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Spatial changes in the vertical distribution of calanoid copepods down to great depths in the North Pacific

Atsushi Yamaguchi[1*], Kohei Matsuno[2] and Tomoe Homma[1]

Abstract

Background: Despite its ecological importance, little information is available regarding the spatial and vertical changes in the calanoid copepod community over large geographical regions. This study investigated the spatial and vertical patterns in calanoid copepod abundance and community structure using zooplankton samples collected between depths of 0 and 2,615 m across the North Pacific from 0° to 56°N.

Results: A total of 211 calanoid copepod species belonging to 66 genera and 24 families were identified. Calanoid copepod abundance decreased with increasing depth, and few latitudinal differences were detected. Across the entire region, species diversity peaked near 500 to 2,000 m in depth. The calanoid copepod community was separated into seven groups with distinct spatial and vertical distributions. For all groups, the number of species was low (28 to 37 species) in the subarctic region (north of 40°N) and high (116 to 121 species) in the subtropical-tropical region. The deepest group in the subtropical-tropical region was composed of cosmopolitan species, and this group was also observed in deep water in the subarctic region.

Conclusions: In deep water, most of the calanoid copepod community consisted of cosmopolitan species, while an endemic community was observed in the subarctic region. Because the food of deep-sea calanoid copepods originates from the surface layer, sufficient and excess flux in the eutrophic subarctic region may be responsible for maintaining the endemic species in the region.

Keywords: Zooplankton; Calanoid copepods; Community structure; Diversity; Deep-sea; North Pacific

Background

Calanoid copepods are the dominant component of the zooplankton biomass throughout the water column in the North Pacific. They consume much of the primary production and are an important link to higher trophic levels; thus, they have an important role in energy transport in marine ecosystems. Calanoid copepods are also an important component of the 'biological pump,' and they transport organic matter to the deep ocean in egested fecal pellets and through diel and seasonal vertical migration (Longhurst 1991; Hernández-León and Ikeda 2005; Kobari et al. 2008b). Because calanoid copepods are the major prey of meso- and bathypelagic fishes (Merrett and Roe 1974; Hopkins and Sutton 1998; Moku

et al. 2000), it is important to clarify the calanoid copepod community structure at depth to better understand marine ecosystems.

Most studies on the community structure of calanoid copepods at great depths have collected samples using plankton nets (cf. Vinogradov 1968). Examples include studies in the Arctic Ocean (Kosobokova and Hirche 2000; Auel and Hagen 2002), Greenland Sea (Richter 1994), Bering Sea (Homma and Yamaguchi 2010), Atlantic Ocean (Roe 1972; Koppelmann and Weikert 1999), subarctic Pacific (Vinogradov 1962; Arashkevich 1972; Yamaguchi et al. 2002; Steinberg et al. 2008), Mediterranean Sea (Scotto di Calro et al. 1984; Weikert and Trinkaus 1990; Koppelmann and Weikert 2007), Arabian Sea (Madhupratap and Haridas 1990; Fabian et al. 2005; Koppelmann and Weikert 2005; Wishner et al. 2008), Red Sea (Weikert 1982; Weikert and Koppelmann 1993), and the Antarctic Ocean (Schnack-Schiel et al.

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Yamaguchi *et al. Zoological Studies* (2015) 54:13

Page 2 of 12

2008). Most of these studies examined biomass, which is easy to measure, but few have identified and evaluated specimens down to species level. Furthermore, few studies have examined the abundance, species diversity, and community structure of calanoid copepods, and most that did were limited to a narrow geographical range. Throughout most of the North Pacific, little is known about the community structure throughout the water column.

During 1965 to 1967, detailed stratified zooplankton samplings from the surface to the deep sea (maximum depth 2,615 m) were made across the North Pacific (0° to 56°N), and the collected calanoid copepods were identified to the species level. In this study, we analyzed the calanoid copepod community down to great depths across the entire North Pacific. Based on this analysis, we discuss what determines the structure of calanoid copepod communities across the North Pacific.

Methods

Field sampling and data gathering

Field sampling was conducted at 12 stations between the equator and 56°N in the Bering Sea and Pacific Ocean during cruises of the T.S. *Oshoro Maru* and R.V. *Hakuho Maru* from 1965 to 1967 (Figure 1). Samples were collected simultaneously from six or seven discrete depths between 0 and 2,615 m by horizontal tows of 3 to 6 Motoda (MTD) horizontal closing nets (mesh size 350 μm, mouth diameter 56 cm; Motoda

1971) (Table 1). The volume of filtered water was calculated assuming a filtering rate of 0.6 (Motoda 1971). After collection, zooplankton samples were preserved in 10% borax-buffered formalin-seawater. In the terrestrial laboratory, 1/32 to 1/2 aliquot subsamples were examined under microscope to identify the calanoid copepods. Although the samplings were conducted at both day and night, the day-night differences are expected to be smaller than the differences due to the large geographical (0° to 56°N) and vertical (0 to 2,615 m) ranges in this study.

Water temperature and salinity were measured using a reversing thermometer and an inductive salinometer, respectively. Data collected by the T.S. *Oshoro Maru* were cited from 'Data Record of Oceanographic Observations and Exploratory Fishing' (Hokkaido University 1967), and those from the R.V. *Hakuho Maru* were provided by the Center for Cruise Coordination, Atmosphere and Ocean Research Institute, the University of Tokyo.

