0.0001$, N.S. : not significant, N.D. : not detectable. For Tukey-Kramer test, any stations not connected by underlines are significantly different ($p<0.05$).

Species	Japan Sea		Okhotsk Sea		Donan	Doto	one-way ANOVA	Tukey-Kramer test					
	J15	J33	O26	O36	P52	P15							
Aidanosagitta reguralis	0.3 (0.0)	0.6 (0.0)	–	–	8.0 (0.6)	0.4 (0.02)	N.S.						
Eukrohnia hamata	–	–	352.8 (39.1)	1,348.2 (75.6)	627.4 (47.3)	1,173.4 (58.1)	****			O26	P52	P15	O36
Flaccisagitta enflata	3.7 (0.3)	3.9 (0.3)	–	–	46.2 (3.5)	3.4 (0.2)	N.S.						
Mesosagitta minima	2.4 (0.2)	22.7 (1.7)	–	4.7 (0.3)	42.2 (3.2)	7.9 (0.4)	N.S.						
Parasagitta elegans	1,193.3 (95.8)	1,228.3 (93.6)	549.2 (60.9)	425.5 (23.9)	417.7 (31.5)	585.0 (29.0)	**	P52	O36	O26	P15	J15	J33
Pseudosagitta lyra	–	–	–	–	9.1 (0.7)	–	N.S.						
Pseudosagitta scrippsae	–	–	–	–	64.7 (4.9)	53.5 (2.7)	N.S.						
Sagitta bipunctata	–	–	–	–	–	0.1 (0.005)	N.S.						
Spadella cephaloptera	–	0.9 (0.07)	–	–	0.9 (0.07)	–	N.S.						
Zonosagitta nagae	45.9 (3.6)	56.2 (4.3)	–	5.6 (0.3)	110.8 (8.3)	194.6 (9.6)	N.S.						
Total chaetognath biomass	1,245.6	1,312.6	902.0	1,784.0	1,327.0	2,018.3	N.S.						
Number of species	5	5	2	3	9	8							

Annual mean biomasses were reported for euphausiids (Kim et al., 2009) and amphipods (Yamada and Ikeda, 2006) based on year-round samplings in the Oyashio region. Based on an oblique tow of a Bongo net between 0-1,000 m, the annual mean biomass of *E. pacifica*, *T. inspinata* and *T. longipes* was 12,220 mg WM m^{-2} (Kim et al., 2009). This value is 20 times higher than the value at St. P15 in the Doto area of the North Pacific (633 mg WM m^{-2}, Table 1). Based on an oblique tow of a Bongo net between 0-500 m, the annual mean biomass of the four dominant amphipod species (*T. japonica*, *T. pacifica*, *P. abyssalis* and *C. challengeri*) was 118 mg WM m^{-2} (Yamada and Ikeda, 2006). This value is two times higher than the value at St. P15 in the Doto area of the North Pacific (559 mg WM m^{-2}, Table 2). Thus, the biomasses of both amphipods and euphausiids in this study were less than the reported values based on an oblique tow of a Bongo net. The greater differences in euphausiids (20 times) compared to amphipods (2 times) may be due to the deeper samplings for euphausiids (0-1,000 m, Kim et al., 2009) than those for amphipods (0-500 m, Yamada and Ikeda, 2006).

Because this study collected samples by vertical hauls of a NORPAC net, the biomass values reported in this study were somewhat underestimated. However, because the sampling methods were consistent throughout the four regions, inter-oceanic comparisons in macrozooplankton biomass is still possible if we assume that the effect of net avoidance is similar for all regions.

Macrozooplankton taxa

For all macrozooplankton taxa, the inter-oceanic variation in species numbers was remarkable. The number of species varied with region : the fewest species (2-4 species) were found in the southern Okhotsk Sea, followed by the northern Japan Sea (3-5 species), and the most species (4-9 species) were in the Donan and Doto areas of the North Pacific (Fig. 3). For various pelagic taxa, the number of species was lower in the Japan Sea than the adjacent North Pacific (Zenkevitch, 1963). For calanoid copepods, 95 species occurred in the Japan Sea, while 390 species occurred in the North Pacific (Morioka, 1980). For euphausiids, 10 species occurred in the Japan Sea, while 28 species occurred in the North Pacific (Endo and Komaki, 1979). For amphipods, two species occurred in the Japan Sea, while 26 species occurred in the North Pacific (Irie, 1959). For chaetognaths,

