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Phenology in large grazing copepods in the Oyashio region, western subarctic Pacific

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Abstract

Seasonal sequence of population structure (=copepodid stage composition) of large grazing copepods (*Metridia pacifica*, *Eucalanus bungii* and *Neocalanus* spp.) was analyzed based on seasonal samples collected with 100 µm mesh nets from 0-500 m stratum at Site H in the Oyashio region, western subarctic Pacific, during 1996-1997 and 2002-2007. On the premise that there are little year-to-year differences, the composite data were arranged to the date of samplings of each year to yield seasonal developmental patterns of each copepod. Seasonal developmental pattern estimated by tracing the sequence of mean copepodid stages of the population at each sampling date revealed that the recruitment season of the population was January for *N. cristatus*, March for *N. flemingeri* and May for *N. plumchrus* and *E. bungii*. In contrast to these copepods with single recruitment seasons in the year, *M. pacifica* exhibited two recruitment seasons (mid-May and August) in a year. Phenology in reproduction and development of these copepods reflects their species-specific differences in energy utilization pattern ; *M. pacifica* and *E. bungii* spawn in phytoplankton-rich surface layer in spring (females need to feed for spawning) while *Neocalanus* spp. spawn in deep layer in winter (females do not feed). Development from C1 to C5 of *N. cristatus*, *N. flemingeri* and *N. plumchrus* was in January to June, March to June and May to August, respectively, thus the three sympatric *Neocalanus* spp. showed a clear temporal separation in the developmental timing in the western subarctic Pacific. This temporal separation in utilizing the surface layer is considered to be a mechanism to reduce inter-specific food competition. Regional comparison of phenology in copepods within the entire subarctic Pacific and its adjacent waters revealed that reproduction timing of the surface spawning *M. pacifica* and *E. bungii* was highly variable, while this was not the case for deep spawning *Neocalanus* spp.

Key words : *Metridia*, *Eucalanus*, *Neocalanus*, Life history, Regional comparison

Introduction

The subarctic Pacific Ocean and its marginal seas (Bering Sea, Okhotsk Sea and Japan Sea) have common sets of zooplankton fauna (Zenkevitch, 1963). Among the zooplankton species, large interzonal copepods such as *Metridia pacifica*, *Eucalanus bungii*, *Neocalanus cristatus*, *N. flemingeri* and *N. plumchrus* make up 73% of annual mean zooplankton biomass in the 0-2,000 m water column of the Oyashio region, western subarctic Pacific (Ikeda et al., 2008). Of these copepods, the life cycle was first evaluated on the regional *N. plumchrus* population in the Strait of Georgia, British Columbia, Canada (Fulton, 1973). Since then, the life cycle and associated ontogenetic vertical migration of oceanic populations of *N. cristatus*, *N. plumchrus*, *E. bungii* and *M. pacifica* were studied in great detail at Ocean Weather Station P (50°N, 145°W) in the Gulf of Alaska in 1980s (Miller et al., 1984 ; Batchelder, 1985). Through these studies at Station P, *N. flemingeri* was separated from *N. plumchrus* as a new species (Miller, 1988), and differences in the life cycle patterns between the two species were reported (Miller and Clemons, 1988).

Compared with the eastern subarctic Pacific, the first reports on the life cycles of the interzonal copepods from the western subarctic Pacific were those of Tsuda et al. (1999) on *N. flemingeri* and *N. plumchrus* and Kobari and Ikeda (1999) on *N. cristatus* both in the Oyashio region. From 2000s, a number of intensive studies have been made on the same and other copepods in the Oyashio region, including those on *N. cristatus* (Tsuda et al., 2004), *N. flemingeri* (Kobari and Ikeda, 2001a ; Tsuda et al., 2001a), *N. plumchrus* (Kobari and Ikeda, 2001b ; Tsuda et al., 2001a), *E. bungii* (Tsuda et al., 2004 ; Shoden et al., 2005), *M. pacifica*, *M. okhotensis* (Padmavati et al., 2004), *Pleuromamma scutullata*, *Heterorhabdus tanneri* (Yamaguchi and Ikeda, 2000a), *Gaidius variabilis* (Yamaguchi and Ikeda, 2000b), *Paraeuchaeta elongata*, *P. birostrata* and *P. rubra* (Yamaguchi and Ikeda, 2001) and four oncaeid copepods (Nishibe and Ikeda, 2007). In addition to

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life cycles of individual copepods, long-term variations in their abundance and its possible causes have been analyzed in recent years (cf. Tadokoro et al., 2005 ; Kobari et al., 2007 ; Chiba et al., 2008).

Despite a wealth of information about the life cycle of each copepod in the Oyashio region, published analyses focused on phenology are currently limited to four studies (e.g., Saito et al., 2002 ; Tadokoro et al., 2005 ; Chiba et al., 2008 ; Ikeda et al., 2008). Since the copepods are the major link between primary production and production of epipelagic fishes (Odate, 1994), micronektonic fishes (Moku et al., 2000) and ground fishes (Yamamura et al., 2002), and because they are mediators of vertical material transport via their active seasonal migration behavior (Kobari et al., 2003), information about phenology in dominant copepods and its control mechanisms is a basis for our better understanding of the trophodynamics of the Oyashio ecosystem.

In the present study, phenological features (timing of life cycle, such as mating, spawning, development and dormancy) in the five dominant copepods (*M. pacifica*, *E. bungii*, *N. cristatus*, *N. flemingeri* and *N. plumchrus*) in the Oyashio region are analyzed by using pooled seasonal data from multi-year sampling programs, as was practiced previously for the study of life cycles of *N. flemingeri* and *N. plumchrus* in the Japan Sea (Miller and Terazaki, 1989) and *Calanus marshallae*, *C. pacificus* and *M. lucens* (=*M. pacifica*) in Dabob Bay, Washington (Osgood and Frost, 1994). Phenological characteristics of the copepods in the Oyashio region are compared to those of the same species inhabiting other regions within the subarctic Pacific and its adjacent seas, and possible causes of the regional variations are discussed.

Materials and Methods

Sequential zooplankton samplings were conducted at Site H (41°30′N-42°30′N, 145°00′E-146°00′E, Fig. 1) in the Oyashio region, western subarctic Pacific, at one to three month intervals from 4 September 1996 through 5 October 1997 and 18 May 2002 through 11 December 2007 (Table 1). Samples were collected with a closing net (60 cm mouth diameter, 100 μm mesh size ; Kawamura, 1968, 1989) from 0-thermocline, thermocline-250 m, and 250-500 m during 1996-1997, and a NORPAC net (45 cm mouth diameter, 100 μm mesh size ; Motoda, 1957) from 0-500 m during 2002-2007. Both closing and NORPAC nets were equipped with a Rigosha flow-meter in the mouth ring to measure the amount of seawater filtered through the nets. After collection, zooplankton samples were immediately preserved in a 5% formalin-seawater solution buffered with borax.