Data analysis

The species diversity index (H') (Shannon and Weaver 1949) for calanoid copepods was calculated as:

$$H' = -\sum n/Ni \, ln \, n/Ni$$

where n is the abundance (individuals (inds.) m^{-3}) of each calanoid species at the ith layer, and Ni is the total abundance of calanoid copepods in the ith layer. This
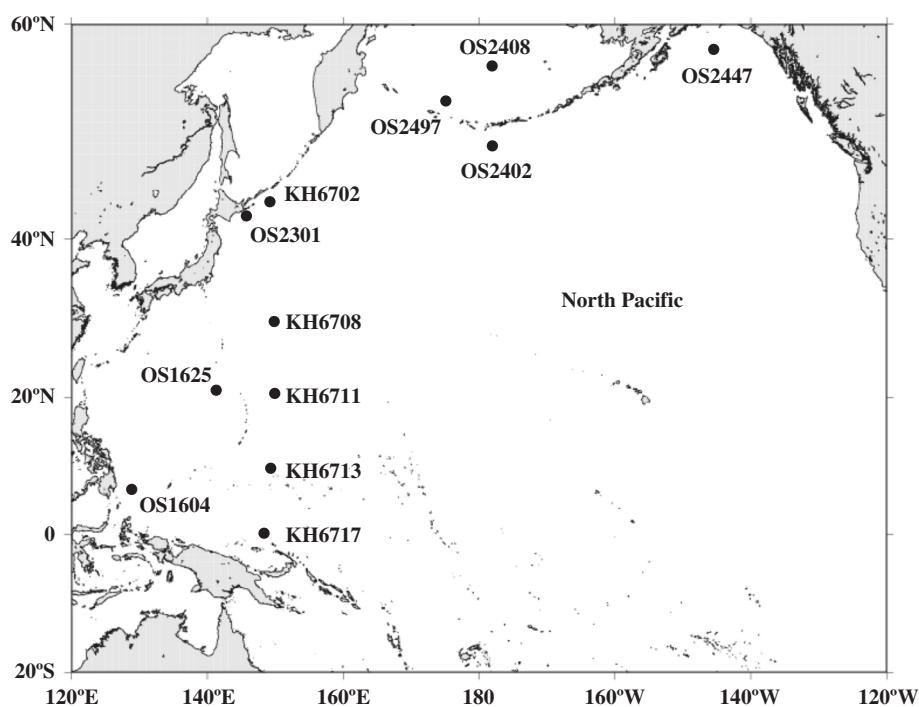

Figure 1 Locations of sampling stations in the Bering Sea and Pacific Ocean.

Yamaguchi *et al. Zoological Studies* (2015) 54:13

Page 3 of 12

Table 1 Zooplankton sampling data used in the present analyses

Area	Station	Position	Sampling date	Local time	Sampled depth (m)
Bering Sea	OS2408	56°00′N 178°00′W	14 June 1967	08:54 to 09:53	0, 130, 270, 610, 983, 1,285
	OS2497	53°08′N 175°02′E	20 June 1967	15:42 to 18:24	0, 40, 105 167, 277, 555, 1,110
		53°08′N 175°02′E	21 June 1967	22:33 to 01:31	0, 85, 170, 260, 430, 860, 1,720
Eastern North Pacific	OS2447	57°33′N 145°56′W	20 August 1967	12:05 to 14:40	0, 65, 137, 200, 333, 665, 1,330
	OS2402	49°00′N 178°00′W	10 June 1967	22:06 to 23:39	0, 87, 177, 355, 432, 800
Western North Pacific	KH6702	43°47′N 149°55′E	6 December 1967	18:43 to 22:53	0, 435, 873, 1,360, 1,745, 2,180, 2,615
	OS2301	42°00′N 146°00′E	23 April 1967	12:06 to 13:61	7, 60, 120, 180, 240, 310, 360
		42°00′N 146°00′E	23 April 1967	22:12 to 23:36	7, 58, 117, 175, 233, 290, 345
	KH6708	29°57′N 150°06′E	13 December 1967	12:06 to 13:61	0, 83, 168, 392, 730, 1,670, 2,500
		29°57′N 150°06′E	13 December 1967	22:12 to 23:36	0, 83, 168, 392, 860, 1,170, 2,500
	OS1625	20°47′N 141°45′E	17 January 1966	09:50 to 13:49	7, 80, 153, 375, 740, 1,475, 2,200
	KH6711	20°04′N 150°07′E	17 December 1967	08:27 to 11:05	0, 75, 152, 380, 583, 835, 1,140
	KH6713	09°53′N 149°51′E	22 December 1967	09:26 to 13:35	0, 65, 122, 317, 637, 1,275, 1,910
		09°53′N 149°51′E	22 December 1967	23:45 to 04:05	0, 80, 140, 347, 685, 2,080
	OS1604	06°52′N 129°24′E	4 December 1965	10:38 to 19:65	9, 47, 85, 383, 755, 1,500
	KH6717	0°02′S 148°52′E	26 December 1967	18:40 to 20:40	0, 50, 105, 258, 518, 1,035, 1,555

All samples were collected with horizontal tows of Motoda horizontal closing nets (Motoda 1971).

diversity is an index of species richness, which includes qualitative evaluation. The value of the index increases when numerous species occur evenly and decreases when a few species dominate.

A Q-mode analysis, which evaluates the similarity between samples (Chiba et al. 2001), was also performed. For the Q-mode analysis, abundance data (X: inds. m^{-3}) were first log transformed (Log$_{10}$[X + 1]). A dissimilarity matrix between each sample was constructed based on the differences in species composition using the Bray-Curtis index (Bray and Curtis 1957). The matrix was analyzed by cluster analysis coupled with the unweighted pair-group method using arithmetic means to classify the samples into several groups with similar community compositions. To minimize the effect of minor species, data from only the 58 most dominant species (i.e., those that composed >10% in total abundance in any sampling layer) were utilized (Table 2). The computer software package BIOSTAT II was employed for this analysis. To verify whether the similarity matrix reflected differences in species composition between groups, each sample was plotted on a two-dimensional map by nonmetric multi-dimensional scaling (NMDS) methods. A close distribution in the NMDS plots indicates a similar community structure. We also conducted a multiple regression analysis to clarify which environmental variables (depth, latitude, and longitude) had a significant relationship with the NMDS plot of the calanoid copepod community. To determine the indicator species for each group, a one-way ANOVA and Fisher's protected least

significant difference (PLSD) test were applied to the calanoid copepod abundance data.

Results

Hydrography

At the sampling stations, the surface temperature ranged from 6.0°C to 29.7°C, and salinity ranged from 32.4 to 35.0 (Figure 2). The study area was classified into three domains based on the locations of the subarctic front (where a 4°C vertical isotherm occurred below 100 m) and the subarctic boundary (where a 34.0 isohaline is stretched vertically). The subarctic domain occurred north of the subarctic front, the transition domain occurred between the subarctic front and the subarctic boundary, and the tropical/subtropical domain occurred south of the subarctic boundary (Favorite et al. 1976; Anma et al. 1990). According to the T-S diagrams, stations located at 42°00′N to 56°00′N occurred in the subarctic domain, and stations at 0°02′S to 29°57′N occurred in the tropical/subtropical domain (Figure 2).

