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Citation	Zoological Studies, 56, 13 https://doi.org/10.6620/ZS.2017.56-13
Issue Date	2017-04-28
Doc URL	http://hdl.handle.net/2115/73467
Type	article
File Information	NakamuraA-2017.pdf

Zoological Studies

Length-weight Relationships and Chemical Composition of the Dominant Mesozooplankton Taxa/species in the Subarctic Pacific, with Special Reference to the Effect of Lipid Accumulation in Copepoda

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Asami Nakamura, Kohei Matsuno, Yoshiyuki Abe, Hiroshi Shimada, and Atsushi Yamaguchi (2017)
While length-weight (L-W) regressions for warm-water zooplankton taxa from the waters neighbouring Japan already exist, they are still missing for comparable cold-water species. In this study, the L-W regressions of 41 species belonging to 12 taxa that are dominant in the Oyashio region were reported. The body length and volume of zooplankton were measured with an image-analysis system, and the effects of lipid accumulation in Copepoda on their mass and chemical composition were quantified. The L-W regressions had a high coefficient of determination (mean r^2 = 0.886). For the chemical composition, the water composition ranged from 69.8 to 95.2% wet mass (WM), carbon (C) composition from 3.8 to 60.8% dry mass (DM) and nitrogen (N) composition from 1.0 to 10.1% DM. Taxon-specific differences in the chemical composition were marked for the gelatinous taxa (Appendicularia, Cnidaria, Salpida), which also had high water and low C composition. Because C is an index of lipids, high water compositions together with low lipid compositions are considered to be characteristics of the gelatinous taxa. The most significant effects of lipid accumulation in the Copepoda are changes in DM and C. Within the same developmental stage, the DM and C compositions of the full lipid-containing specimens showed 495% and 741% increases, respectively, over those of the low lipid-containing specimens. These differences exceeded the changes after moulting (78.1%) for general copepod species. Thus, lipid accumulation should be evaluated for the accurate mass estimation of boreal Copepoda by image analysis.

Key words: Mass, L-W equation, Zooplankton, C/N, Lipids, Oil sac volume, Image analysis.

BACKGROUND

In the marine ecosystem, mesozooplankton play an important role as a vital link connecting primary producers and higher trophic levels (Hunt et al. 1998; Beamish et al. 1999; Ikeda et al. 2008). The feeding preference of fishes is affected by the size of mesozooplankton (Sheldon et al. 1977), and the energy cost, growth and mortality of fishes also vary with the size of mesozooplankton (van der Meeren and Næss 1993). These facts indicate that information about mesozooplankton's size and biomass are of prime importance when evaluating energy transfer in marine ecosystems. On the other hand, mesozooplankton play an important role in the vertical material flux down to the deep layer. Mesozooplankton feed on phytoplankton, egest fast-sinking faecal pellets, and actively

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transport materials by the diel vertical migration (DVM), thus they have central role in the "biological pump" (Longhurst and Harrison 1989). Because the flux of the faecal pellets egested during DVM is correlated with mesozooplankton's size and biomass (Paffenhöfer and Knowles 1979; Uye and Kaname 1994), an accurate estimation of the biomass and size of mesozooplankton is also of primary importance from the perspective of the biological pump.

The chemical composition of mesozooplankton varies by taxon. For instance, the Cnidaria, Appendicularia, and Salpida are known to have high water and lower organic compositions and are called "gelatinous taxa" (Larson 1986; Gorsky et al. 1988; Molina-Ramírez et al. 2015). The chemical composition is also known to vary with region and depth (*e.g.*, geographically and vertically). For instance, the organic composition and lipid levels are higher for high-latitude species (Lee et al. 1971; Båmstedt 1986), while higher carbon and low nitrogen compositions are reported for deep-sea species (Ikeda et al. 2006). Chemical composition differences may also affect length-weight (L-W) relationships, and these relationships also vary widely by taxon and region (Uye 1982; Mizdalski 1988; Hirst 2012). Concerning the waters around Japan, information on the L-W relationships and chemical compositions of mesozooplankton is available for the warm-water regions (Uye 1982); however, little information is available for the cold-water (Oyashio) region.

In the Oyashio region, large amounts of nutrients are provided at the surface layer by strong wintertime mixing; phytoplankton form massive diatom blooms during the spring (Kasai et al. 1997). The mesozooplankton in this region is dominated by Copepoda, which utilize the spring phytoplankton bloom as energy for their growth and reproduction (Miller et al. 1984). For instance, the dominant copepods in this region, *Neocalanus* spp., achieve growth at the surface layer during the spring bloom, store lipids, and then migrate down to the deep layers for diapause and reproduction (Kobari and Ikeda 1999; Tsuda et al. 1999), during which the stored lipids are used for energy (Lee et al. 1970; Miller et al. 1998; Jónasdóttir 1999). Thus, the C/N ratio of copepods is known to vary seasonally and to be correlated with the amount of the lipid store (Omori 1969). While the importance of their lipid store is known, information on the effects of the lipid store of Copepoda on their L-W relationship and chemical compositions is scarce.

In this study we report the L-W relationships

of various taxa (41 species belonging to 12 taxa) that are dominant in the mesozooplankton community in the Oyashio region. For the chemical composition, the water, carbon and nitrogen compositions were quantified and the differences were evaluated by separating gelatinous and semi-gelatinous taxa (Larson, 1986). For the Copepoda, the amount of stored lipid was quantified using image-analysis methods (Shimada and Oku 2014). Based on the amounts of stored lipids, the body volume, mass and chemical compositions of the Copepoda were compared and the effects of the lipid stores were evaluated for each parameter.

MATERIALS AND METHODS

Present study is a compilation of published and unpublished studies, some of which has been submitted as theses project of Hokkaido University.

Field sampling

Specimens of 41 species belonging to 12 taxa used for the L-W relationship estimation were mainly collected between the sea surface and a depth of 3000 m in the Oyashio region in the western subarctic Pacific Ocean and the adjacent northern Japan Sea (Table 1).

Zooplankton samples were collected at four stations (41°N, 145°E; 43°N, 155°E; 40°N, 155°E; 37°N, and 148°E) by vertical tows of a NORPAC net (45 cm mouth diameter, 335 μm mesh) at depths of 150 m or 500 m to the sea surface between 8 and 19 May 2015. The freshly collected samples were taken according to the procedures discussed below. Additional samples were collected by a 0-300 m vertical tow of a NORPAC net at St. O26 (45°N, 143°E) in the southern Okhotsk Sea on 5 June 2015.

Samples for analysing the effect of the lipid stores of copepods were collected for five species: *Eucalanus bungii* copepodid stage six female (C6F), *Metridia okhotensis* C5M, C6F, *Neocalanus cristatus* C5, *N. flemingeri* C5 and C6F, and *N. plumchrus* C5. The specimens were sorted into three categories of lipid storage amounts (low, medium, and full) as defined by the following references: Shoden et al. (2005) for *E. bungii*, Padmavati et al. (2004) for *M. okhotensis* and Ikeda et al. (1990) for *Neocalanus* spp.

Table 1. Summary on mass-length regressions for various zooplankton taxa/species which dominated in the western subarctic Pacific and their adjacent seas. Note that length units are μm for meso-size taxa (Ostracoda, Copepoda and Appendicularia) and mm for the remaining macro-size taxa. For masses, units are in μg for all taxa. WM: wet mass, DM: dry mass, C: carbon, N: nitrogen, BH: bell height, TL: total length, SL: standard length, PL: prosome length, BL: body length, L: length, TrL: trunk length. Detailed diagrams of measured parts are shown in figures 1 and 2