In the land laboratory, *M. pacifica*, *E. bungii*, *N. cristatus*, *N. flemingeri*, and *N. plumchrus* were sorted from all of or half aliquots of the preserved zooplankton samples and counted under a dissecting microscope. The morphological features used to distinguish developmental stages of *M. pacifica* and *E. bungii* are given by Morioka (1976) and Johnson (1937), respectively. For *N. flemingeri* and *N. plumchrus*, species identification was possible based on relative size of maxilla to their body size from C2 onward (Tsuda et al., 1999 ; Kobari and Ikeda, 2001a). Since the seasonal abundance of C1 stage of *N. flemingeri/N. plumchrus* showed bimodal peak (cf. Fig. 4 of Kobari and Ikeda, 2001a), we assumed the early spring peak (mostly before April) is of *N. flemingeri* and the late spring peak (after May) is of *N. plumchrus* in this study.

Abundance of each copepodid stage was expressed as individuals m^{-2} in the 0-500 m water column. Since most of the species treated in this study have diapause phase in deep layer and reproduction of *Neocalanus* spp. is known to be occurred >500 m, we refer that mating or spawning of *Neocalanus* spp. from literatures (Tsuda et al., 1999 ; Kobari and Ikeda, 1999, 2001a, 2001b). Percent stage composition to the total abundance was calculated for each sample. Then the stage composition data were combined according to date since January 1 of each year (“Day of year” in Table 1). Prior to analysis, we made statistical test on annual variation in abundance and

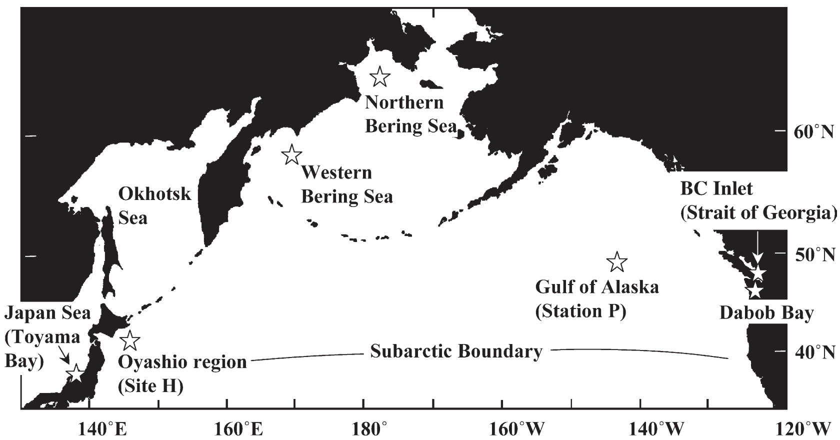

Fig. 1. Location of the sampling stations where the life history of the dominant copepods were reported (stars, cf. Fig. 6) in the subarctic Pacific and adjacent marginal seas.

Table 1. Zooplankton sampling dates at Site H in the western subarctic Pacific. Samples were collected from 0–500 m with stratified vertical hauls of closing net in 1996–1997 and of twin NORPAC net during 2002–2007. Mesh sizes of the both nets were the same (100 µm).

1996/1997		2002/2003		2004/2005		2006/2007	
Date	Day of year	Date	Day of year	Date	Day of year	Date	Day of year
4 Sep. 96	248	18 May 02	139	7 Feb 04	39	10 Mar. 06	70
19 Sep. 96	263	6 June 02	158	9 Mar 04	70	11 Mar. 06	71
1 Oct. 96	275	12 July 02	194	13 Mar 04	74	9 May 06	130
1 Dec. 96	335	12 Aug. 02	225	15 Mar 04	76	18 May 06	139
8 Dec. 96	342	8 Oct. 02	282	9 May 04	131	23 May 06	144
13 Jan. 97	13	17 Dec. 02	352	1 June 04	154	2 June 06	154
20 Feb. 97	51	11 Feb. 03	42	11 June 04	164	29 July 06	181
11 Apr. 97	101	11 Mar. 03	71	25 June 04	178	25 Oct. 06	299
5 May 97	126	10 May 03	131	21 Aug. 04	235	26 Oct. 06	300
3 June 97	155	20 May 03	141	4 Sep. 04	249	27 Oct. 06	301
22 June 97	174	3 June 03	155	5 Sep. 04	250	14 Dec. 06	349
1 July 97	183	14 June 03	166	14 Dec. 04	349	15 Dec. 06	350
17 Aug. 97	229	27 June 03	179	15 Dec. 04	350	8 May 07	129
26 Aug. 97	238	22 Aug. 03	235	19 Mar. 05	79	18 May 07	139
5 Oct. 97	278	4 Oct. 03	278	10 May 05	131	1 July 07	183
		16 Dec. 03	351	21 May 05	142	25 Aug. 07	238
				29 May 05	150	10 Dec. 07	345
				3 June 05	155	11 Dec. 07	346
				13 June 05	165		
				27 June 05	179		
				22 Aug. 05	235		
				14 Dec. 05	349		

mean stage of copepods, and found no significant annual variation (p=0.223–0.876, one-way ANOVA). On the premise that year-to-year differences in the timings of life cycles are minor, the eight years of data (1996–1997, 2002–2007) were combined to yield an averaged picture of annual cycles of percent stage composition of each copepod. Uneven gaps between sampling dates were interpolated to generate a sequenced estimate 15 days each over the year, and the resulting time series was smoothed by a 30-day running mean. Mean stage composition (*Mean S*) was computed : $Mean\ S = \sum (i \times N_i)/N$, where N_i is the number of ith copepodid stage (i=1 to 6), and N is the total number of copepodids.

Results

All copepodid stages (C1–C6) of *M. pacifica* occurred throughout the year (Fig. 2a). In January, the population structure of *M. pacifica* was characterized by the dominance of C6 (34% of the total population). The proportion of C6 increased progressively until the end of March, and reached its annual maximum (63% of the whole population) in early April. From May to August, the proportion of C6 was low (7–15%), and the most numerous stage was C1 (>18%). During this period (May–August), C1 had two abundance peaks : late May and August (Fig. 2a). After September, the proportion of C6 to the total population increased again, and stabilized at around 30–37% toward the end of the year. Mean stage composition (*Mean S*) of *M. pacifica* fluctuated between 2.9 in early June and 4.8 in November, indicating the copepodid recruitment season to be mainly in May–August (Fig. 2a). Since female/male separation was possible from C4 to C6 for *M. pacifica*, female and male population structures (C4–C6) are shown separately (Fig. 2b, c). While population structures of females and males were basically parallel, that is, C4 and C5 were both abundant during June–August, and C6 in March–April, the dominance of C6 was slightly earlier (March) for males than for females (April) (Fig. 2b, c).