Abundance and species diversity

Vertical changes in abundance are shown in Figure 3a. Calanoid copepod abundance ranged from 0.072 to 591.8 inds. m^{-3}; it was the greatest in the subarctic domain (40° to 50°N) and lowest in the tropical/subtropical domain (0° to 10°N). Calanoid copepod abundance decreased exponentially with increasing depth over the entire region (Figure 3a).

Table 2 List of families and species of calanoid copepods identified in this study

Acartiidae	Calanidae	Heterorhabdidae	Pontellidae
Acartia longiremis (Lilljeborg, 1853)	*Calanus pacificus* Brodsky, 1948	*Disseta palumbii* Giesbrecht, 1889	*Calanopia minor* Scott A., 1902
Acartia negligens Dana, 1849	*Canthocalanus pauper* (Giesbrecht, 1888)	*Heterorhabdus abyssalis* (Giesbrecht, 1889)	*Labidocera acutifrons* (Dana, 1849)
Acartia erythraea Giesbrecht, 1889	*Cosmocalanus darwinii* (Lubbock, 1860)	*Heterorhabdus clausi* (Giesbrecht, 1889)	*Labidocera detruncata* (Dana, 1849)
Aetideidae	*Megacalanus princeps* Wolfenden, 1904	*Heterorhabdus norvegicus* (Boeck, 1872)	*Labidocera japonica* Mori, 1935
Aetideus armatus (Boeck, 1872)	*Mesocalanus tenuicornis* (Dana, 1849)	*Heterorhabdus pacificus* Brodsky, 1950	*Labidocera pavo* Giesbrecht, 1889
Aetideus giesbrechti Cleve, 1904	*Nannocalanus minor* (Claus, 1863)	*Heterorhabdus papilliger* (Claus, 1863)	*Pontella chierchiae* Giesbrecht, 1889
Chiridius poppei Giesbrecht, 1893	*Neocalanus cristatus* (Krøyer, 1848)	*Heterorhabdus spinifrons* (Claus, 1863)	*Pontella denticauda* Scott A., 1909
Chiridius sp.	*Neocalanus flemingeri* Miller, 1988	*Heterorhabdus tanneri* (Giesbrecht, 1895)	*Pontella securifer* Brady, 1883
Chirundina streetsii Giesbrecht, 1895	*Neocalanus gracilis* (Dana, 1852)	*Heterostylites longicornis* (Giesbrecht, 1889)	*Pontella spinicauda* Mori, 1937
Chirundina sp.	*Neocalanus plumchrus* (Marukawa, 1921)	*Heterostylites major* (Dahl F., 1894)	*Pontellina plumata* (Dana, 1849)
Euchirella bitumida With, 1915	*Neocalanus robustior* (Giesbrecht, 1888)	*Paraheterorhabdus compactus* (Sars G.O., 1900)	Rhincalanidae
Euchirella curticauda Giesbrecht, 1888	*Undinula vulgaris* (Dana, 1849)	*Paraheterorhabdus robustus* (Farran, 1908)	*Rhincalanus nasutus* Giesbrecht, 1888
Euchirella messinensis (Claus, 1863)	Candaciidae	Lucicutiidae	*Rhincalanus rostrifrons* (Dana, 1849)
Euchirella pulchra (Lubbock, 1856)	*Candacia armata* Boeck, 1872	*Lucicutia bicornuta* Wolfenden, 1905	Scolecitrichidae
Euchirella rostrata (Claus, 1866)	*Candacia bipinnata* (Giesbrecht, 1889)	*Lucicutia clausi* (Giesbrecht, 1889)	*Amallothrix curticauda* (Scott A., 1909)
Euchirella truncata Esterly, 1911	*Candacia bispinosa* (Claus, 1863)	*Lucicutia curta* Farran, 1905	*Amallothrix tenuiserrata* (Giesbrecht, 1893)
Euchirella venusta Giesbrecht, 1888	*Candacia catula* (Giesbrecht, 1889)	*Lucicutia flavicornis* (Claus, 1863)	*Amallothrix valida* (Farran, 1908)
Gaetanus armiger Giesbrecht, 1888	*Candacia columbiae* Campbell, 1929	*Lucicutia grandis* (Giesbrecht, 1895)	*Lophothrix frontalis* Giesbrecht, 1895
Gaetanus brachyurus Sars G.O., 1907	*Candacia curta* (Dana, 1849)	*Lucicutia longiserrata* (Giesbrecht, 1889)	*Pseudoamallothrix inornata* (Esterly, 1906)
Gaetanus brevicornis Esterly, 1906	*Candacia ethiopica* (Dana, 1849)	*Lucicutia magna* Wolfenden, 1903	*Pseudoamallothrix ovata* (Farran, 1905)
Gaetanus brevispinus (Sars G.O., 1900)	*Candacia longimana* (Claus, 1863)	*Lucicutia maxima* Steuer, 1904	*Pseudoamallothrix profunda* (Brodsky, 1950)
Gaetanus miles Giesbrecht, 1888	*Candacia simplex* (Giesbrecht, 1889)	*Lucicutia orientalis* Brodsky, 1950	*Racovitzanus antarcticus* Giesbrecht, 1902
Gaetanus pileatus Farran, 1903	*Candacia truncata* (Dana, 1849)	*Lucicutia ovalis* (Giesbrecht, 1889)	*Racovitzanus levis* Tanaka, 1961
Gaetanus tenuispinus (Sars G.O., 1900)	Centropagoidae	*Lucicutia pacifica* Brodsky, 1950	*Scaphocalanus affinis* (Sars G.O., 1905)
Gaetanus spp.	*Centropages abdominalis* Sato, 1913	*Lucicutia polaris* Brodsky, 1950	*Scaphocalanus brevicornis* (Sars G.O., 1900)
Pseudochirella obesa Sars G.O., 1920	*Centropages bradyi* Wheeler, 1900	*Lucicutia sewelli* Tanaka, 1963	*Scaphocalanus echinatus* (Farran, 1905)
Pseudochirella obtusa (Sars G.O., 1905)	*Centropages calaninus* (Dana, 1849)	Metridiidae	*Scaphocalanus elongatus* Scott A., 1909
Undeuchaeta intermedia Scott A., 1909	*Centropages elongatus* Giesbrecht, 1896	*Metridia asymmetrica* Brodsky, 1950	*Scaphocalanus magnus* (Scott T., 1894)
Undeuchaeta major Giesbrecht, 1888	*Centropages furcatus* (Dana, 1849)	*Metridia brevicauda* Giesbrecht, 1889	*Scaphocalanus major* (Scott T., 1894)
Undeuchaeta plumosa (Lubbock, 1856)	*Centropages gracilis* (Dana, 1849)	*Metridia curticauda* Giesbrecht, 1889	*Scolecithricella bradyi* (Giesbrecht, 1888)
Arietellidae	*Centropages longicornis* Mori, 1932	*Metridia okhotensis* Brodsky, 1950	*Scolecithricella dentata* (Giesbrecht, 1893)
Arietellus setosus Giesbrecht, 1893	*Centropages violaceus* (Claus, 1863)	*Metridia ornata* Brodsky, 1950	*Scolecithricella globulosa* Brodsky, 1950
Arietellus simplex Sars G.O., 1905	Clausocalanoidae	*Metridia pacifica* Brodsky, 1950	*Scolecithricella longifurca* (Giesbrecht, 1888)