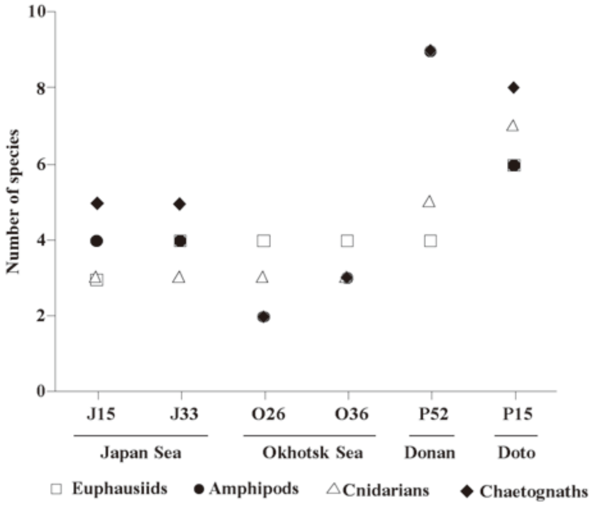

Fig. 3. Regional comparison of the number of species of macrozooplankton taxa : euphausiids, amphipods, cnidarians and chaetognaths in the northern Japan Sea (J15 and J33), southern Okhotsk Sea (O26 and O36), and Donan (P52) and Doto (P15) areas of the North Pacific during February 2013 to February 2015.

17 species occurred in the Japan Sea, while 21 species occurred in the North Pacific (Kitou, 1974). The most prominent taxon was decapods, with 75 species occurring in the North Pacific and no species occurring in the Japan Sea (Hayashi, 1991). For micronektonic fishes, 75 species occurred in the western North Pacific, while only one Gonostomatoid, *Maurolicus japonicas*, occurred in the Japan Sea (Okiyama, 1971 ; Kawaguchi, 1974). In the present study, the species composition of macrozooplankton taxa showed substantial inter-oceanic differences, as mentioned above. Following, we discuss inter-oceanic characteristics of each taxon.

Euphausiids were dominated by *E. pacifica* throughout the four regions (Table 1). Based on year-round observations in the Oyashio region, *E. pacifica* occurs across a broad thermal range (2-16˚C) (Kim et al., 2009). The eurythermal distribution of *E. pacifica* may explain the dominance of this species throughout all four regions around Hokkaido Island. When the surface water temperature exceeds the thermal limit of *E. pacifica* (16˚C), it is known to stay in the cold deep-layer during the day and night and cease feeding and growth (Iguchi et al., 1993). *T. raschii* and *T. longipes* had the highest biomasses in the southern Okhotsk Sea (Table 1). In the western North Pacific, *T. raschii* and *T. longipes* are reported to be "arctic boreal" and "subarctic," respectively (Sogawa et al., 2013). In the Oyashio region, the thermal range of *T. longipes* was reported to be 0.3-5.1˚C, which is much lower than that of *E. pacifica* (2-16˚C) (Kim et al., 2009). The southern Okhotsk Sea was characterized by a cold dicothermal layer (Kitani, 1973 ; Fig. 1), which can explain the dominance of two boreal *Thysanoessa* species, *T. raschii* and *T. longipes*, in this region.

The amphipod communities were dominated by *T. japonica* throughout the regions (Table 2). *T. japonica* predominated (composing 89-99% of the total amphipod biomass) in the northern Japan Sea and southern Okhotsk Sea. However, in the North Pacific (the Doto and Donan areas), the proportion of *T. japonica* decreased (42-50% of biomass) because of the substantial biomass of *T. pacifica*, *P. abyssalis* and *C. challenger* (Table 2). Due to the low number of species in the Japan Sea, the ecologies of *T. japonica* and *P. abyssalis* in this sea are different than in the adjacent North Pacific (Yamada et al., 2002, 2004). Compared to the North Pacific populations, the Japan Sea populations exhibit higher abundance and biomass, faster growth, and later maturation (Yamada et al., 2002, 2004). The higher biomass of *T. japonica* in the northern Japan Sea than in the North Pacific is confirmed in this study (Table 2). Faster growth and later maturation in the Japan Sea are considered to be related to lower predation pressure by pelagic decapods and micronektonic fishes, and lower competition between amphipods (Yamada et al., 2002). Interestingly, two dominant species in the North Pacific, *C. challengeri* (20-29%) and *T. pacifica* (7-24%), were not observed in the southern Okhotsk Sea (Table 2). Inter-oceanic differences in pelagic fauna between the Japan Sea and the North Pacific have been explained by the shallow strait depths (maximum in 140 m) connecting to the North Pacific (Nishimura, 1969). The straits connecting the Okhotsk Sea and the North Pacific are much deeper (2,200 m), and faunal differences between the Okhotsk Sea and the North Pacific could not be explained by depth topography. The two dominant species in the North Pacific (*C. challengeri* and *T. pacifica*) were absent in the southern Okhotsk Sea. Their absence may be due to the cold dicothermal layer or ice cover during winter, but detailed mechanisms remain unknown.