The population of *E. bungii* was composed of C3–C6 during January to March and the proportion of C6 gradually increased from 3% to 26% during the period (Fig. 3a). The occurrence of C1 and C2 was restricted to April–September. After October to the end of the year, C3–C6 became the major component of the population. The annual minimum of *Mean S*, 3.2 were observed in June–July. It increased rap-

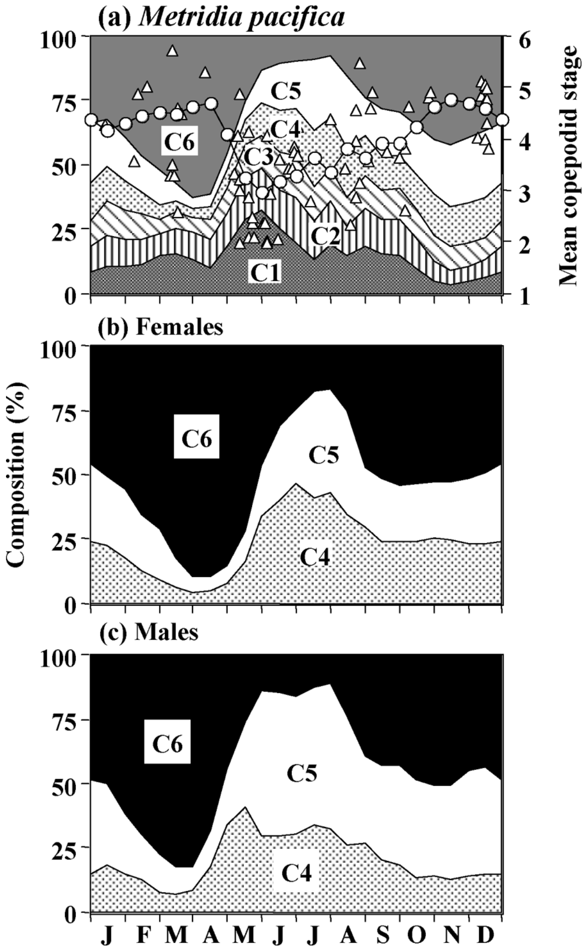

Fig. 2. Seasonal changes in stage composition and mean copepodid stage (triangles : raw data, circles : mean data) of *Metridia pacifica* (a) and their population structure (C4–C6) of females (b) and males (c) in the Oyashio region, western subarctic Pacific.

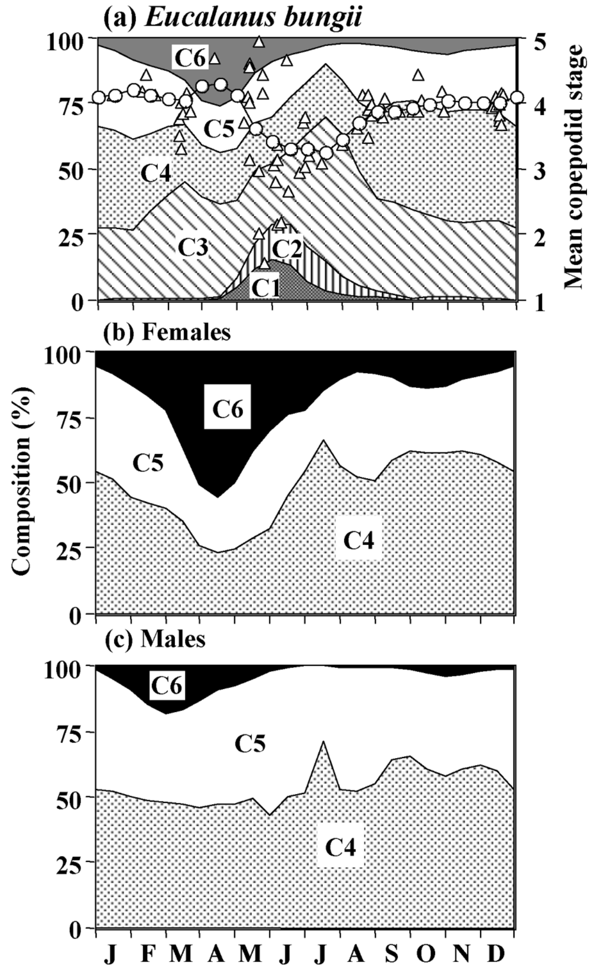

Fig. 3. Seasonal changes in stage composition and mean copepodid stage (triangles : raw data, circles : mean data) of *Eucalanus bungii* (a) and their population structure (C4–C6) of females (b) and males (c) in the Oyashio region, western subarctic Pacific.

idly to 4 in October (Fig. 3a), then more gradually toward the annual maximum of 4.3 in April of the next year. That was maturation of the overwintering population. Then, *Mean S* returned to the annual minimum in June because of recruitment of new population. Since the separation by sex was possible from C4 to C6 for *E. bungii*, population structures (C4–C6) of females and males were constructed separately (Fig. 3b, c). Females were dominated by C4 during July–November (>60%), C5 during January–February (>40%) and C6 during April–May (>50%) (Fig. 3b). In contrast, the population structure of males was stable throughout the year, with only an exception for C6, which was most numerous in February–March (>15%) or two months earlier than that (April–May) of the C6 females (Fig. 3b, c).

C1–C5 stages of *N. cristatus* occurred throughout the year, but C6 was found only occasionally in small numbers (<1% of the total population) (Fig. 4a). Annual population structure of *N. cristatus* was characterized by the predominance of C1 in early January (70% of the total population), C2 in February–April (26–27%), C3 in April–May (26–29%), C4 in May–June (22–25%) and C5 in August (38–39%) (Fig. 4a). During the June to October period, there were only minor changes in population structure. A small number of C1 continued to occur during the same period (June to October). After October, the proportion of C1 stage increased rapidly and reached its annual maximum (75%) at the end of December. *Mean S* of *N. cristatus* was the lowest during December–January (1.5), increased progressively from January to May, and reached its annual maximum in May (3.9). During May to October, *Mean S* decreased to 3.0, followed by a rapid decline to the annual minimum (1.5) at the end of December (Fig. 4a).