Yamaguchi et al. Zoological Studies (2015) 54:13

Page 4 of 12

Table 2 List of families and species of calanoid copepods identified in this study *(Continued)*

Augaptilidae	*Clausocalanus arcuicornis* (Dana, 1849)	*Metridia princeps* Giesbrecht, 1889	*Scolecithricella minor* (Brady, 1883)
Augaptilus lamellifer Esterly, 1911	*Clausocalanus pergens* Farran, 1926	*Metridia similis* Brodsky, 1950	*Scolecithricella orientalis* Mori, 1937
Augaptilus longicaudatus (Claus, 1863)	*Microcalanus pusillus* Sars G.O., 1903	*Metridia venusta* Giesbrecht, 1889	*Scolecithricella spinipedata* Mori, 1937
Augaptilus spp.	*Microcalanus pygmaeus* (Sars G.O., 1900)	*Pleuromamma abdominalis* (Lubbock, 1856)	*Scolecithricella vittata* (Giesbrecht, 1893)
Centraugaptilus porcellus Johnson M.W., 1936	*Pseudocalanus minutus* (Krøyer, 1845)	*Pleuromamma gracilis* Claus, 1863	*Scolecithrix danae* (Lubbock, 1856)
Centroaugaptilus sp.	*Pseudocalanus newmani* Frost, 1989	*Pleuromamma quadrungulata* (Dahl F., 1893)	*Scottocalanus longispinus* Scott A., 1909
Euaugaptilus angustus (Sars G.O., 1905)	Eucalanidae	*Pleuromamma scutullata* Brodsky, 1950	*Scottocalanus persecans* (Giesbrecht, 1895)
Euaugaptilus facilis (Farran, 1908)	*Eucalanus bungii* Giesbrecht, 1893	*Pleuromamma xiphias* (Giesbrecht, 1889)	*Scottocalanus securifrons* (Scott T., 1894)
Euaugaptilus gracilis (Sars G.O., 1905)	*Eucalanus californicus* Johnson M.W., 1938	Nullosetigeridae	Spinocalanidae
Euaugaptilus gracilis (Sars G.O., 1905)	*Eucalanus elongatus* (Dana, 1848)	*Nullosetigera bidentata* (Brady, 1883)	*Monacilla typica* Sars G.O., 1905
Euaugaptilus grandicornis Sars G.O., 1920	*Pareucalanus attenuatus* (Dana, 1849)	*Nullosetigera helgae* (Farran, 1908)	*Spinocalanus longicornis* Sars G.O., 1900
Euaugaptilus hecticus (Giesbrecht, 1893)	*Subeucalanus crassus* (Giesbrecht, 1888)	*Nullosetigera impar* (Farran, 1908)	*Spinocalanus* spp.
Euaugaptilus hyperboreus Brodsky, 1950	*Subeucalanus mucronatus* (Giesbrecht, 1888)	*Nullosetigera integer* (Esterly, 1911)	Temoridae
Euaugaptilus nodifrons (Sars G.O., 1905)	*Subeucalanus subcrassus* (Giesbrecht, 1888)	Paracalanidae	*Temora discaudata* Giesbrecht, 1889
Euaugaptilus pacificus Matthews, 1972	*Subeucalanus subtenuis* (Giesbrecht, 1888)	*Acrocalanus gibber* Giesbrecht, 1888	*Temora stylifera* (Dana, 1849)
Euaugaptilus palumboi (Giesbrecht, 1889)	Euchaetidae	*Acrocalanus gracilis* Giesbrecht, 1888	Tortanidae
Euaugaptilus propinquus Sars G.O., 1920	*Euchaeta concinna* Dana, 1849	*Acrocalanus monachus* Giesbrecht, 1888	*Tortanus discaudatus* (Thompson & Scott 1897)
Euaugaptilus squamatus (Giesbrecht, 1889)	*Euchaeta indica* Wolfenden, 1905	*Calocalanus pavo* (Dana, 1852)	
Haloptilus acutifrons (Giesbrecht, 1893)	*Euchaeta longicornis* Giesbrecht, 1888	*Mecynocera clausi* Thompson I.C., 1888	
Haloptilus longicirrus Brodsky, 1950	*Euchaeta marina* (Prestandrea, 1833)	*Paracalanus parvus* (Claus, 1863)	
Haloptilus longicornis (Claus, 1863)	*Euchaeta media* Giesbrecht, 1888	Phaennidae	
Haloptilus mucronatus (Claus, 1863)	*Euchaeta plana* Mori, 1937	*Cephalophanes frigidus* Wolfenden, 1911	
Haloptilus pseudooxycephalus Brodsky, 1950	*Paraeuchaeta californica* (Esterly, 1906)	*Cornucalanus chelifer* (Thompson I.C., 1903)	
Haloptilus sp.	*Paraeuchaeta elongata* (Esterly, 1913)	*Onchocalanus affinis* With, 1915	
Bathypontiidae	*Paraeuchaeta propinqua* (Esterly, 1906)	*Onchocalanus magnus* (Wolfenden, 1906)	
Temorites elongata (Sars G.O., 1905)	*Paraeuchaeta rubra* Brodsky, 1950	*Talacalanus greenii* (Farran, 1905)	
Temorites similis (Tanaka, 1965)	*Paraeuchaeta tonsa* (Giesbrecht, 1895)	*Xanthocalanus pulcher* Esterly, 1911	