Taxa	Species (taxonomic category)	Regression	Unit Mass	Length	r^2	n	p	References
Cnidaria	*Aglantha digitale*	$Log_{10}DM = 1.125(Log_{10}BH)^2 + 1.268Log_{10}BH+0.667$	DM (μg)	BH (mm)	0.976	72		Ikeda and Imamura (1996)
	Other Cnidaria spp.	$Log_{10}DM = 2.94Log_{10}TL+0.82$	DM (μg)	TL (mm)	0.620	35		Imao (2005)
Annelida	Annelida spp.	$Log_{10}DM = 1.53Log_{10}TL+1.49$	DM (μg)	TL (mm)	0.810	43		Imao (2005)
Ostracoda	*Discoconchoecia pseudodiscophora*	$Log_{10}DM = 2.61Log_{10}SL-7.751$	DM (μg)	SL (μm)	0.992	8		Kaeriyama and Ikeda (2002)
	Metaconchoecia skogsbergi	$Log_{10}DM = 2.42Log_{10}SL-7.143$	DM (μg)	SL (μm)	0.996	7		Kaeriyama and Ikeda (2002)
	Orthoconchoecia haddoni	$Log_{10}DM = 2.53Log_{10}SL-7.511$	DM (μg)	SL (μm)	0.996	8		Kaeriyama and Ikeda (2002)
Copepoda	*Calanus pacificus* (C1-C5)	$Log_{10}DM = 1.871Log_{10}PL-4.309$	DM (μg)	PL (μm)	0.783	21	< 0.001	Ueda et al. (2008)
		$Log_{10}C = 3.573Log_{10}PL-11.008$	C (μg)	PL (μm)	0.857	20	< 0.001	Ueda et al. (2008)
		$Log_{10}N = 2.382Log_{10}PL-7.788$	N (μg)	PL (μm)	0.625	13	< 0.01	Ueda et al. (2008)
	Eucalanus bungii (C1-C5)	$Log_{10}DM = 2.052Log_{10}PL-5.408$	DM (μg)	PL (μm)	0.771	93	< 0.001	Ueda et al. (2008)
		$Log_{10}C = 2.828Log_{10}PL-8.97$	C (μg)	PL (μm)	0.879	92	< 0.001	Ueda et al. (2008)
		$Log_{10}N = 2.727Log_{10}PL-9.63$	N (μg)	PL (μm)	0.788	53	< 0.001	Ueda et al. (2008)
	Gaetanus variabilis (C1-C6)	$Log_{10}DM = 3.169Log_{10}PL-8.317$	DM (μg)	PL (μm)	0.982	34		Yamaguchi and Ikeda (2000a)
	Heterorhabdus tanneri (C3-C6)	$Log_{10}DM = 3.530Log_{10}PL-9.579$	DM (μg)	PL (μm)	0.998	20		Yamaguchi and Ikeda (2000b)
	Metridia pacifica (C1-C5)	$Log_{10}DM = 1.405Log_{10}PL-2.865$	DM (μg)	PL (μm)	0.689	45	< 0.001	Ueda et al. (2008)
		$Log_{10}C = 2.967Log_{10}PL-9.113$	C (μg)	PL (μm)	0.924	44	< 0.001	Ueda et al. (2008)
		$Log_{10}N = 2.902Log_{10}PL-9.209$	N (μg)	PL (μm)	0.940	45	< 0.001	Ueda et al. (2008)
	Neocalanus cristatus (C1-C5)	$Log_{10}DM = 2.418Log_{10}PL-6.242$	DM (μg)	PL (μm)	0.890	67	< 0.001	Ueda et al. (2008)
		$Log_{10}C = 2.964Log_{10}PL-8.931$	C (μg)	PL (μm)	0.900	67	< 0.001	Ueda et al. (2008)
		$Log_{10}N = 3.115Log_{10}PL-10.288$	N (μg)	PL (μm)	0.893	62	< 0.001	Ueda et al. (2008)
	Neocalanus flemingeri (C4-C5)	$Log_{10}DM = 4.954Log_{10}PL-15.005$	DM (μg)	PL (μm)	0.669	15	< 0.001	Ueda et al. (2008)
		$Log_{10}C = 6.395Log_{10}PL-20.449$	C (μg)	PL (μm)	0.681	14	< 0.001	Ueda et al. (2008)
		$Log_{10}N = 4.905Log_{10}PL-16.345$	N (μg)	PL (μm)	0.306	14		Ueda et al. (2008)
	Neocalanus plumchrus (C1-C5)	$Log_{10}DM = 2.044Log_{10}PL-4.881$	DM (μg)	PL (μm)	0.933	49	< 0.001	Ueda et al. (2008)
		$Log_{10}C = 3.237Log_{10}PL-9.794$	C (μg)	PL (μm)	0.957	49	< 0.001	Ueda et al. (2008)
		$Log_{10}N = 2.235Log_{10}PL-7.043$	N (μg)	PL (μm)	0.874	49	< 0.001	Ueda et al. (2008)
	Paraeuchaeta birostrata (Egg-C6)	$Log_{10}DM = 2.882Log_{10}PL-7.252$	DM (μg)	PL (μm)	0.991	358		Yamaguchi and Ikeda (2002)
	Paraeuchaeta elongata (Egg-C6)	$Log_{10}DM = 3.167Log_{10}PL-8.358$	DM (μg)	PL (μm)	0.975	359		Yamaguchi and Ikeda (2002)
	Paraeuchaeta rubra (Egg-C6)	$Log_{10}DM = 2.854Log_{10}PL-7.1102$	DM (μg)	PL (μm)	0.984	172		Yamaguchi and Ikeda (2002)
	Pleuromamma scutullata (C1-C6)	$Log_{10}DM = 2.723Log_{10}PL-6.892$	DM (μg)	PL (μm)	0.995	28		Yamaguchi and Ikeda (2000b)
	Pseudocalanus newmani (N2-N6)	$Log_{10}DM = 2.515Log_{10}TL-6.57$	DM (μg)	TL (μm)	0.951	5		Lee et al. (2003)
	Pseudocalanus newmani (C1-C5)	$Log_{10}DM = 2.08Log_{10}TL-5.456$	DM (μg)	TL (μm)	0.988	9		Lee et al. (2003)
	Scolecithricella minor (C2-C6)	$Log_{10}DM = 3.669Log_{10}PL-9.739$	DM (μg)	PL (μm)	0.989	22		Yamaguchi (1999)
	Cyclopoid Copepoda (3 species, C1-C6)	$Log_{10}DM = 1.997Log_{10}PL-5.3245$	DM (μg)	PL (μm)	0.755	56		Kaneko (2005)
	Poecilostomatoid Copepoda (12 species, C5-C6)	$Log_{10}DM = 2.875Log_{10}PL-7.458$	DM (μg)	PL (μm)	0.976	24	< 0.0001	Nishibe (2005)
	Other Copepoda spp.	$Log_{10}DM = 2.62Log_{10}TL-6.40$	DM (μg)	TL (μm)	0.670	242		Imao (2005)
Mysidacea	*Meterythrops microphtalma*	$Log_{10}DM = 3.10Log_{10}BL+0.26$	DM (μg)	BL (mm)	0.987	46		Ikeda (1992)
Amphipoda	*Cyphocaris challengeri*	$Log_{10}DM = 2.83Log_{10}BL+0.69$	DM (μg)	BL (mm)	0.992	17	< 0.0001	Yamada (2002)
	Primno abyssalis	$Log_{10}DM = 2.71Log_{10}BL+0.76$	DM (μg)	BL (mm)	0.992	22	< 0.0001	Yamada et al. (2002)
	Themisto japonica	$Log_{10}DM = 2.12Log_{10}BL+1.11$	DM (μg)	BL (mm)	0.912	30	< 0.0001	Yamada (2002)
	Themisto pacifica	$Log_{10}DM = 2.72Log_{10}BL+0.690$	DM (μg)	BL (mm)	0.992	21	< 0.0001	Yamada (2002)
Euphausiacea	*Euphausia pacifica* (Furcilia-Adult)	$Log_{10}WM = 3.130Log_{10}BL+0.914$	WM (μg)	BL (mm)	0.990	67	< 0.01	Kim (2009)
	Thysanoessa inspinata (Furcilia-Adult)	$Log_{10}WM = 3.190Log_{10}BL+1.041$	WM (μg)	BL (mm)	0.988	53	< 0.01	Kim (2009)
	Thysanoessa longipes (Furcilia-Adult)	$Log_{10}WM = 3.263Log_{10}BL+0.929$	WM (μg)	BL (mm)	0.992	55	< 0.01	Kim (2009)
Chaetognatha	*Eukrohnia fowleri*	$Log_{10}DM = 3.32Log_{10}TL-1.14$	DM (μg)	TL (mm)	0.950	85		Imao (2005)
	Sagitta elegans	$Log_{10}DM = 2.91Log_{10}TL-0.79$	DM (μg)	TL (mm)	0.970	54		Imao (2005)
	Other Chaetognatha spp.	$Log_{10}DM = 2.80Log_{10}TL-0.6$	DM (μg)	TL (mm)	0.900	96		Imao (2005)
Doliolida	*Dolioletta toritonis* (nurse)	$Log_{10}WM = 2.16Log_{10}L+1.56$	WM (μg)	L (mm)	0.915	20		Aono (1999)
	Dolioletta toritonis (phorozooid)	$Log_{10}WM = 2.24Log_{10}L+1.77$	WM (μg)	L (mm)	0.895	7		Aono (1999)
	Dolioletta toritonis (gonozooid)	$Log_{10}WM = 2.39Log_{10}L+1.66$	WM (μg)	L (mm)	0.934	23		Aono (1999)
Salpida	*Cyclosalpa bakeri*	$Log_{10}DM = 3.03Log_{10}L+0.2$	DM (μg)	L (mm)	0.968	14		Aono (1999)
	Salpa aspera	$Log_{10}DM = 3.66Log_{10}L-0.74$	DM (μg)	L (mm)	0.963	25		Aono (1999)
	Salpa fusiformis	$Log_{10}DM = 2.73Log_{10}L+0.36$	DM (μg)	L (mm)	0.947	24		Aono (1999)
	Thalia democratica (solitary zooid)	$Log_{10}DM = 2.26Log_{10}L+0.86$	DM (μg)	L (mm)	0.839	19		Aono (1999)
	Thalia democratica (aggregate zooid)	$Log_{10}DM = 2.86Log_{10}L+0.53$	DM (μg)	L (mm)	0.939	25		Aono (1999)
Appendicularia	*Oikopleura longicauda*	$Log_{10}DM = 1.988Log_{10}TL-4.264$	DM (μg)	TrL (μm)	0.982	29	< 0.001	Shichinohe (2000)
Mollusca	Mollusca spp.	$Log_{10}DM = 1.13Log_{10}TL+2.29$	DM (μg)	TL (mm)	0.440	9		Imao (2005)