While C4 and C6 stages of *N. flemingeri* were found throughout the year, C1–C3 and C5 occurred only seasonally (Fig. 4b). The fraction of C1 stage was low in January, but it increased and reached its annual peak (25%) in mid-March (Fig. 4b). Abundance of C2 and C3 was also high (20–25%) during March–April and April–May, respectively. C1–C3

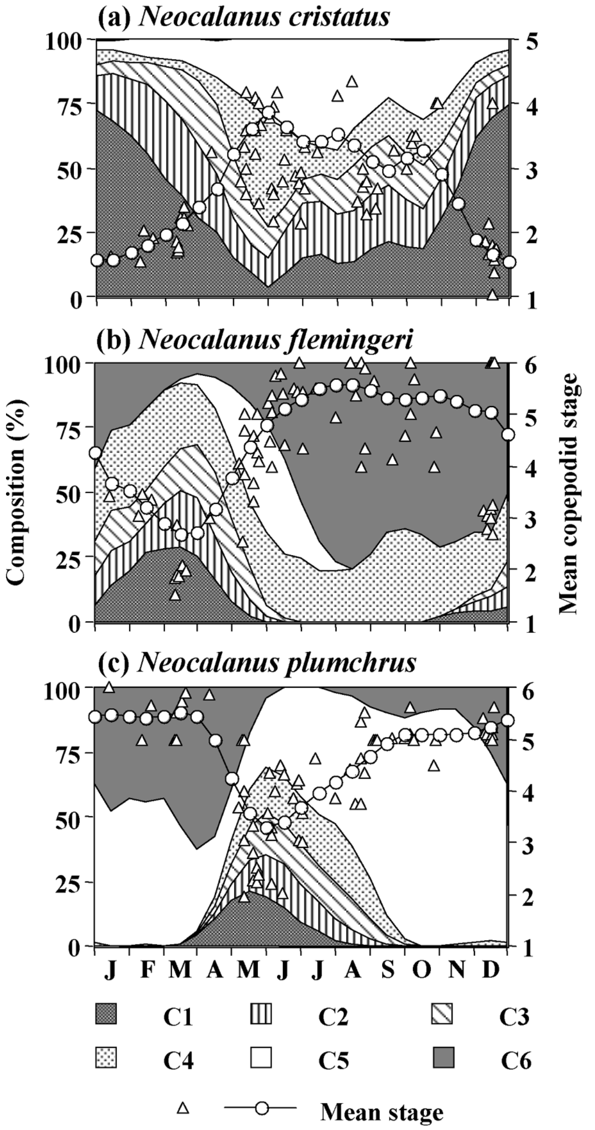

Fig. 4. Seasonal changes in stage composition and mean copepodid stage (triangles : raw data, circles : mean data) of *Neocalanus cristatus* (a), *N. flemingeri* (b) and *N. plumchrus* (c) in the Oyashio region, western subarctic Pacific.

were not observed during July to September, and C6 was the major component of the population during this period (60–70% of the total population). C5 was found only from March to July. The annual pattern of *Mean S* of *N. flemingeri* showed a smooth curve, characterized by the annual minimum (2.7) in March and the annual maximum (5.5) in August (Fig. 4b).

Unlike *N. flemingeri*, C5 was the only stage of *N. plumchrus* that was found throughout the year (Fig. 4c). This is because C5 is the only dormant stage for *N. plumchrus*. During January to March, C5 and C6 of *N. plumchrus* were the predominant component of the population. C1 increased from March and peaked in mid-May. Fractions of C2, C3 and C4 were greater (>10%) during May-August. C5 predominated (>70%) during September to December, then were replaced by C6 during January to March. In terms of *Mean S*, the population structure of *N. plumchrus* was stable at 5.5 during January-March, decreased rapidly during April to May, and reached the annual minimum in late May. *Mean S* increased from May to September, and was stable October through end of November, then increased maturation in December and early January.

Discussion

Potential source of errors (annual variation and depth limitation)

In contrast to our premise that the time schedule of life cycle of the copepods is stable across the years studied, year-to-year variations in the developmental timing of *N. plumchrus* in response to ocean climate fluctuations have been reported at Station P in the Gulf of Alaska between 1956 and 2005 (Mackas et al., 1998, 2007). In the Oyashio region, Tadokoro et al. (2005) reported inter-annual variation in the abundance of *N. cristatus*, *N. flemingeri* and *N. plumchrus* in spring and summer during 1972 to 1999. According to Tadokoro et al. (2005), the developmental stage index (*DSI*= *Mean S* in this study) of *N. cristatus* varied from 4.17 (1978–1989) to 3.87 (1990–1999) during summer. The indices of *N. flemingeri* and *N. plumchrus* changed little through the regime shifts in 1976/1977 and 1988/1989 (Tadokoro et al., 2005). According to recent analysis of Chiba et al. (2008), the change in the copepod population structures in the Oyashio region occurred immediately or shortly following the significant changes in ocean climate and atmospheric forcing. To evaluate presence or absence of climatic regime shifts in the Oyashio region during our study period (1996–2007), we analyzed climate indices from the websites, including Arctic Oscillation (AO) index (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml), North Pacific Index (NPI) (http://www.cgd.ucar.edu/cas/jhurrell/npindex.html), and Pacific Decadal Oscillation (PDO) (ftp://ftp.atmos.washington.edu/mantua/pnw_impacts/iNDICES/PDO.latest). None of these indices (AO, NPI and PDO) showed any drastic regime shifts during the 1996–2007 period. In support of this conclusion, temperature and salinity profiles at our study site during 1996–2007 showed repetition of the same pattern (cf. Fig. 2 of Kobari and Ikeda, 1999). Statistical test on abundance and mean stage of copepods also showed no inter-annual changes (p=0.223–0.876), and raw data on mean stage showed similar repetition during the study period (Figs. 2a, 3a, 4).

As another source of error, the copepod data we used in the present analyses are from the 0–500 m water column, whereas the copepods often extend their vertical distribution range deeper than 500 m (Vinogradov, 1968). The populations below 500 m (mostly late copepodid stages) are not taken into account in our analyses. These overlooked populations affect the population structure and calculation of *Mean S* of each copepod (Figs. 2–4). Nevertheless, active growth of all the copepods in this study is achieved in the 0–500 m water column, so the omission of part of the population (late stages) below 500 m likely little affects our analyses of inter-specific differences in the phenology in spawning events and development patterns of the large copepods in this study. For deep-spawning species (*Neocalanus* spp.), we determined mating season from literatures (Kobari and Ikeda, 1999, 2001a, 2001b ; Tsuda et al., 1999, 2004), and spawning period from abundance of early copepodid stage and development time observed by laboratory rearing (Saito and Tsuda, 2000).

Phenology in life cycles of copepods

Based on the present analyses and literature data, average phenology in mating, spawning, growth and dormancy (quiescence and diapause) of the large dominant copepods in the Oyashio region are summarized in Fig. 5.