*Species composing >10% of the total copepod abundance in at least one sample used for cluster and NMDS analyses (cf. Figure 4).
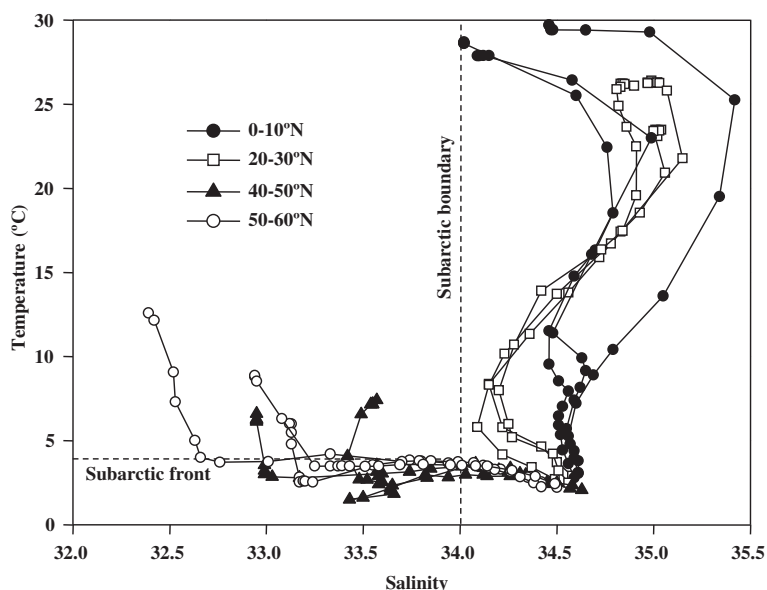
Figure 2 T-S diagram from all stations of this study in the Bering Sea and Pacific Ocean. Horizontal and vertical dashed lines indicate the locations of the subarctic front and boundary, respectively (Favorite et al. 1976; Anma et al. 1990).

Vertical changes in species diversity (H′) are shown in Figure 3b. H′ varied from 0.04 to 3.4; it was low near the surface, high at depths of approximately 500 to 2,000 m, and decreased below 2,000 m. H′ was high in the tropical/subtropical domain (0° to 10°N, 20° to 30°N) and low in the subarctic domain (40° to 60°N; Figure 3b).

A total of 211 calanoid copepod species belonging to 66 genera and 24 families were identified (Table 2). A total of 58 species composed >10% of the total abundance in at least one sampling layer; therefore, these species were applied in the cluster analysis. Thus, most species (153) were minor species that made up less than 10% of the total abundance in all sampling layers. The highest number of species (86 from 36 families) was observed at St. KH6708 in the subtropical domain, while the lowest number of species (20 from 14 families) was observed at St. OS2301 in the subarctic domain. This low number may have been caused by the limited sampling range (0 to 360 m) at this station (Table 1).

Community structure
Q-mode analysis classified the calanoid copepod community into seven groups (A to G) at 65% and 94% dissimilarity levels (Figure 4a). The number of samples in each group ranged from 4 to 23. Calanoid copepod abundance was greatest in group A with 229 ± 166 inds. m^{-3} (mean ± sd), followed by group E. Species diversity (H′) was lowest in group B (1.8 ± 0.3) and greatest in group F (2.4 ± 0.4). The number of species in each group varied between 28 and 121. Groups A to D had fewer species (28 to 37), and groups E to G had more (112 to 121; Figure 4a).

In the NMDS plots, the distributions of groups A to D and E to G were clearly separated (Figure 4b). Depth, latitude, and longitude each showed a significant relationship with calanoid copepod group ordination. Group F occurred at low latitudes, groups A and B occurred at high latitudes, and group G occurred at great depths.

The vertical and horizontal distributions of each group are shown in Figure 5. In the subarctic domain, group A occurred at the surface, group B occurred at 100 to 500 m, group C occurred at 500 to 1,000 m, and group D occurred at 500 to 2,250 m. In the tropical/subtropical domain, group E occurred at 0 to 1,000 m, group F occurred at 500 to 1,500 m, and group G occurred at 750 to 2,615 m. The horizontal distributions of each group were clearly separated, and the greatest discrepancy was observed between 30° and 40°N. Group G was the only group collected from deep water in both the subarctic and tropical/subtropical domains.