Mass and chemical composition measurements

Fresh specimens/samples were removed from seawater, placed on a 100-μm mesh and then rinsed briefly with distilled water to remove salt. Samples on the mesh were then placed on clean dry tissues to remove water. The water-free samples were then placed in a pre-weighed aluminium pan and frozen at -20°C. In a laboratory on land, the wet mass (WM) was measured using a microbalance (Mettler Toledo MT5) with a precision of 1 μg, and the sample was freeze-dried for five hours and stored in a drying oven at 60°C for twelve hours. After cooling in a desiccator for several hours, the dry mass (DM) was measured with a microbalance. The water compositions (% of WM) were calculated according to the differences in masses (water = 100 (WM - DM)/WM). The dried samples were ground, weighed, and placed in a tin cup, after which carbon (C) and nitrogen (N) were measured by a CHN coder (Vrio EL III). The C and N compositions were expressed as a percentage of the DM.

Body length and volume measurements

The measurements of the lengths of the body parts of the various taxa treated in this study are shown in figure 1. The bell height (BH) of the Cnidaria, total length (TL) of the Annelida, standard length (SL) of the Ostracoda, body length (BL) of the Mysidacea, body length (BL) of the Amphipoda, body length (BL) of the Euphausiacea, total length (TL) of the Chaetognatha, length (L) of the Doliolida, length (L) of the Salpida, trunk length (TrL) of the Appendicularia, and total length (TL) of the Mollusca were measured.

For the Copepoda, only the prosome length (PL) was measured for all of the species (Fig. 2A). The lipid stores were quantified for five species (see later), and image analyses from the dorsal and lateral views were performed using the equipment of Shimada and Oku (2014). The length (*L*) and width (*W*) of the prosome (PL and PW), urosome (UL and UW) and oil sac (OSL and OSW) were measured to a precision of 1 μm with the aid of Image J software (Figs. 2A, B). The volumes (V: mm^3 ind.$^{-1}$) of the prosome (PV), urosome (UV) and oil sac (OSV) were calculated with the following equation (Escribano and McLaren 1992): $V = 1/6 \times L \times \pi \times (W/2)^2$.

The total volume (TV) was calculated as the sum of the PV and UV (TV = PV + UV). To evaluate the effect of the viewing direction (dorsal
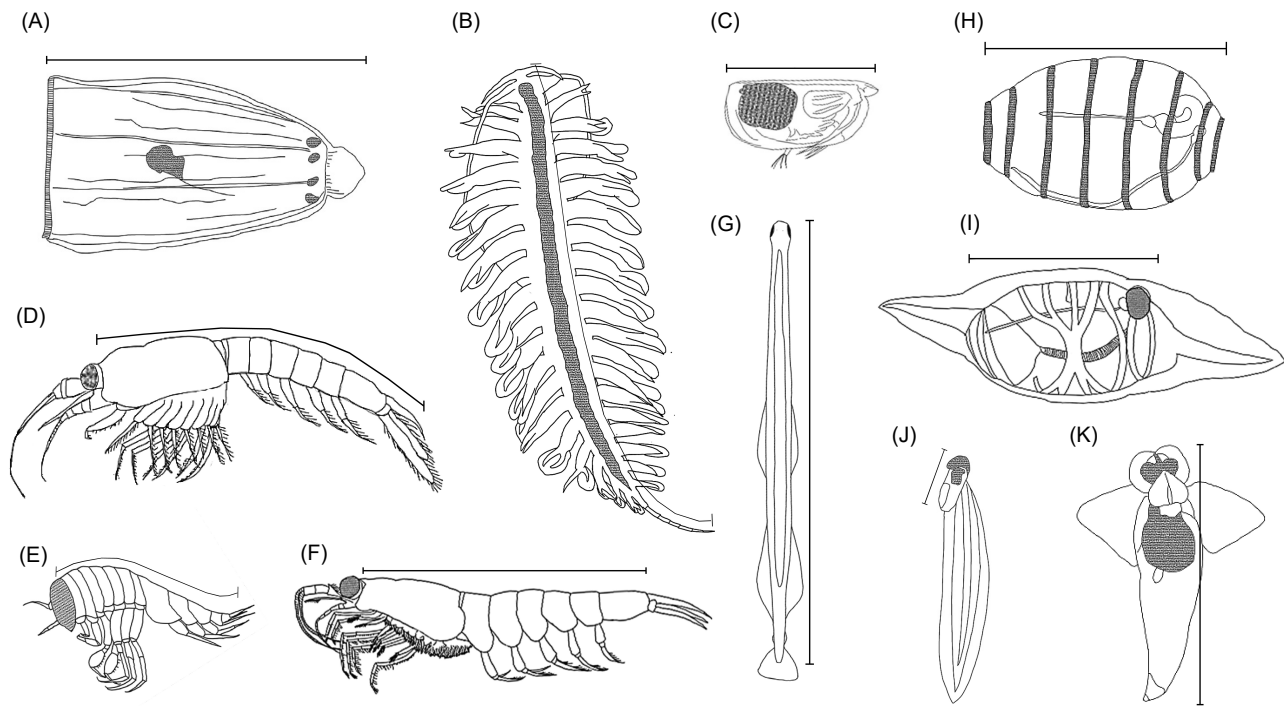
Fig. 1. Illustration showing the length measurements of various zooplankton taxa. A: bell height (BH) of Cnidaria, B: total length (TL) of Annelida, C: standard length (SL) of Ostracoda, D: body length (BL) of Mysidacea, E: body length (BL) of Amphipoda, F: body length (BL) of Euphausiacea, G: total length (TL) of Chaetognatha, H: length (L) of Doliolida, I: length (L) of Salpida, J: trunk length (TrL) of Appendicularia, K: total length (TL) of Mollusca. Note that the length measurements for Copepoda are summarized in figure 2.

and lateral views) on the volume value, we compared the volumes from both the dorsal (V_D) and lateral (V_L) views.

Length-weight equation and analysis

To express the L-W relationship, we applied the power-law equation, which was also used by Uye (1982) for the warm-water region of Japan: $Log_{10}M = a \times Log_{10}L + b$, where *a* and *b* are fitted constants, *M* is the mass in μg and *L* is the length in μm for mesozooplankton (Ostracoda, Copepoda and Appendicularia) and in mm for macrozooplankton taxa (Uye 1982). For the cnidarian *Aglantha digitale*, we applied an expression in a quadratic equation based on the literature (Ikeda and Imamura 1996). Most of the L-W relationships were unpublished data in theses submitted to Hokkaido University.