Metridia pacifica repeat two generations in the year, although recruitment of young continues in all seasons (Fig. 2a). The first generation is characterized by rapid development during just after the spring phytoplankton bloom (generation length : 2–3 months), and the second generation by slow development (generation length : 9–10 months) and overwintering at C5 in deeper-layers (up to 1,000–2,000 m) (Padmavati et al., 2004). Based on the egg-hatching time and naupliar development time determined by laboratory-rearing experiments (Padmavati and Ikeda, 2002), spawning is considered to occur 1.5–2 months before the abundance peak of C1. Thus, the first major spawning is during the phytoplankton bloom, and the second spawning after the bloom. The first major spawning in March–April coincides with the peak of C6F (Fig. 2b). Slightly faster development to C6M (Fig. 2c) than to C6F is also reported for the populations in Toyama Bay, southern Japan Sea (Hirakawa and Imamura, 1993). The overwintering copepodid stage is C5, most of which reside >500 m (Padmavati et al., 2004). The population structure during winter season in Fig. 2a is just those in the upper 500 m. According to Padmavati et al. (2004), the energy needs of overwintering *M. pacifica* are likely supplied by both feeding in winter and lipid stored in the body. Dependence on dual energy sources may be due to a higher energy demand to sustain continuous glide-swimming at depth by *M. pacifica*, a trait that contrasts to the cessation of feeding and reduced swimming activity of overwintering *Neocalanus* spp. and *E. bungii* mentioned below.

Eucalanus bungii spawn in April/May in the surface layer (Fig. 5). Resultant C1 form prominent abundance peaks in early June (Fig. 3a). The C1 develop and reach C3–C5 by August. From August onwards, C3–C5 sink to depth, and enter diapause to overwinter at >500 m depth (Shoden et al., 2005). The C5M molt to C6M in February (Fig. 3c) and C5F molt to C6F in April (Fig. 3b). Faster development of male than female in C5–C6 is also reported in the Gulf of Alaska (Miller et al., 1984) and Oyashio region (Shoden et al., 2005).

Both *E. bungii* and *M. pacifica* exhibit active spawning during spring phytoplankton bloom (Fig. 5), suggesting that the females of both species obtain energy needed for spawning from recent feeding on rich phytoplankton. For *E. bungii*, the amount of lipid droplets stored in the body is much less than that of *Neocalanus* spp. Nevertheless, a calculation of metabolic energy requirement for *E. bungii* C5 in diapause showed that they could live for 222 days or 7.4 months by utilizing the stored lipid as sole energy source (Shoden et al., 2005). Thus, *E. bungii* C5 could overwinter without feeding until next spring bloom.

Neocalanus cristatus releases eggs throughout the year below 500 m depth, with a peak from October to December (Kobari and Ikeda, 1999). The eggs and nauplii float/migrate upward. In the surface layer, the C1 develop and reach C5 by early June. C5 migrate to deeper layers in July and August, where they molt to adults, mate and spawn again (Kobari and Ikeda, 1999 ; Tsuda et al., 2004). The developmental time from eggs to C1 has been estimated to be about 40 days at 2°C in laboratory experiments (Saito and Tsuda, 2000). From the naupliar development time and the peak season of C1 (January, cf. Fig. 4a), the spawning date can be back-calculated as late November in this study (Fig. 5). It is noted that the copepodid developmental time of *N. cristatus* (6 months) is much longer than those (about 3 months) of *N. flemingeri* and *N. plumchrus* (Fig. 5).

Neocalanus flemingeri overwinters as adults and spawns at 250–1,000 m in January–February (Kobari and Ikeda, 2001a). Hatched nauplii migrate upward. The young develop in the

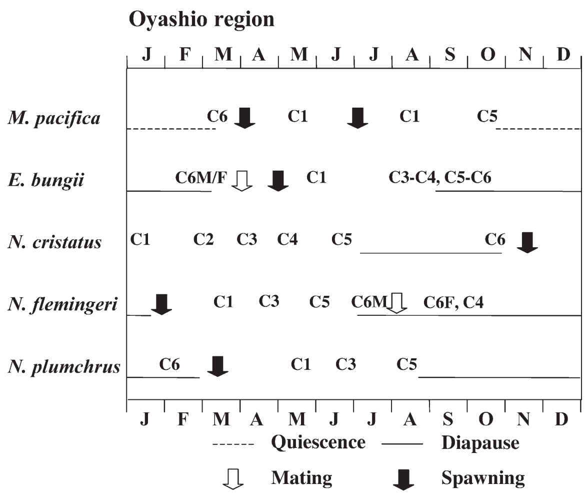

Fig. 5. Schematic diagram showing life cycle timing (mating, spawning, quiescence and diapause) of five dominant copepods in the Oyashio region, western subarctic Pacific. Dominant copepodid stages are also shown in the panel.

surface layer and reach C5 by early June (the end of the phytoplankton bloom). While most C5 sink to depth, part of the population remains as C4 and resides at about 300 m (Kobari and Ikeda, 2001a). C5 molt to C6 males (May to July) and C6 females with immature gonads (June to December). C6 males die shortly after descent, and gonads of C6 females mature in January to February. The life cycle of *N. flemingeri* was estimated as annual for most of the populations, but the part of the population overwintering as C4 may have a biennial life cycle (Kobari and Ikeda, 2001a ; Tsuda et al., 2001a). The specific ratio of C4 : C6 was 30 : 70 during resting period (August to October) (Fig. 4b). The dominance of C6 during their resting period suggests that the majority of the population has an annual life cycle. As a notable feature of overwintering copepodid stages, that of *N. flemingeri* is C4 and C6 females in contrast to C5 for the other *Neocalanus* spp. (Fig. 5).

Neocalanus plumchrus spawns in October to April below 250 m depth (Kobari and Ikeda, 2001b). The arrival of nauplii and early copepodids in the surface layer, and their subsequent development to C5 occur in the mid- to late spring phytoplankton bloom (Tsuda et al., 1999 ; Kobari and Ikeda, 2001b). The C5 migrate to the deeper layers in July-August where they molt to adults. Development time of C5 to C6 is highly variable. Among the *Neocalanus* spp., an anomalous feature of the life cycle of *N. plumchrus* is their long spawning period (October to April) (Kobari and Ikeda, 2001b). This long spawning (the maturation onset is much earlier and more prolonged) is also the case of Gulf of Alaska (Miller et al., 1984). While our data set showed that the maturation of adults was later (end of the year and beginning of the next year) and was relatively brief (Fig. 4c), which is the similar phenomenon reported in the eastern fjord (Georgia Strait) (Fulton, 1973). Judging from the C1 peak in May (Fig. 4c) and estimated development time (40 days) between egg to C1 at 2°C (Saito and Tsuda, 2000), their reproduction peak is estimated to be in March.