An ANOVA and Fisher's PLSD test were used to determine indicator species for each group (Table 3). The indicator species were as follows: *Neocalanus plumchrus* and *Pseudocalanus minutus* for group A; *Eucalanus bungii, Racovitzanus antarcticus,* and *Scolecithricella minor* for group B; *Neocalanus cristatus* and *N. plumchrus* for group C; *Metridia pacifica, Metridia okhotensis, Paraeuchaeta elongata,* and *Pleuromamma scutullata* for group D; *Aetideus giesbrechti, Clausocalanus arcuicornis, Euchaeta marina, Cosmocalanus darwinii,* and *Undinula vulgaris* for group E; *Haloptilus longicornis, Metridia venusta,* and *Pleuromamma xiphias* for group F; and *Pleuromamma abdminalis* and *Pleuromamma gracilis* for group G.
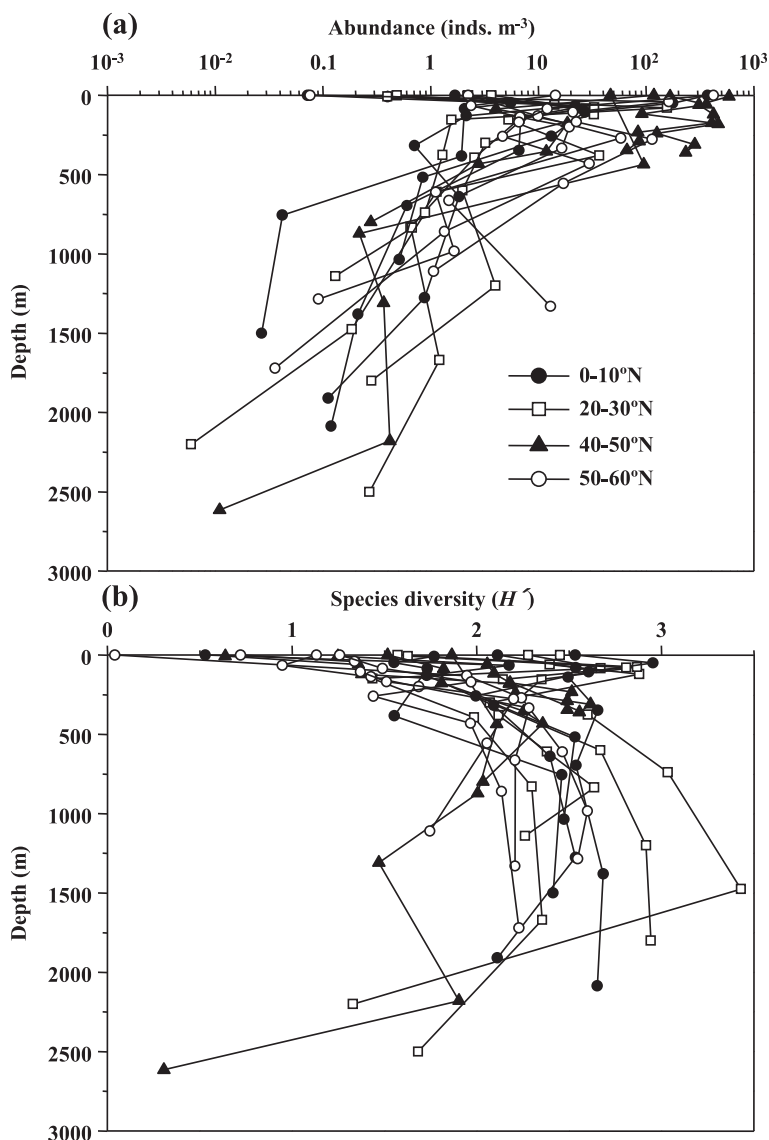
Yamaguchi *et al. Zoological Studies* (2015) 54:13

Page 7 of 12

Figure 3 Vertical distribution of calanoid copepod abundance (a) and species diversity (b) in the Bering Sea and Pacific Ocean.

Discussion

Abundance and species diversity

Many studies have shown that zooplankton biomass decreases with depth, but few have examined abundance. This is partly because biomass is easier to measure and contains more useful information. Zooplankton biomass between the surface and 4,000 m in the North Pacific is greater in the subarctic than in the tropical/subtropical domain; in both regions, the biomass decreases with increasing depth (Vinogradov 1962). The rate of biomass decrease with increasing depth is similar in all domains, and the influence of the surface layer is known to extend over 4,000 m into the water column (Vinogradov 1962, 1968). Across the North Pacific, 65% of the zooplankton biomass between depths of 0 and 4,000 m occurs at 0 to

500 m, and this percentage is similar through all regions because zooplankton food in the deep sea depends on sinking particles provided by the upper layer. Therefore, biomass in the deep sea is proportionate to the biomass in the surface layer (Vinogradov and Tseitlin 1983; Vinogradov 1997). Although much is known about biomass, only limited information is available on abundance and species diversity. This is partly because of the difficulty in counting and identifying zooplankton under a microscope, which requires taxonomic knowledge and a significant time investment.

The most remarkable characteristic of the vertical changes in abundance described in this study was that while latitudinal differences are common in biomass (more biomass in the subarctic and less in the subtropical, cf.
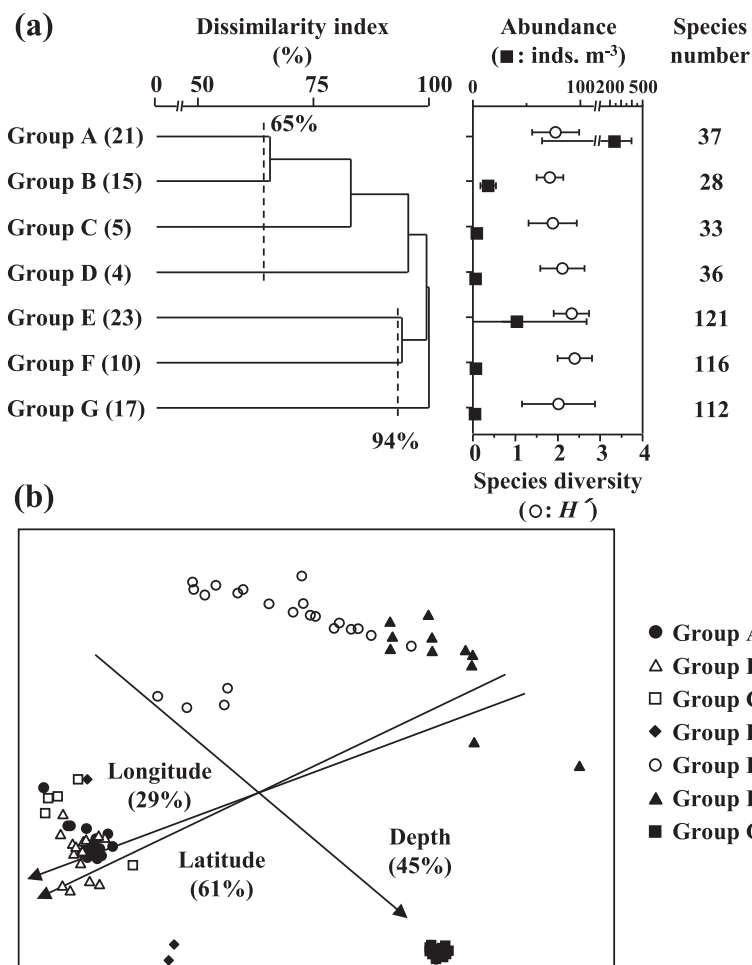
Yamaguchi *et al. Zoological Studies* (2015) 54:13

Page 8 of 12

Figure 4 Results of cluster analysis (Bray-Curtis connected with UPGMA) on calanoid copepod community (a) and their NMDS plots (b). Seven groups (A to G) were identified from the cluster analysis, and the number of stations belonging to each group is shown in parentheses. The mean and standard deviation of their abundance and species diversity (cf. Figure 3) were calculated, and the number of species in each group is shown in the right column of (a). Arrows and values in (b) indicate the directions and r^2 values of the environmental parameters that showed a significant correlation with the NMDS ordination.