To evaluate the changes in the volume and mass together with the lipid store (from low to medium and full lipid), we calculated the "percentage change" index according to Hopkins et al. (1984) for *E. bungii* C6F, *M. okhotensis* C6F and *N. cristatus* C5. This value means that the percentage changes in the volume and mass from the values at low lipid store are expressed as 100%: Percent change = 100 × ([*Full* or *Medium*] - [*Low*]) / *Low*, where *Full*, *Medium*, and *Low* indicate the values at full, medium and low lipid levels, respectively (Hopkins et al. 1984). The percentage changes were calculated for volumes (PV, OSV and TV), masses (μg WM and μg DM), and chemical compositions (μg Water, μg C and
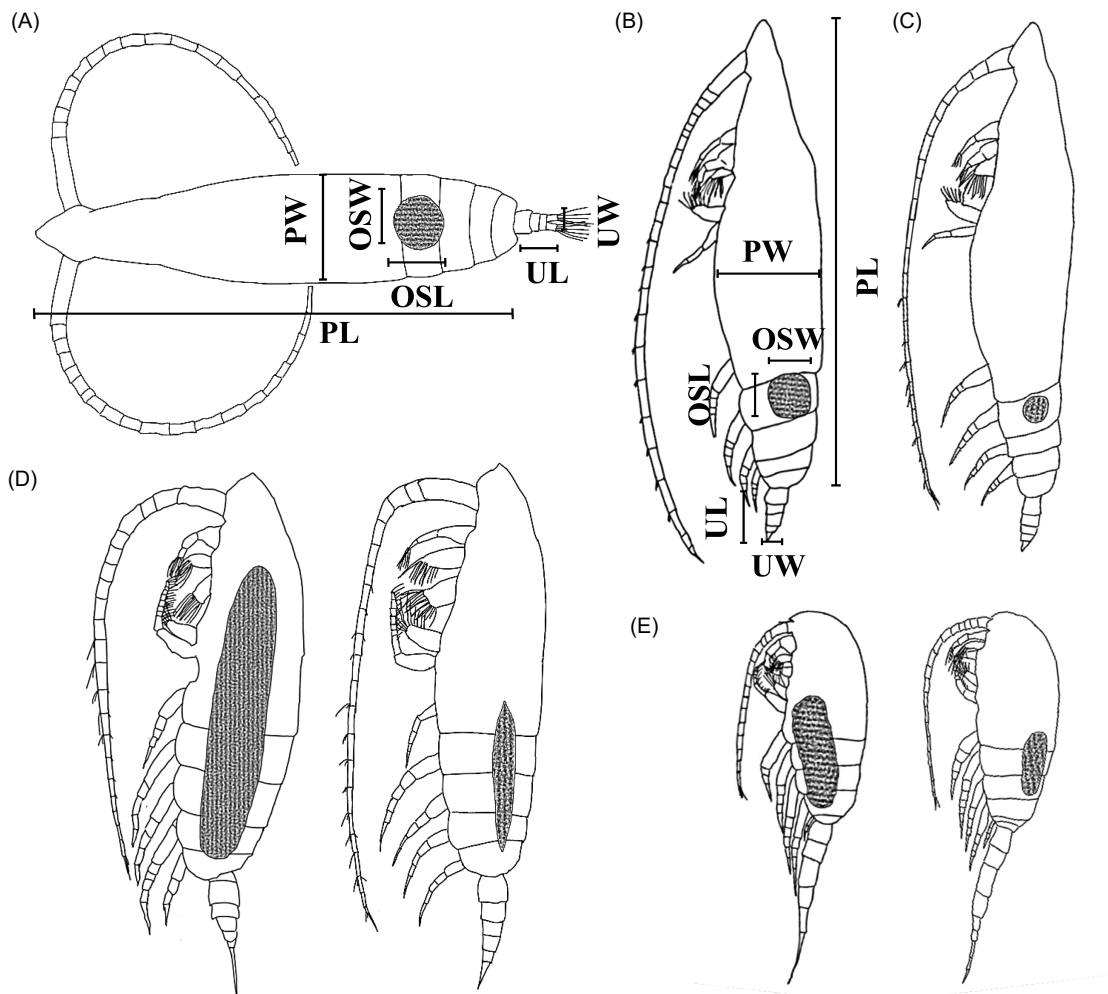
Fig. 2. Diagrams of the length and volume measurements of Copepoda (*Eucalanus bungii* C6F with full lipid) in dorsal (A) and lateral (B) views. C: *E. bungii* C6F with low lipid, D: *Neocalanus cristatus* C5 with full lipid (left) and low lipid (right), E: *Metridia okhotensis* C5F with full lipid (left) and low lipid (right). PL: prosome length, PW: prosome width, OSL: oil sac length, OSW: oil sac width, UL: urosome length, UW: urosome width.

μg N); the effects of lipid storage on the volume, mass, and chemical compositions were then evaluated.

RESULTS

Length-weight equations and chemical compositions

The L-W equations of 41 species belonging to 12 taxa are summarized in table 1. For the Euphausiacea and Doliolida, the mass units were in WM and were in DM for the other taxa. For five species of Copepoda (*Calanus pacificus*, *E. bungii*, *Metridia pacifica*, *N. cristatus*, *N. flemingeri* and *N. plumchrus*), the units of C and N are also shown as presented in Ueda et al. (2008). The coefficient of determination (r^2) ranged between 0.306 and 0.998, and the mean value was 0.886 ± 0.145 (mean ± 1 SD).

The water, C, and N compositions of each taxon are summarized in table 2. The water compositions ranged between 69.8% WM (*Thysanoessa longipes*) and 95.2 ± 0.5%WM (*Aglantha digitale*). The C compositions ranged

Table 2. Summary on water composition (% of wet mass, %WM), carbon (C) and nitrogen (N) composition (% of dry mass, %DM) for various zooplankton taxa/species which dominated in the western subarctic Pacific and their adjacent seas. Values are mean ± 1 SD