For cnidarians, *A. digitale* was dominant throughout the regions (22-90% of cnidarian biomass, Table 3). The biomass of *A. digitale* was significantly higher in the northern Japan Sea than other regions ($p<0.01$, Table 3), which corresponds with previous studies. The previously reported biomass of *A. digitale* was 225 mg DM m^{-2} in the Japan Sea (Ikeda and Imamura, 1996) and 186 mg DM m^{-2} in the Oyashio region (Takahashi and Ikeda, 2006). In addition to *A. digitale*, diphyid cnidarians (Siphonophorae) were dominant throughout the regions (*Abylopsis* sp. : 6.1-56.5% ; Diphyidae spp. : 3.4-44.3%) (Table 3). These findings suggest that the less studied siphonophores may have an important role in marine ecosystems around Hokkaido Island, and future studies on the ecology of siphonophores is needed. The significantly high biomass of both *A. digitale* and siphonophores in the northern Japan Sea may be related to the poor micronektonic fauna there, which implies low predation pressure on cnidarians in this region.

Two chaetognaths, *E. hamata* and *P. elegans*, were the dominant species and composed more than 80% of the total biomass in the Donan and Doto areas of the North Pacific and the southern Okhotsk Sea (Table 4). In the northern Japan Sea, *P. elegans* predominated, composing 93-95% of the total biomass (Table 4). *P. elegans* is an epipelagic species in the North Pacific. Because of the lack of deep-water competitors (*E. hamata* and *E. bathypelagica*) in the Japan Sea, *P. elegans* has several ecological adaptations. This species extends its vertical distribution down to mesopelagic depths, and it exhibits morphological changes characteristic of deep-sea species, including elongated teeth and lipid storage in its body (Terazaki, 1993). The cold southern Okhotsk Sea had the fewest chaetognath species because of a lack of warm-water species (Table 4). In the Doto and Donan areas, the occurrence of warm-water species led to high chaetognath diversity in these regions.

Inter-oceanic comparison in marine ecosystem structure

The feeding modes of the four macrozooplankton taxa varied. Euphausiids are herbivores (Brinton, 1962), and the other taxa (amphipods, cnidarians and chaetognaths) are carnivores (Feigenbaum, 1991 ; Purcell, 1991 ; Yamada and Ikeda, 2006). The remaining mesozooplankton biomasses were dominated by calanoid copepods, which mainly consisted of herbivores (Mauchline, 1998). Inter-oceanic differences in the mass-balance of these taxa indicate differences in energy flow within the lower marine trophic levels. Based on the means of two years of sampling, inter-oceanic differences in marine ecosystem structure are described below for four regions around Hokkaido Island (Fig. 4).

In the northern Japan Sea, carnivorous amphipods, cnidarians and chaetognaths were dominant, while herbivorous euphausiids and mesozooplankton were less common (Fig. 4). As mentioned above, because of the topography, the abundance and biomass of micronektonic species are low in the Japan Sea (Okiyama, 1971 ; Ikeda, 1992 ; Davydova et al., 2006). The reduced predation pressure of micronekton on macrozooplankton may lead to a high biomass of carnivorous macrozooplankton. The dominance of carnivorous macrozooplankton may produce high predation pressure on herbivorous mesozooplankton and euphausiids. Thus, such top-down control may reduce herbivore biomass in the northern Japan Sea.

In the southern Okhotsk Sea, the biomass of carnivorous macrozooplankton taxa was low compared to the northern Japan Sea, but the biomasses of herbivorous mesozooplankton and euphausiids were extremely high (Fig. 4). The mass-balances within these lower trophic levels may indicate the dominance of bottom-up control (predominance of herbivores) in the southern Okhotsk Sea. There were seven species belonging to four genera of fish micronekton, which are predators of macrozooplankton, in the Japan Sea and 35 species belonging to 17 genera in the Okhotsk Sea (Davydova et al., 2006). Because of the high predation pressure of micronekton, the biomass of carnivorous macrozooplankton taxa may be low in the southern Okhotsk Sea. The reduced predation pressure of carnivorous macrozooplankton may lead to a dominance of herbivorous mesozooplankton and euphausiids in the southern Okhotsk Sea. For euphausiids, the year-round presence of a cold dicothermal layer (Fig. 1) may explain the dominance of boreal *T. longipes* and *T. raschii*. Together with the eurythermal *E. pacifica*, the dominance of these cold-water *Thysanoessa* spp. leads to high euphausiid biomass in the southern Okhotsk Sea.