Overall, phenology in life cycle patterns of interzonal copepods in the Oyashio region differs from one species to the next. The five species not only partition space (depth) and time (season) of spawning, but also two species need to feed immediately prior to spawning (*M. pacifica* and *E. bungii*), while three others do not (*Neocalanus* spp.). Nevertheless, the spring phytoplankton bloom is the most important annual event for all these copepods through which they achieve rapid development than the other season and accumulate large amounts of lipid in the body as an energy source for overwintering and reproduction at depth without feeding (as an exception, *M. pacifica* may continue to feed). The three sympatric *Neocalanus* spp. have clear seasonal separation in copepodid developmental timing (Fig. 5), a mechanism that reduces niche-overlap among species with similar morphology (=similar food habits). While developmental timing of *N. cristatus* is overlapped with both *N. flemingeri* and *N. plumchrus*, vertical separation (shallow : *N. flemingeri* and *N. plumchrus* vs. deep : *N. cristatus*) is reported within the same period (Mackas et al., 1993 ; Sato et al., in press).

Regional comparison

Within the subarctic Pacific and its adjacent seas, a large regional variation in spawning periods is evident for *M. pacifica* populations in Dabob Bay, Gulf of Alaska, northern and western Bering Sea and Japan Sea, and *E. bungii* populations in British Columbia Inlet, Gulf of Alaska and western Bering Sea (Fig. 6). On the other hand, such large between-region variation is not present for the spawning periods of *Neocalanus* spp. from Gulf of Alaska, Strait of Georgia, western Bering Sea or Japan Sea (Fig. 6). The differences seen in the regional variation patterns may reflect their dissimilar spawning traits ; because *M. pacifica-E. bungii* need to feed before spawning they must adjust their spawning to match the incidence of local phytoplankton bloom. Because *Neocalanus* spp. do not feed for spawning, their spawning timing is not constrained by the incidence of regional phytoplankton blooms.

Generation number per year of *M. pacifica* varied also with region : one (northern Bering Sea and Japan Sea), two (Oyashio region), three (Dabob Bay and Gulf of Alaska) and four (western Bering Sea) per year (Fig. 6). The reproductive period of *M. pacifica* (which coincides with phytoplankton bloom periods) is delayed with increasing latitude (Fig. 1) : January in the southern Japan Sea, February in Dabob Bay, Washington, USA, March in the Gulf of Alaska, April in the Oyashio region, May in the western Bering Sea and July in the northern Bering Sea (July) (Figs. 5, 6). In theoretical mean, there are two peaks of phytoplankton abundance in temperate latitudes, while only one peak at summer in higher latitudes (cf. Fig. 3.9 of Lalli and Parsons, 1997). Assuming this schema on seasonal cycle of phytoplankton, we concluded that reproductive season of *M. pacifica* was corresponded with the phytoplankton bloom at each region. For the populations in the Bering Sea, Oyashio region and Japan Sea, quiescence of *M. pacifica* at C5 stage has been known. This quiescence occurs during winter in the Oyashio region and Bering Sea, but in summer (aestivation) in the Japan Sea. Aestivation in the Japan Sea is considered to avoid high thermal condition of the surface layer during summer (Hirakawa and Imamura, 1993).

Generation length of *E. bungii* also varies with location, i.e. one year (British Columbia Inlet, western Bering Sea and Oyashio region), vs. two to three years in the Gulf of Alaska (Miller et al., 1984). Their reproductive periods also varied with location. Within the same habitats, *E. bungii* spawn about two months after *M. pacifica.* For example, respective spawning periods of *E. bungii* and *M. pacifica* are April and February in British Columbia Inlet, June and March in the

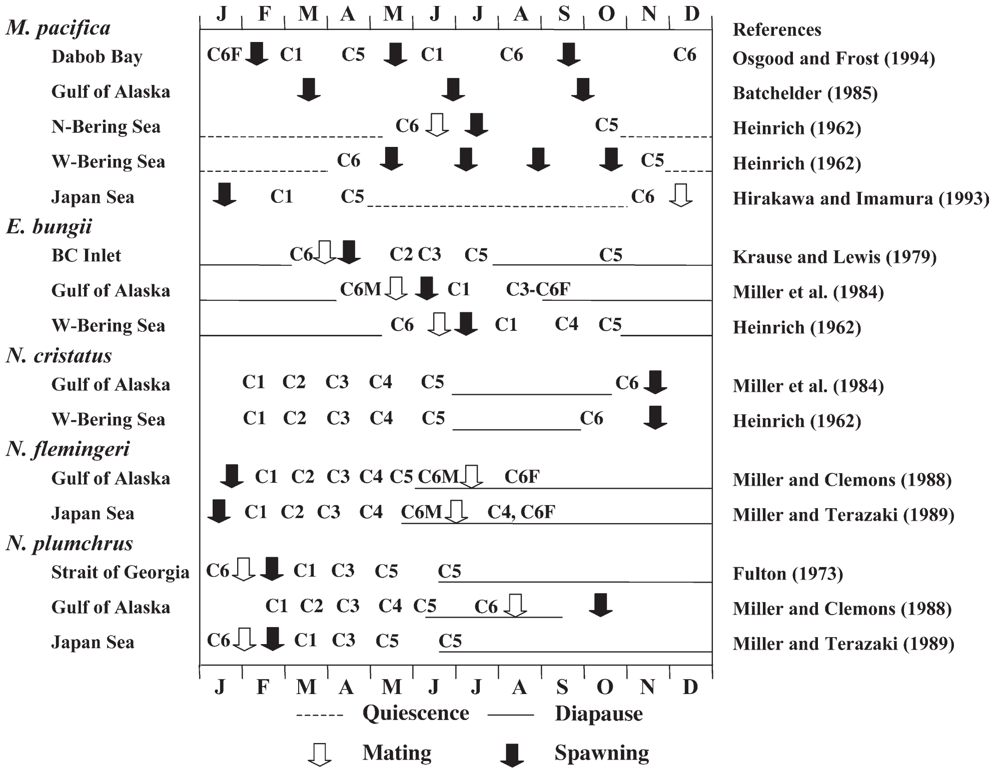

Fig. 6. Schematic diagram showing life cycle timing (mating, spawning, quiescence and diapause) of five dominant copepods in the subarctic Pacific (except Oyashio region, Fig. 5) and their marginal seas. Sources of references are shown in the right column.

Gulf of Alaska, and July and May in the western Bering Sea (Fig. 6). Delay in spawning of *E. bungii* in response to phytoplankton bloom is due to the need of extra time for the development of C3–C5 stages in diapause to mature. Unlike *E. bungii*, *M. pacifica* in quiescence as C6F can respond quickly to the phytoplankton bloom and spawn in a short time.

Major diapause stage of *E. bungii* has been reported as C5 in the British Columbia Inlet (Krause and Lewis, 1979) and western Bering Sea (Heinrich, 1962), C3–C4 in the Gulf of Alaska (Miller et al., 1984) and C3–C5 in the Oyashio region (Shoden et al., 2005). These differences in diapause stages may be related to the differences in development of newly born individuals achieved by the beginning of winter as a result of complex interactions among environmental conditions (temperature, foods etc.) (Saito et al., 2011). From this viewpoint, populations entering diapause at C5 are the result of earlier birth dates (British Columbia Inlet) or rich phytoplankton in summer (western Bering Sea). Conversely, the major attributes for the populations entering diapause at C3–C4 in the Gulf of Alaska or C4–C5 in the Oyashio region are considered to be low phytoplankton abundance and short developmental period which caused by the high thermal condition for the former region.