Taxa	Species (taxinomic category)	Water (%WM)	C (%DM)	N (%DM)	References
Cnidaria	*Aglantha digitale*	95.2 ± 0.5	15.4 ± 1.6	4.3 ± 0.4	Ikeda (2014a)
	Other Cnidaria spp.		3.8 ± 4.3	1.0 ± 1.4	This study
Annelida	Annelida spp.	85.2 ± 1.15	32.8 ± 4.28	7.9 ± 0.71	This study
Ostracoda	*Discoconchoecia pseudodiscophora*	75.9	50.8 ± 4.7	7.8 ± 0.8	Ikeda (1990), Kaeriyama and Ikeda (2004)
	Metaconchoecia skogsbergi		39.8 ± 1.6	9.4 ± 0.5	Kaeriyama and Ikeda (2004)
	Orthoconchoecia haddoni		44	8.95	Kaeriyama and Ikeda (2004)
Copepoda	*Calanus pacificus* (C1-C5)		18.9 ± 13.4	3.0 ± 2.3	Ueda et al. (2008)
	Eucalanus bungii (C1-C5)	92.8 ± 1.5	15.1 ± 5.8	1.5 ± 0.7	Shoden (2000), Ueda et al. (2008)
	Gaetanus variabilis (C5-C6)	79.7 ± 3.5	47.1 ± 4.9	10.1 ± 1.1	Ikeda et al. (2006)
	Heterorhabdus tanneri (C6)	88.1	43.2	9.4	Ikeda et al. (2006)
	Metridia pacifica (C1-C5)		8.0 ± 5.3	1.5 ± 0.8	Ueda et al. (2008)
	Neocalanus cristatus (C1-C5)	83.9 ± 8.5	30.9 ± 20.5	3.8 ± 2.3	Kobari et al. (2003), Ueda et al. (2008)
	Neocalanus flemingeri (C4-C5)	81.6 ± 6.3	47.8 ± 11.6	4.5 ± 1.8	Kobari et al. (2003), Ueda et al. (2008)
	Neocalanus plumchrus (C1-C5)	86.9 ± 4.5	22.2 ± 15.0	4.5 ± 2.1	Kobari et al. (2003), Ueda et al. (2008)
	Paraeuchaeta birostrata (C5-C6)	70.7 ± 4.1	58.8 ± 2.2	7.5 ± 0.5	Ikeda et al. (2006)
	Paraeuchaeta elongata (C4-C6)	75.0 ± 5.0	56.5 ± 2.8	7.9 ± 0.9	Ikeda et al. (2006)
	Paraeuchaeta rubra (C5-C6)	69.9 ± 2.6	60.8 ± 3.1	7.5 ± 0.6	Ikeda et al. (2006)
	Pleuromamma scutullata (C6)	80.3	47.7	9.6	Ikeda et al. (2006)
	Pseudocalanus newmani (C6)		47.9 ± 5.3	9.7 ± 1.3	Lee et al. (2001)
	Scolecithricella minor (C4-C6)	80.9 ± 2.3			Yamaguchi (1999)
	Cyclopoid Copepoda (3 species)	81.4 ± 5.1	44.8 ± 5.9	9.8 ± 1.8	Ikeda (2014b)
	Poecilostomatoid Copepoda (12 species, C6)		52.9 ± 5.3	8.5 ± 1.3	Nishibe and Ikeda (2008)
	Other Copepoda spp.	81.4 ± 5.1	51.6 ± 7.5	9.8 ± 1.8	Imao (2005), Ikeda (2014b)
Mysidacea	*Meterythrops microphtalma*	84.8 ± 1.7	46.1 ± 8.0	8.6 ± 1.9	Ikeda (1992), Ikeda (2013b)
Amphipoda	*Cyphocaris challengeri*	80.1 ± 4.7	36.8 ± 4.8	6.8 ± 0.9	Yamada and Ikeda (2003)
	Primno abyssalis	77.4 ± 4.2	54.3 ± 5.4	7.6 ± 0.3	Yamada and Ikeda (2003)
	Themisto japonica	77.7 ± 2.6	46.3 ± 2.3	8.8 ± 0.5	Yamada and Ikeda (2003)
	Themisto pacifica	77.2 ± 2.8	47.9 ± 7.2	8.3 ± 1.1	Yamada and Ikeda (2003)
Euphausiacea	*Euphausia pacifica* (Adult)	76.8 ± 0.9	34.5 ± 1.7	9.3 ± 0.2	Kim (2009)
	Thysanoessa inspinata (Adult)	77.2 ± 1.6	36.3 ± 1.0	9.8 ± 0.3	Kim (2009)
	Thysanoessa longipes (Juvenile-Adult)	69.8	41.0 ± 9.8	8.6	Iguchi and Ikeda (2005)
Chaetognatha	*Eukrohnia fowleri*	90.3 ± 1.5	41.1 ± 10.3	8.5	Imao (2005), Ikeda and Takahashi (2012)
	Sagitta elegans	91.0 ± 0.2	44.2 ± 4.5	12.1	Imao (2005), Ikeda and Takahashi (2012)
	Other Chaetognatha spp.	89.6 ± 2.5	39.5 ± 5.3	9.9 ± 2.0	Imao (2005), Ikeda and Takahashi (2012)
Doliolida	*Dolioletta toritonis*				
Salpida	*Salpa fusiformis*		4.6 ± 0.2	1.0 ± 0.03	This study
Appendicularia	*Oikopleura longicauda*		29.5 ± 2.9	7.3 ± 2.0	Shichinohe (2000)
Mollusca	Mollusca spp.	80.2 ± 7.7	28.0 ± 0.9	5.2 ± 2.6	Imao (2005), Ikeda (2014b)

from 3.8 ± 4.3% DM (various cnidarian species) to 60.8 ± 3.1% DM (*Paraeuchaeta rubra*). The N compositions were observed between 1.0 ± 0.03% DM (*Salpa fusiformis*) and 10.1 ± 1.1% DM (*Gaetanus variabilis*).

The relationships among water, C, and N compositions are shown with scatter plots (Fig. 3).
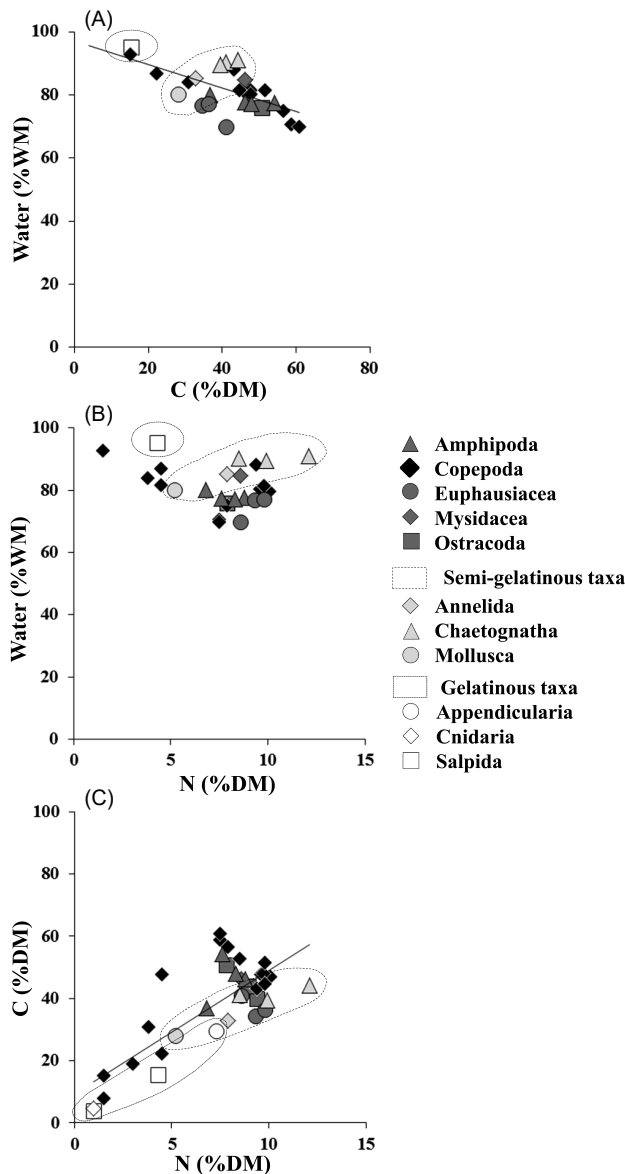
Fig. 3. Scatter plots of the water (water, % wet mass [WM]), carbon (C, % dry mass [DM]) and nitrogen (N, % DM) compositions for various zooplankton taxa (cf. Table 2). Plotted areas for the gelatinous taxa (Annelida, Appendicularia, Chaetognatha, Cnidaria, Mollusca and Salpida) are indicated by dashed circles. For taxa other than the gelatinous taxa, regression lines are calculated for each panel. The separation of gelatinous and semi-gelatinous taxa was derived from Larson (1986).

When comparing the water and C compositions, a significant negative correlation (high C composition implying low water composition) was detected for the non-gelatinous taxa ($p < 0.01$, Fig. 3A). The gelatinous taxa plotted at positions of high water and low C compositions. The plots of the semi-gelatinous taxa appear between the other two types of taxa. The comparison between the N and water compositions showed no correlation among them (Fig. 3B). The comparison between the C and N compositions were positively correlated in both gelatinous and non-gelatinous taxa ($p < 0.0001$, Fig. 3C).

Effect of lipid storage in Copepoda

The mean values of the body volumes (PV, OSV, and TV), masses (WM and DM) and chemical compositions (water, C, and N) of the Copepoda were summarized for the three lipid-accumulation categories (low, medium, and full) (Table 3). Lateral (V_L) view body volumes were smaller than the dorsal view (V_D) values (Table 3). From a regression analysis between V_L and V_D in the form of $V_L = a \times V_D$, where a is a fitted constant, highly significant correlations were observed for all volume units ($p < 0.0001$) (Fig. 4). The slopes (a) of the regressions ranged between 0.538 and 0.896. Based on the mean slope values, the volume values from the lateral view (VL) were 82.1 ± 5.4% of the dorsal view (VD) for PV, 82.4 ± 5.5% for TV and 70.0 ± 12.6% for OSV (Fig. 4).

By applying the "percent change" of Hopkins et al. (1984), we analysed the volume and mass changes along with the lipid accumulation (Fig. 5). Within the treated units, the value increases were prominent, especially for OSV, DM, and C (Fig. 5). For OSV, the percent changes of the values for the medium and full lipids were 550% and 3212% of the values for the low lipids, respectively (Fig. 5). These observed values indicate a 5-fold and 32-fold OSV increase from the low-lipid accumulation to specimens with medium and full lipid accumulations, respectively. The maximum percentage change was 495% and 741% for DM and C, respectively. Species-specific differences were also detected; thus, small increases of volume and mass along with a change in lipids were observed for *E. bungii* C6F, while the greatest increases were observed for *N. cristatus* C5; the *M. okhotensis* C6F values were between those of these two species (Fig. 5).