As is characteristic of the marine ecosystem in the Doto area of the North Pacific, the biomass of chaetognaths was high compared to other macrozooplankton taxa (Fig. 4). In addition to the common dominant chaetognath species (*E. hamata* and *P. elegans*), the occurrence of warm-water species (*Pseudosagitta lyra* and *M. minima*) and large *P. scrippsae* may explain the high chaetognath biomass in the Doto area (Table 4).

Compared with the Doto area, the zooplankton community

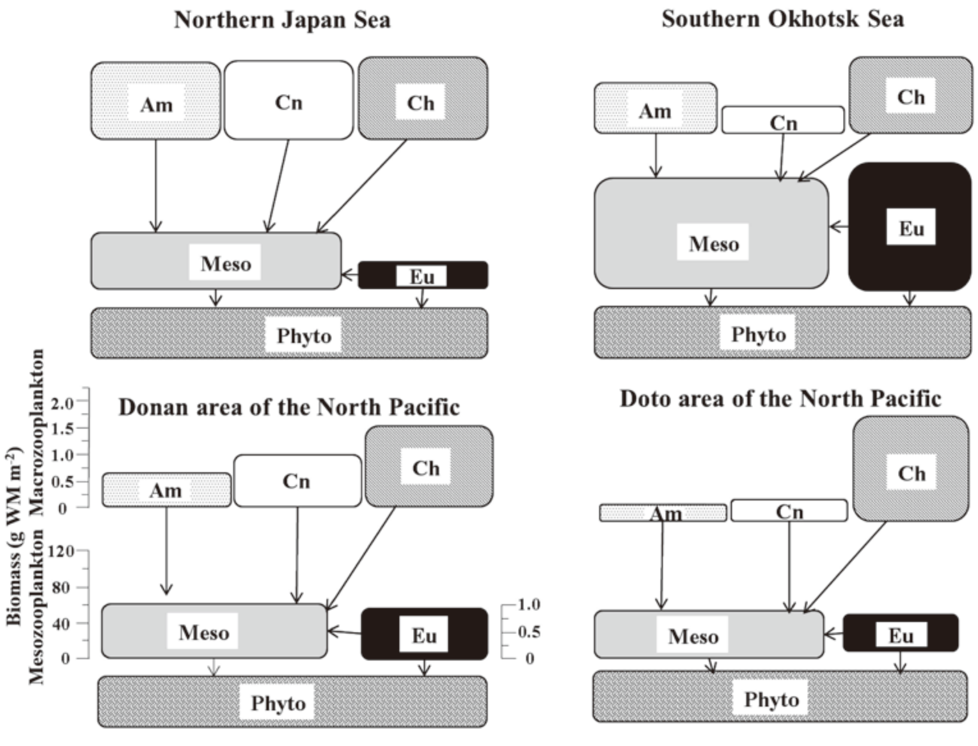

Fig. 4. Diagram showing the biomasses of zooplankton (wet mass : WM), mesozooplankton (Meso), macrozooplankton taxa : euphausiids (Eu), amphipods (Am), cnidarians (Cn) and chaetognaths (Ch) in the northern Japan Sea, southern Okhotsk Sea, and Donan and Doto areas of the North Pacific during February 2013 to February 2015. The values are annual means in each region. The box heights indicate biomass values. Note that the scales are varied between the mesozooplankton and macrozooplankton taxa.

in the Donan area was characterized by relatively high biomasses of amphipods and cnidarians (Fig. 4). The Donan area experiences marked seasonal intrusions of Coastal Oyashio Water from the Doto area and the Tsugaru Warm Current from the northern Japan Sea (Ohtani, 1971). These two water masses were observed in this study (Fig. 1). The zooplankton community in the northern Japan Sea, from which the Tsugaru Warm Current originates, is characterized by the dominance of amphipods and cnidarians (Fig. 4). The seasonal intrusion of these two different water masses may explain why the zooplankton community structure in the Donan area has mixed characteristics of the Doto area and the northern Japan Sea.

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