Yamaguchi et al. 2005), no differences were observed in abundance (Figure 3a). In all domains, calanoid copepods are the most abundant mesozooplankton taxa in terms of biomass (Yamaguchi et al. 2004). The latitudinal differences in zooplankton units may be caused by the latitudinal differences in individual mass. Thus, the individual size of calanoid copepods (=biomass) is expected to be larger in the subarctic domain than in the subtropical domain. In fact, Yamaguchi et al. (2004) reported that the individual size of calanoid copepods is smaller in the subtropics, while large calanoid copepods (i.e., *Neocalanus* spp. and *Eucalanus* spp.) are dominant in the subarctic, composing more than 50% of the mesozooplankton biomass in deep water.

Environmental factors that affect the vertical distribution of zooplankton abundance include the thermocline and the oxygen minimum zone (Sameoto 1986). In zooplankton biomass, a vertical minimum occurs below the thermocline throughout the year near the Kuril-Kamchatka Trench (100 to 200 m) (Bogorov and Vinogradov 1955) and in the Sea of Japan (Morioka and Komaki 1978). In the oxygen minimum zone of the Red Sea, the number of common calanoid copepod species is low, while the number of specialized species is high (Weikert 1982). In the present study, the abundance and species diversity of calanoid copepods did not show a clear decrease in either the thermocline or the oxygen minimum zone (Figure 3a,b). This may be an artifact of the sampling design in this study. Because MTD nets collect samples from irregular layers during simultaneous, multi-layer, horizontal tows, the small-scale vertical distribution changes in the thermocline or oxygen minimum zone would have been difficult to evaluate.

A unique finding of this study was the vertical change in species diversity, which was low at the surface and
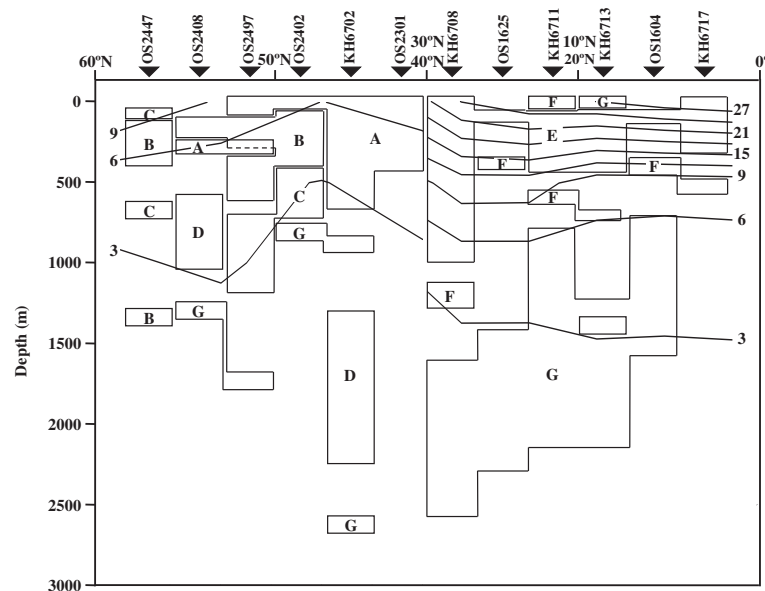
Yamaguchi *et al. Zoological Studies* (2015) 54:13

Page 9 of 12

Figure 5 Horizontal and vertical distributions of seven calanoid copepod communities identified by cluster analysis (see Figure 4a). Stations are arranged from north (left) to south (right). Approximate positions of latitudes are shown in the upper margin. Temperature profiles along the latitudinal transect are superimposed.

Table 3 Mean abundance of copepods in each group identified through in-cluster analysis of the copepod community (see Figure 4a)

Species	Group and abundance (log10[inds. m^{-3} + 1])							*F*	Results of one-way ANOVA
	A	B	C	D	E	F	G		
Aetideus giesbrechti	0.00	0.00	0.00	0.00	*0.26*	0.10	0.04	3.37	**
Clausocalanus arcuicornis	0.00	0.00	0.l00	0.00	*0.67*	0.29	0.04	16.70	***
Eucalanus bungii	1.10	*1.68*	1.20	0.51	0.00	0.00	0.17	44.00	***
Euchaeta marina	0.00	0.00	0.00	0.00	*0.65*	0.42	0.11	10.10	***
Haloptilus longicornis	0.00	0.00	0.00	0.00	0.24	*0.40*	0.11	0.01	*
Metridia pacifica	1.03	0.84	0.52	*1.52*	0.00	0.00	0.43	12.10	***
Metridia okhotensis	0.33	0.00	0.00	*0.48*	0.00	0.00	0.06	4.93	***
Metridia venusta	0.00	0.00	0.00	0.00	0.00	*0.24*	0.21	3.90	**
Neocalanus cristatus	0.58	0.56	*0.94*	0.85	0.02	0.00	0.28	11.30	***
Neocalanus plumchrus	*1.13*	0.86	*1.13*	1.07	0.11	0.08	0.28	19.70	***
Paraeuchaeta elongata	0.01	0.11	0.16	*0.33*	0.00	0.00	0.16	2.63	*
Pleuromamma abdminalis	0.00	0.00	0.00	0.00	0.35	1.07	*0.36*	13.50	***
Pleuromamma gracilis	0.00	0.00	0.00	0.00	0.47	1.03	*0.48*	9.97	***
Pleuromamma scutullata	0.32	0.45	0.39	*0.61*	0.00	0.00	0.19	5.70	***
Pleuromamma xiphias	0.00	0.00	0.00	0.00	0.11	*0.35*	0.03	4.43	***
Pseudocalanus minutus	*0.67*	0.53	0.49	0.35	0.00	0.00	0.20	7.70	***
Racovitzanus antarcticus	0.19	*0.44*	0.00	0.02	0.00	0.00	0.20	3.90	**
Scolecithricella minor	0.37	*0.53*	0.14	0.00	0.00	0.00	0.00	11.20	***
Cosmocalanus darwinii	0.00	0.00	0.00	0.00	*0.64*	0.08	0.32	9.20	***
Undinula vulgaris	0.00	0.00	0.00	0.00	*0.36*	0.13	0.04	5.48	***
Total copepods	*2.24*	1.13	0.44	0.26	1.08	0.36	0.08	61.4	***

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Groups where the significant greatest abundance was observed were italicized.