The proportion of OSV to TV was standardized by calculating OSV/TV, and

correlation analyses were then performed on the chemical compositions (water, C and N) (Fig. 6). With increasing OSV/TV, the water compositions decreased (r^2 = 0.85, p < 0.0001, Fig. 6A), while the C compositions increased (r^2 = 0.64, p < 0.001, Fig. 6B). For the N compositions, no correlations were observed for OSV/TV (Fig. 6C).

DISCUSSION

Length-weight Equation

Throughout this study, species-specific differences in L-W equations were noted, even within the same taxa. For the Copepoda, the body sizes of *Paraeuchaeta* spp., *Neocalanus* spp. and *E. bungii* were similar, but marked differences in

Table 3. Comparison on body volume, mass and chemical composition of Copepoda (*Eucalanus bungii*, *Metridia okhotensis*, *Neocalanus cristatus*, *Neocalanus flemingeri* and *Neocalanus plumchrus*) between full, medium and low lipid contents

Species	Lipid	Stage	(n)	PV_L	PV_D	OSV_L	OSV_D	TV_L	TV_D
						Volume (mm³ ind.⁻¹)			
E. bungii	Full	C6F	7	10.504	12.760	0.210	0.330	10.559	12.809
	Medium	C6F	9	9.413	11.199	0.034	0.036	9.463	11.247
	Low	C6F	1	11.028	10.145	0.000	0.000	11.087	10.202
M. okhotensis	Full	C5M	5	1.110	1.274	0.247	0.288	1.140	1.308
	Full	C6F	2	2.195	2.069	0.407	0.388	2.271	2.153
	Medium	C6F	6	2.259	2.592	0.052	0.104	2.354	2.685
	Low	C6F	2	2.011	2.214	0.012	0.012	2.095	2.290
N. cristatus	Full	C5	6	18.553	22.383	2.944	2.488	18.795	22.623
	Medium	C5	16	12.929	17.381	0.398	0.497	13.135	17.579
	Low	C5	6	7.114	11.337	0.226	0.292	7.243	11.459
N. flemingeri	Full	C5	9	4.110	4.678	1.333	1.826	4.157	4.719
	Full	C6F	2	7.521	9.219	2.141	2.013	7.632	9.345
	Medium	C5	10	3.168	3.676	0.478	1.012	3.213	3.719
	Low	C6F	1	4.791	7.521	0.000	0.000	4.907	7.657
N. plumchrus	Medium	C5	12	2.103	2.672	0.138	0.134	2.134	2.705

Species	Lipid	Stage	(n)	WM	DM	(n)	Water (%WM)	(n)	C (%DM)	N (%DM)
				Mass (mg ind.⁻¹)				Chemical Composition		
E. bungii	Full	C6F	5	12.399	1.158	5	90.48	3	34.27	7.057
	Medium	C6F	5	11.152	0.768	5	93.09	2	28.60	7.730
	Low	C6F	2	11.501	0.861	2	92.49	1	28.00	6.470
M. okhotensis	Full	C5M	6	1.167	0.370	6	68.22	2	54.20	6.725
	Full	C6F	2	2.738	0.665	2	75.72	2	46.35	6.080
	Medium	C6F	15	2.760	0.548	15	80.14	6	43.83	8.685
	Low	C6F	2	2.720	0.393	2	85.47	1	37.40	10.220
N. cristatus	Full	C5	25	22.989	6.047	25	73.74	15	54.65	6.942
	Medium	C5	35	17.394	1.927	35	89.24	14	39.91	8.061
	Low	C5	11	11.059	1.016	11	90.91	6	38.63	9.740
N. flemingeri	Full	C5	9	5.418	1.959	9	66.69	11	51.86	7.445
	Full	C6F	1	11.093	3.813	1	65.63	1	60.40	5.900
	Medium	C5	26	3.963	1.171	26	71.11	18	53.04	7.472
	Low	C6F	1	5.963	0.334	1	94.39	1	18.50	2.610
N. plumchrus	Medium	C5	6	2.663	0.420	6	84.95	2	43.90	7.365

PV: prosome volume, OSV: oil sac volume, TV: total volume (= PV + urosome volume [UV]), WM: wet mass, DM: dry mass, Water: water content, C: carbon content, N: nitrogen content. Lower letters in volume indicate observed direction: i.e., L: lateral and D: dorsal views. (*n*): observed number.
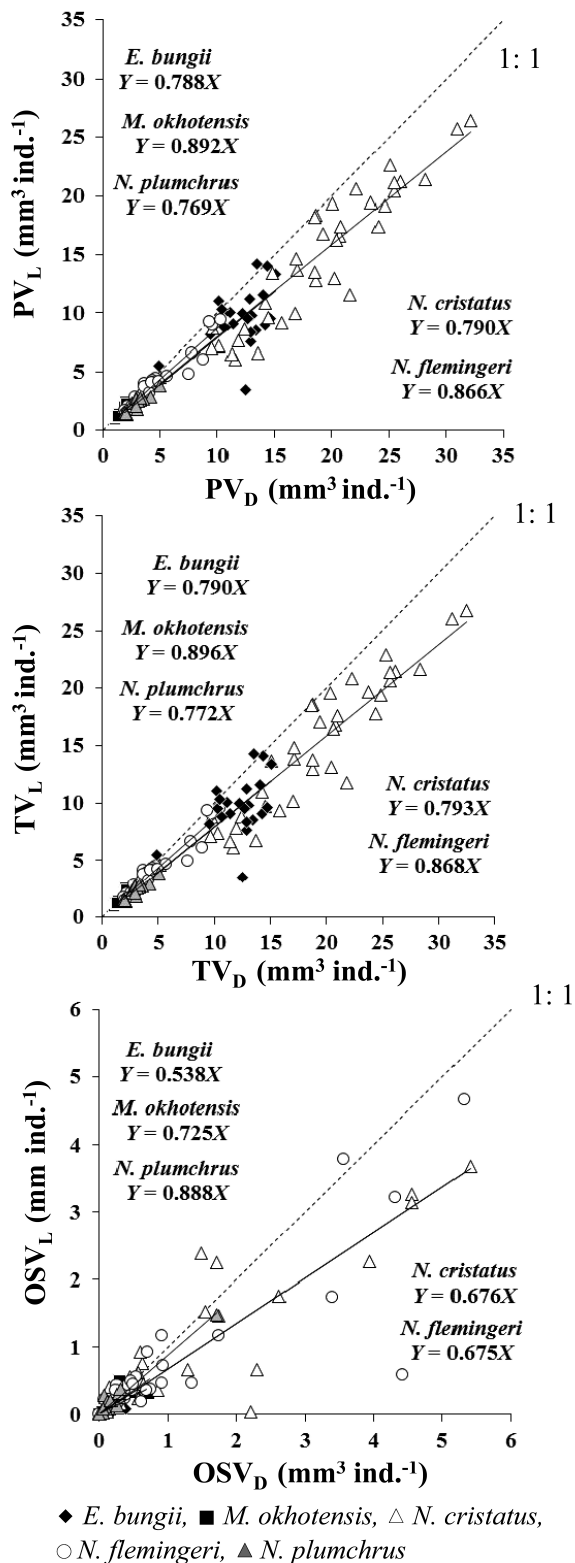
Fig. 4. Comparison of volumes (prosome volume: PV, total volume: TV, oil sac volume: OSV) of five copepod species between those in lateral views (*Y*-axis) and dorsal views (*X*-axis). Positions of 1:1 are shown with dashed lines. All regressions were significant (*p* < 0.0001).

mass were observed. Thus, for the same body size (PL = 3 mm), the DM values of *Neocalanus* spp. and *Paraeuchaeta* spp. were 3 or 12 times greater than that of *E. bungii* (Fig. 7). These species-specific differences in mass may be caused by their species-specific differences in chemical composition. Flint et al. (1991) revealed that the lipid and protein compositions of *Eucalanus* spp. were extremely low, 1/7-1/10 (lipid) and 1/5-1/20 (protein), respectively, of those in *Calanus* spp., which are called "jelly-bodied copepods" because of their low organic and high water compositions. The water composition of *E. bungii* evaluated in this study (92.8 ± 1.5%) (Table 2) was similar to those of the gelatinous zooplankton (*i.e.*, > 95%, Alldredge and Madin 1982). According to Ohman (1997), the water compositions of three sympatric copepods (*Rhincalanus nasutus*, *C. pacificus* and *M. pacifica*) (82.3-84.3%) differed significantly from those of *Eucalanus californicus* (92.9%). These facts suggest that the chemical compositions of *Eucalanus* spp. may be similar to those of previously reported gelatinous zooplankton taxa.