Compared with *M. pacifica* and *E. bungii*, which exhibit highly variable life cycle patterns within the subarctic North Pacific and its adjacent seas, *Neocalanus* spp. showed rather stable life cycle patterns across the subarctic North Pacific (Fig. 6). Briefly, *N. cristatus* spawn in winter, hatched nauplii develop C1–C5 in January–June, then descend to deep layer to enter diapause (as C5), and subsequent maturation and reproduction (annual life cycle, Fig. 6). *N. flemingeri* reproduce early in the year (January or February), develop to C1–C5 in February–May, then descend to deep layer in July. *N. flemingeri* overwinter as C6F (annual life cycle), but part of the population overwinter as C4 in the Japan Sea and Oyashio region and need two years for maturation (two year life cycle). *N. plumchrus* releases eggs in March, and resulting offspring develop to C1–C5 in May to July, then sink to depth in July–August to enter diapause (as C5), followed by maturation and reproduction (Fig. 6). While several differences in developmental timing is reported spatially (Goldblatt et al., 1999) and temporally (Mackas et al., 1998, 2007), well-synchronized developmental timing of three *Neocalanus* copepods throughout their broad geographical distribution (Fig. 6) suggests that the presence of endogenous clock with a strong implication to achieve niche-separation within sympatric congener species in the surface layer.

Within the *Neocalanus* species, the resting stage is C5 for *N. cristatus* and *N. plumchrus*, but is C6F or C4 for *N. flemingeri* (Miller and Terazaki, 1989). Not only anomalous resting stages (compared to other species of *Neocalanus*), but cooccurrence of two distinct size populations (large-form and small-form) are observed for *N. flemingeri* in the western subarctic Pacific (Tsuda et al., 1999, 2001b ; Kobari and Ikeda, 2001a). It should be an important local variation in life histories of this species.

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Literature cited

Batchelder, H.P. (1985) Seasonal abundance, vertical distribution, and life history of *Metridia pacifica* (Copepoda : Calanoida) in the oceanic subarctic Pacific. *Deep-Sea Res.*, **32A**, 949-964.

Chiba, S., Aita, M.N., Tadokoro, K., Saino, T., Sugisaki, H. and Nakata, K. (2008) From climate regime shifts to lower-trophic level phenology : Synthesis of recent progress in retrospective studies of the western North Pacific. *Prog. Oceanogr.*, **77**, 112-126.

Fulton, J. (1973) Some aspects of the life history of *Calanus plumchrus* in the Strait of Georgia. *J. Fish. Res. Bd Canada*, **30**, 811-815.

Goldblatt, R.H., Mackas, D.L. and Lewis, A.G. (1999) Mesozooplankton community characteristics in the NE subarctic Pacific. *Deep-Sea Res. II*, **46**, 2619-2644.

Heinrich, A.K. (1962) On the production of copepods in the Bering Sea. *Int. Rev. Ges. Hydrobiol.*, **47**, 465-469.

Hirakawa, K. and Imamura, A. (1993) Seasonal abundance and life history of *Metridia pacifica* (Copepoda : Calanoida) in Toyama Bay, southern Japan Sea. *Bull. Plankton Soc. Japan*, **40**, 41-54.

Ikeda, T., Shiga, N. and Yamaguchi, A. (2008) Structure, biomass distribution and trophodynamics of the pelagic ecosystem in the Oyashio region, western subarctic Pacific. *J. Oceanogr.*, **64**, 339-354.

Johnson, M.W. (1937) The developmental stages of the copepod *Eucalanus elongatus* Dana var. *bungii* Giesbrecht. *Trans. Am. Microsc. Soc*., **56**, 79-98.

Kawamura, A. (1968) Performance of Peterson type closing net. *Bull. Plankton Soc. Japan*, **15**, 11-12.

Kawamura, A. (1989) Fast sinking mouth ring for closing NORPAC net. *Bull. Japan. Soc. Sci. Fish*., **55**, 1121.

Kobari, T. and Ikeda, T. (1999) Vertical distribution, population structure and life cycle of *Neocalanus cristatus* (Crustacea : Copepoda) in the Oyashio region, with notes on its regional variations. *Mar. Biol.*, **134**, 683-696.

Kobari, T. and Ikeda, T. (2001a) Life cycle of *Neocalanus flemingeri* (Crustacea : Copepoda) in the Oyashio region, western subarctic Pacific, with notes on its regional variations. *Mar. Ecol. Prog. Ser*., **209**, 243-255.

Kobari, T. and Ikeda, T. (2001b) Ontogenetic vertical migration and life cycle of *Neocalanus plumchrus* (Crustacea : Copepoda) in the Oyashio region, with notes on regional variations in body sizes. *J. Plankton Res.*, **23**, 287-302.

Kobari, T., Shinada, A. and Tsuda, A. (2003) Functional roles of interzonal migrating mesozooplankton in the western subarctic Pacific. *Prog. Oceanogr.*, **57**, 279-298.

Kobari, T., Tadokoro, K., Sugisaki, H. and Itoh, H. (2007) Response of *Eucalanus bungii* to oceanographic conditions in the western subarctic Pacific Ocean : Retrospective analysis of the Odate Collections. *Deep-Sea Res. II*, **54**, 2748-2759.

Krause, E.P. and Lewis, A.G. (1979) Ontogenetic migration and the distribution of *Eucalanus bungii* (Copepoda ; Calanoida) in British Columbia inlets. *Can. J. Zool.*, **57**, 2211-2222.

Lalli, C.M. and Parsons, T.R. (1997) *Biological Oceanography An Introduction Second Edition*. Butterworth Heinemann, Oxford.

Mackas, D.L., Sefton, H., Miller, C.B. and Raich, A. (1993) Vertical habitat partitioning by large calanoid copepods in the oceanic subarctic Pacific during spring. *Prog. Oceanog.*, **32**, 259-294.

Mackas, D.L., Goldblatt, R. and Lewis, A.G. (1998) Interdecadal variation in developmental timing of *Neocalanus plumchrus* populations at Ocean Station P in the subarctic North Pacific. *Can. J. Fish. Aquat. Sci.*, **55**, 1878-1893.

Mackas, D.L., Batten, S. and Trudel, M. (2007) Effects on zooplankton of a warmer ocean : Recent evidence from the Northeast Pacific. *Prog. Oceanogr*., **75**, 3-252.