Yamaguchi *et al. Zoological Studies* (2015) 54:13

Page 10 of 12

peaked at 500 to 2,000 m (Figure 3b). Increases in the number of species and species diversity in the mesopelagic zone (200 to 1,000 m) and bathypelagic zone (1,000 to 3,000 m) have been reported in the North Atlantic (Roe 1972), the Mediterranean Sea (Scotto di Calro et al. 1984), the western North Pacific (Yamaguchi et al. 2002), and the Bering Sea (Homma and Yamaguchi 2010). This suggests that an increase in the number of calanoid copepod species in the meso- and bathypelagic zones is a common phenomenon of the ocean worldwide. The differentiation of calanoid copepod species is reported to strongly influence their feeding habits, and an increased number of species in the meso- and bathypelagic zones are reported to reflect diverse feeding modes in these zones (Ohtsuka and Nishida 1997). In fact, detritivores attached to marine snow do not occur in the surface layer but constitute more than 50% of the total calanoid copepod abundance in the meso- and bathypelagic zones of the western subarctic Pacific and Bering Seas (Yamaguchi et al. 2002; Homma and Yamaguchi 2010). Large sinking particles (e.g., marine snow and giant larvacean house) play an important role as microcosms in the deep sea. The abundance of zooplankton attached to marine snow in the deep sea is reported to be 200 times higher than those in the surrounding waters (Steinberg et al. 1994, 1998).

Community structure

In the North Pacific, calanoid copepod communities in the surface layer generally correspond to the ocean current system and can be separated into subarctic and tropical/subtropical communities. The number of species is greater in the tropical/subtropical than in the subarctic (McGowan and Walker 1979; Ohtsuka and Ueda 1999). Much is known about calanoid copepod communities in the surface layer; however, little is known about those in the deep sea. In the present study, deep-sea calanoid copepods were divided into seven groups (A to G; Figure 4a), and the distribution of each group was clearly separated (Figure 5). Groups A to D occurred north of 40°N and consisted of a small number (28 to 37 species) of species. Groups E to G occurred mainly south of 30°N in the tropical/subtropical domain, and group G occurred in deep water in both the subarctic and tropical/subtropical domains where the temperature was below 3°C (Figure 5). Groups E to G contain a large number (116 to 121 species) of species, indicating that the number of species was high in both shallow and deep water in the tropical/subtropical domain.

The wide distribution of Group G indicates that this group consists of cosmopolitan species that occur widely throughout the uniform environmental condition of the deep sea (Figure 5). Concerning the regional distribution of the deep-sea calanoid copepod genus *Paraeuchaeta*, Park (1994) noted that the cosmopolitan species occurred

widely in the oligotrophic region, while endemic species were found in the deep sea of the eutrophic region (e.g., subarctic Pacific and Antarctic). Park suggested that most food of deep-sea zooplankton sinks from the surface and that the low flux of sinking material in the oligotrophic region could maintain only cosmopolitan species; in contrast, the higher flux in the eutrophic region could sustain the endemic species (Park 1994). Group D in the deep sea of the subarctic domain consisted of endemic species in the subarctic Pacific (Table 3; *M. pacifica, M. okhotensis, P. elongata*, and *P. scutullata*) and corresponded to the endemic deep-sea species group observed in the eutrophic region (Park 1994). The uniform low temperature (≤3°C) in the deep sea indicates that there is no barrier to the distribution of deep-sea cosmopolitan species. This is presumably why group G (cosmopolitan species) was the only calanoid copepod community observed in both the subarctic and tropical/subtropical domains (Figure 5).

Some zooplankton have bipolar distributions; for instance, the chaetognath *Eukrohnia hamata* occurs at the surface layer at high latitudes and below 1,000 m near the equator (Pierrot-Bults and Nair 1991). For calanoid copepods, a bipolar distribution is considered to be possible for carnivorous or omnivorous species but may be difficult for herbivorous species that feed on phytoplankton in the epipelagic layer (Machida et al. 2006). In the present study, the species characterizing each group were identified (Table 3), but the limited study area (North Pacific) prevented an evaluation of bipolar distributions.

N. plumchrus was the only species that occurred in all groups (A to G) (Table 3). *N. plumchrus* is a subarctic species that occurs in the surface layer during the spring phytoplankton bloom and descends to deep water during the rest of the year (Miller and Clemons 1988; Kobari and Ikeda 2001). Various authors have reported that the diapause stages C5 and C6 of *Neocalanus* spp. are transported to the deep sea in the subtropical domain by the submerged Oyashio undercurrent (Omori and Tanaka 1967; Oh et al. 1991; Shimode et al. 2006; Kobari et al. 2008a). Within the tropical/subtropical community (groups E, F, and G), the order of depth distribution was E < F < G, and the shallowest group (E) was also occasionally observed at 1,000 m (St. KH6708, Figure 5). Thus, the transported *N. plumchrus* might have occurred in all tropical/subtropical community groups (groups E to G). Concerning the southern limit of transported *Neocalanus* spp., Yamaguchi et al. (2004) reported that they occur at 30°N, but not at 25°N; this agrees with the southern limit of their distribution (28°N) reported by Omori (1967). While *Neocalanus* spp. transported south of 40°N are important in terms of adding additional biomass to the deep-sea subtropical domain (Yamaguchi et al. 2004), this is considered to be an

Yamaguchi *et al. Zoological Studies* (2015) 54:13

Page 11 of 12

abortive transport, and they are not thought to reproduce in the subtropical domain (Oh et al. 1991).

Conclusions

In deep water, most of the calanoid copepod community consists of cosmopolitan species, while an endemic community was observed in the subarctic region. Because the food of deep-sea calanoid copepods originates on the surface layer, sufficient and excess flux in the eutrophic subarctic region may be responsible for maintaining endemic species in the region.

Authors' contributions
AY and TH wrote the manuscript. KM participated in the design of the study and assisted with the statistical analyses. All authors read and approved the final manuscript.

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Yamaguchi *et al. Zoological Studies* (2015) 54:13

Page 12 of 12

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