The C and N compositions of *E. bungii* were 15.1% and 1.5% DM, respectively; those of *Neocalanus* spp. were 22.2-47.8% and 3.8-4.5% DM respectively; and those of *Paraeuchaeta* spp. were 56.5-60.8% and 7.7-7.9% DM (Table 2), respectively. *Paraeuchaeta* spp., the heaviest DM species with the same body size, had high C and N compositions, while both the C and N compositions were the lowest for the lightest, *E. bungii*, and all of the values of *Neocalanus* spp. were intermediate between these two species. For zooplankton, C and N are the lipid and protein indices, respectively (Postel et al. 2000). The low C and N compositions of *E. bungii* suggest that individuals of this species have low lipid and protein compositions in their bodies. Because of the low organic compositions (lipid and protein), *E. bungii* show high water compositions as well as a transparent body colour and structure, which may function to reduce predation pressure by visual predator fishes.

From the viewpoint of feeding modes, *Paraeuchaeta* spp. are categorized as carnivores (Yen 1983), while *Eucalanus* spp. mainly feed on phytoplankton (Ohtsuka et al. 1993), and *Neocalanus* spp. are suspension feeders (Dagg 1993; Gifford 1993). For carnivorous *Paraeuchaeta* spp., high protein compositions may provide a high swimming ability, which allows them to capture prey. For herbivorous *Eucalanus* spp., a high swimming ability may not be required;

thus, low protein and low organic compositions (= light DM) are characteristic of this species. For the chemical compositions of Copepoda from a water column of 0 to 5000 m, a rapid decrease in the N compositions with increasing depth is explained by freedom from visual predators in the deep-water layers, allowing them to have a low swimming ability and thus low organic and protein compositions (Ikeda et al. 2006).

In this study, the low C composition of *E. bungii* suggests that this species stores lower amounts of lipids in their bodies. According
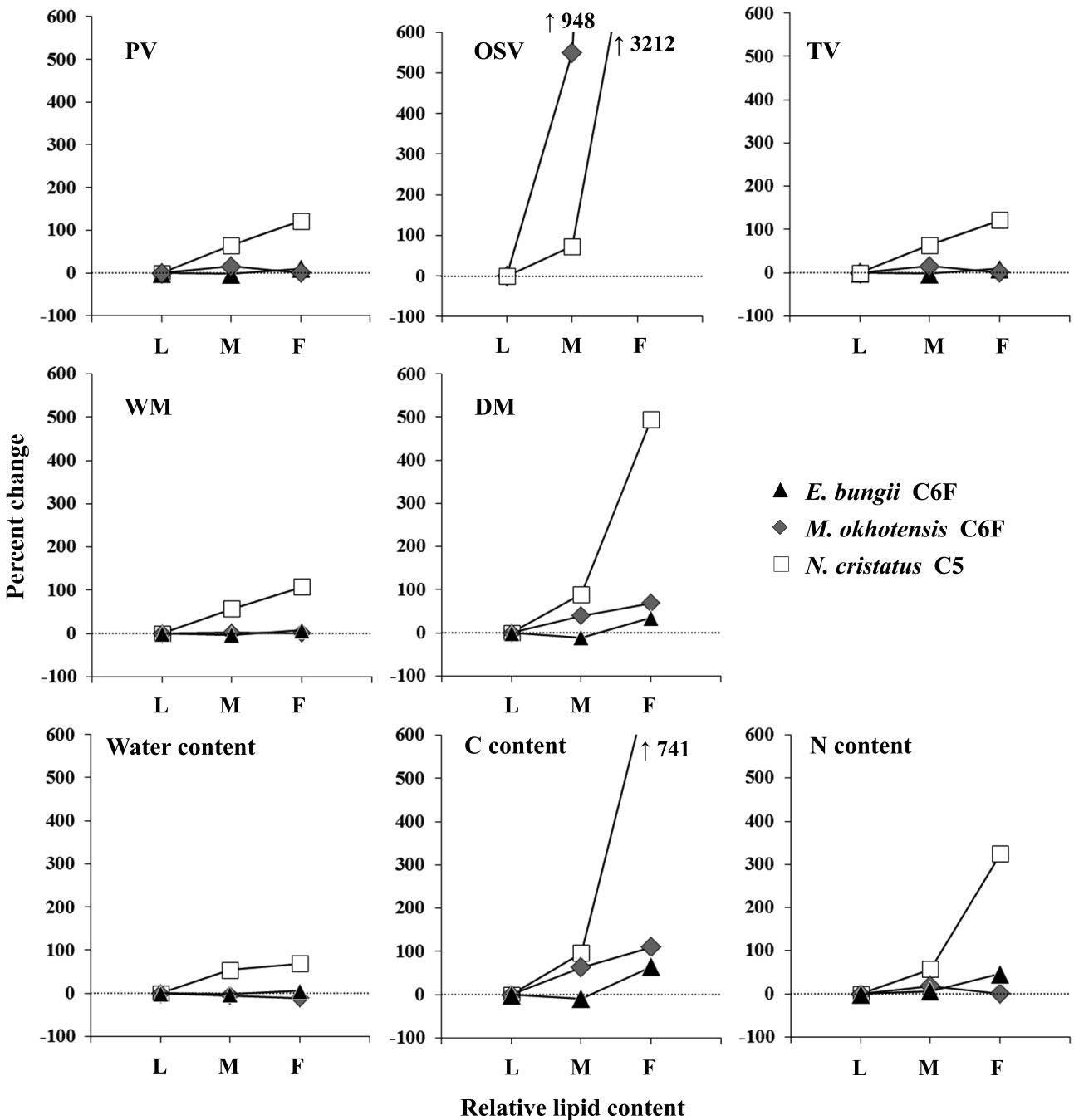

Fig. 5. Percent changes in the volumes, masses and chemical compositions of *Eucalanus bungii* C6F, *Metridia okhotensis* C6F and *Neocalanus cristatus* C5 along with relative lipid contents (low: L, medium: M and full: F) (cf. Table 3). PV: prosome volume, OSV: oil sac volume, TV: total volume (= PV + urosome volume [UV]), WM: wet mass, DM: dry mass, C: carbon, N: nitrogen. For volumes, the mean values of the lateral and dorsal views were applied for these calculations.
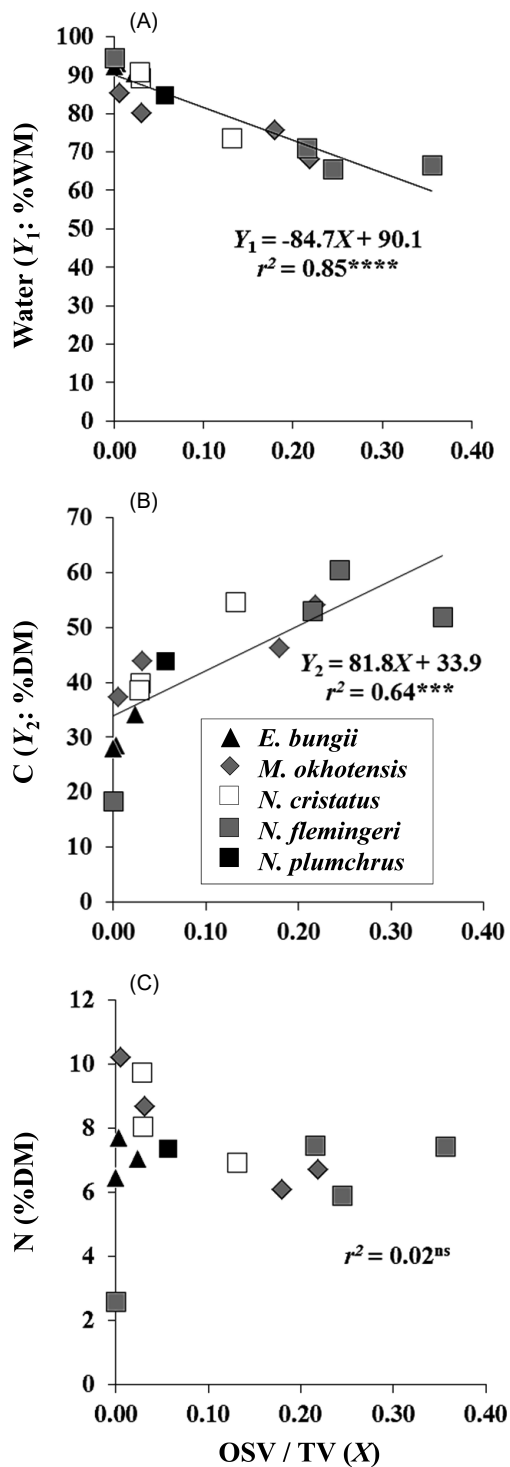
Fig. 6. Relationships between the chemical compositions (water composition: water in % wet mass (WM), carbon composition: C in % dry mass (DM) and nitrogen composition: N in % DM) and relative composition of the oil sac volume (OSV) to the total volume (TV) for various Copepoda in the subarctic Pacific Ocean (cf. Table 3). For significant relationships, regressions were calculated; ***: $p < 0.001$, ****: $p < 0.0001$, ns: not significant. The values for volume were the applied mean values of the lateral and dorsal views.