Miller, C.B. (1988) *Neocalanus flemingeri*, A New Species of Calanidae (Copepoda : Calanoida) from the Subarctic Pacific Ocean, with a comparative redescription of *Neocalanus plumchrus* (Marukawa) 1921. *Prog. Oceanogr.*, **20**, 223-273.

Miller, C.B. and Clemons, M.J. (1988) Revised life history analysis for large grazing copepods in the subarctic Pacific Ocean. *Prog. Oceanogr.*, **20**, 293-313.

Miller, C.B. and Terazaki, M. (1989) The life histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* in the Sea of Japan. *Bull. Plankton Soc. Japan*, **36**, 27-41.

Miller, C.B., Frost, B.W., Batchelder, H.P., Clemons, M.J. and Conway, R.E. (1984) Life histories of large, grazing copepods in a subarctic ocean gyre : *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the Northeast Pacific. *Prog. Oceanogr.*, **13**, 201-243.

Moku, M., Kawaguchi, K., Watanabe, H. and Ohno, A. (2000) Feeding habits of three dominant myctophid fishes, *Diaphus theta*, *Stenobrachius leucopsarus* and *S. nannochir*, in the subarctic and transitional waters of the western North Pacific. *Mar. Ecol. Prog. Ser.*, **207**, 129-140.

Morioka, Y. (1976) Vertical invasion of boreal calanoid copepods into the shallow warm stratum. *Bull. Japan Sea Reg. Fish. Res. Lab.*, **27**, 91-101.

Motoda, S. (1957) North Pacific standard plankton net. *Inform. Bull. Planktol. Japan*, **4**, 13-15 (in Japanese with English abstract).

Nishibe, Y. and Ikeda, T. (2007) Vertical distribution, population structure and life cycles of four oncaeid copepods in the Oyashio region, western subarctic Pacific. *Mar. Biol.*, **150**, 609-625.

Odate, K. (1994) Zooplankton biomass and its long-term variation in the western North Pacific Ocean, Tohoku sea area, Japan.

Bull. Tohoku Natl. Fish. Res. Inst., **56**, 115-173 (in Japanese with English abstract).

Osgood, K.E. and Frost, B.W. (1994) Comparative life histories of three species of planktonic calanoid copepods in Dabob Bay, Washington. *Mar. Biol*., **118**, 627-636.

Padmavati, G. and Ikeda, T. (2002) Development of *Metridia pacifica* (Crustacea : Copepoda) reared at different temperatures in the laboratory. *Plankton Biol. Ecol*., **49**, 93-96.

Padmavati, G., Ikeda, T. and Yamaguchi, A. (2004) Life cycle, population structure and vertical distribution of *Metridia* spp. (Copepoda : Calanoida) in the Oyashio region (NW Pacific Ocean). *Mar. Ecol. Prog. Ser*., **270**, 181-198.

Saito, H. and Tsuda, A. (2000) Egg production and early development of the subarctic copepods *Neocalanus cristatus*, *N. plumchrus* and *N. flemingeri*. *Deep-Sea Res. I*, **47**, 2141-2158.

Saito, H., Tsuda, A. and Kasai, H. (2002) Nutrient and plankton dynamics in the Oyashio region of the western subarctic Pacific Ocean. *Deep-Sea Res. II*, **49**, 5463-5486.

Saito, R., Yamaguchi, A., Saitoh, S.-i., Kuma, K. and Imai, I. (2011) East-west comparison of the zooplankton community in the subarctic Pacific during summers of 2003-2006. *J. Plankton Res*., **33**, 145-160.

Sato, K.-i., Yamaguchi, A., Ueno, H., Ikeda, T. (2011) Vertical segregation within four grazing copepods in the Oyashio region during early spring. *J. Plankton Res.* (in press).

Shoden, S., Ikeda, T. and Yamaguchi, A. (2005) Vertical distribution, population structure and life cycle of *Eucalanus bungii* (Copepoda : Calanoida) in the Oyashio region, with notes on its regional variations. *Mar. Biol*., **146**, 497-511.

Tadokoro, K., Chiba, S., Ono, T., Midorikawa, T. and Saino, T. (2005) Interannual variation in *Neocalanus* biomass in the Oyashio waters of the western North Pacific. *Fish. Oceanogr*., **14**, 210-222.

Tsuda, A., Saito, H. and Kasai, H. (1999) Life histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* (Calanoida : Copepoda) in the western subarctic Pacific. *Mar. Biol*., **135**, 533-544.

Tsuda, A., Saito, H. and Kasai, H. (2001a) Life history strategies of subarctic copepods *Neocalanus flemingeri* and *N. plumchrus*, especially concerning lipid accumulation patterns. *Plankton Biol. Ecol*., **48**, 52-58.

Tsuda, A., Saito, H. and Kasai, H. (2001b) Geographical variation of body size of *Neocalanus cristatus*, *N. plumchrus* and *N. flemingeri* in the subarctic Pacific and its marginal seas : implications for the origin of large form of *N. flemingeri* in the Oyashio area. *J. Oceanogr*., **57**, 341-352.

Tsuda, A., Saito, H. and Kasai, H. (2004) Life histories of *Eucalanus bungii* and *Neocalanus cristatus* (Copepoda : Calanoida) in the western subarctic Pacific Ocean. *Fish. Oceanogr*., **13**, S10-S20.

Vinogradov, M.E. (1968) *Vertical Distribution of the Oceanic Zooplankton.* Academy of Science of the U.S.S.R., Institute of Oceanography, Moscow. (in Russian, translated by Israel Program for Scientific Translations in 1970) Keter Press, Jerusalem.

Yamaguchi, A. and Ikeda, T. (2000a) Vertical distribution, life cycle, and body allometry of two oceanic calanoid copepods (*Pleuromamma scutullata* and *Heterorhabdus tanneri*) in the Oyashio region, western North Pacific Ocean. *J. Plankton Res*., **22**, 29-46.

Yamaguchi, A. and Ikeda, T. (2000b) Vertical distribution, life cycle and developmental characteristics of mesopelagic calanoid copepod *Gaidius variabilis* (Aetideidae) in the Oyashio region, western North Pacific Ocean. *Mar. Biol*., **137**, 99-109.

Yamaguchi, A. and Ikeda, T. (2001) Abundance and population structure of three mesopelagic *Paraeuchaeta* species (Copepoda : Calanoida) in the Oyashio region, western subarctic Pacific Ocean with notes on their carcasses and epizoic ciliates. *Plankton Biol. Ecol*., **48**, 104-113.

Yamamura, O., Honda, S., Shida, O. and Hamatsu, T. (2002) Diets of walleye pollock *Theragra chalcogramma* in the Doto area, northern Japan : ontogenetic and seasonal variations. *Mar. Ecol. Prog. Ser*., **238**, 187-198.

Zenkevitch, L. (1963) *Biology of the Seas of the U.S.S.R.* George Allen and Unwin Ltd, London.