to Larson (1986), high water and low organic compositions in zooplankton function to substantially reduce metabolism. These facts suggest that the metabolic demand of *E. bungii* may be low and the low lipid (C) compositions of this species may be sufficient. While *E. bungii* have a diapause phase in their life cycle, a mass-balance estimation between metabolic demand and lipid stores showed that the stored lipids of *E. bungii* are sufficient to maintain their population during the resting phase in the deep layer (Shoden et al. 2005).

As we show in this study, even the L-W equations within the same taxa showed large species-specific differences, which are related to the feeding mode, life cycle, and habitat depths of each species. The chemical compositions of marine zooplankton vary greatly with the taxa, which may be caused not only by the internal state (developmental stage, sex and nutritional condition) but also by the external conditions (season, region, geography and depth) (Omori 1969; Ikeda 1974; Båmstedt 1986). For instance, other than the Copepoda, the chemical compositions of the Amphipoda are known to be lower in C and higher
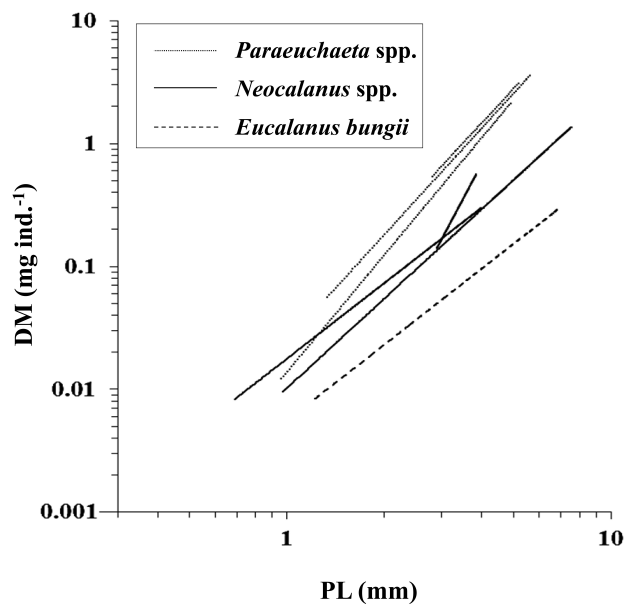
Fig. 7. Comparison of the dry mass (DM) - prosome length (PL) regressions of Copepoda of similar body sizes belonging to three genera (*Paraeuchaeta*, *Neocalanus* and *Eucalanus bungii*). For details of the regressions, see table 1.

in water compositions with increasing habitat depth (Ikeda 2013a). To make an exact biomass estimation, application of the general L-W equation to all taxa is not adequate. Differences between species should be considered.

Chemical compositions

For the chemical compositions of the zooplankton, noticeable differences exist between the gelatinous taxa and other taxa. In this study, we divided the zooplankton taxa into three categories according to Larson (1986). Thus, the gelatinous taxa include the Appendicularia, Cnidaria and Salpida; the non-gelatinous taxa contain the Amphipoda, Copepoda, Euphausiacea, Mysidacea and Ostracoda; and the remaining taxa, the Annelida, Chaetognatha and Mollusca, are categorized as semi-gelatinous (Larson 1986). The water compositions were 95.2% WM for the gelatinous taxa, 85.2-90.3% WM for the semi-gelatinous taxa and 69.8-86.9% WM (except for *E. bungii*, as previously mentioned) for the other taxa (Table 2). It should be noted that the water composition of *E. bungii* was extremely high (92.8% WM) as previously noted.

Proteins contain C and N at 51.3% and 17.8% DM, respectively, while for lipids, C and N constitute 69% and 0.6% DM, respectively (Rogers 1927). On the basis of these differences in the chemical compositions between protein and lipids, C is treated as an index of lipids and N as an index of the amount of protein (Postel et al. 2000). A negative correlation between the C and water compositions suggests that high lipid-containing specimens (= high C composition) may contain relatively less water as a percent of body volume. This pattern (inverse relationship between C and water composition) is reported for fishes and crustaceans (Love 1970; Ikeda et al. 2004).

The comparison of N and water composition showed no correlation between them (Fig. 3B). The gelatinous taxa were plotted at a high water composition, while the semi-gelatinous taxa were plotted at similar positions to those of the other taxa, and fewer taxonomic differences were detected for the N compositions (Fig. 3B). The amount of protein may thus have little effect on the water composition, and the DM protein compositions show little difference between the gelatinous and non-gelatinous taxa.

Both the gelatinous and non-gelatinous taxa showed positive correlations between the C and N compositions ($p < 0.0001$, Fig. 3C). Compared with the non-gelatinous taxa, the gelatinous taxa were characterized by low C, while both taxa had similar N composition. The high water composition of the gelatinous taxa may reduce the relative levels of C (= lipid), while they had less effect on the N compositions (= protein).

Bailey et al. (1995) noted that gelatinous taxa are characterized by high water and ash and low C and N compositions. As a function of a lower organic composition of their bodies, reduced metabolism and faster growth rates are reported (Larson 1986). With regard to the feeding mode, the gelatinous zooplankton are divided into two categories, filter feeders (*i.e.*, Salpida and Doliolida) and carnivores (Cnidaria). The relationship between the WM and CM is reported to vary with the feeding mode; specifically, exponential increases for filter feeders and linear increases for carnivores (Molina-Ramírez et al. 2015). The rapid increase in WM with increasing CM for filter feeders may serve to increase the surface area and increase the food-capture surfaces (Molina-Ramírez et al. 2015). For the Cnidaria, chemical composition varies according to the body part (Larson 1986). These facts suggest that the chemical compositions exhibit large variability and diversity for the taxa/species within the gelatinous taxa.

Effect of lipid accumulation in Copepoda

In all copepods, the volumes (PV, OSV, and TV) observed from the dorsal view (V_D) were greater than those observed from the lateral view (V_L) (Fig. 4). This indicates that the proportions of the copepod prosome and urosome, as well as their oil sacs, are dorsally flattened shapes. Using an image-analysis system, Miller et al. (2000) quantified the OSV of the copepod *Calanus finmarchicus* from both the dorsal and lateral views and reported that the V_D was greater than the V_L, which corresponded with the results of this study.

For copepod species in general, the percentage change in the individual DM as a result of one moulting ranged from 61.7 to 94.0% (78.1 ± 13.7% [mean ± 1 SD]) (Mauchline 1998). In this study, the DM within the same copepodid stage showed changes of 495% depending on the amount of lipid accumulation (*N. cristatus* C5, Table 3). These differences in the DM are much higher than those of the copepodid moulting stage. To accurately estimate the DM of Copepoda from L-W relationships, the effect of lipid accumulation should be considered.

The C:N ratio is known to be an index of lipid accumulation (Postel et al. 2000). Omori (1969) reported that the C:N ratio of *Calanus cristatus* (= *N. cristatus*) had a maximum in May and a minimum in December, with a twofold seasonal difference in the C:N ratio. Similar seasonal changes were also reported for *C. plumchrus* (= *N. plumchrus*) and *M. okhotensis* (Omori 1969). The amount of food availability is also known to be a critical factor for determining lipid accumulation (Escribano and McLaren 1992).

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