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Seasonal, regional, and diel changes in the abundance of five large, dominant copepods in the western subarctic Pacific : Insights from Continuous Plankton Recorder surveys

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Abstract

In the marine ecosystem, mesozooplankton, especially large copepods, have an important role both in the mediation of primary production to higher trophic levels and in the transportation of organic materials from the surface to the deep ocean, termed the biological pump. Continuous Plankton Recorder (CPR) surveys have been used as a long-term monitoring method for mesozooplankton over wide geographical areas, including the North Pacific, where a CPR survey began in 2000. In this study, we used CPR samples collected in the western subarctic Pacific during 2001–2015 to investigate the abundance and population structure of five large, dominant copepods (*Neocalanus cristatus*, *N. flemingeri*, *N. plumchrus*, *Eucalanus bungii* and *Metridia pacifica*) and evaluate the differences in season, region, and diel scales between species. Significant seasonal changes in abundance and population structure were detected, and these changes were considered to reflect the life history of each species. Regional differences were detected for the three *Necalanus* species and were considered to be related to sea surface temperature and food availability. Diel changes in abundance were observed for *N. cristatus* and *M. pacifica*, with both species more abundant near the surface at night suggesting diel vertical migration.

Key words : Continuous Plankton Recorder, Copepods, *Eucalanus bungii, Metridia pacifica*, *Neocalanus* spp., Western Subarctic Pacific

Introduction

In the marine ecosystem, mesozooplankton, especially large copepods, have an important role both in the mediation of primary production to higher trophic levels and in the transportation of organic materials from the surface to the deep ocean, termed the biological pump (Kobari et al., 2003 ; Jónasdóttir et al., 2015). Continuous Plankton Recorder (CPR) instruments, which are towed by commercial vessels, have been used in the North Atlantic since 1931 as a long-term monitoring method for large copepods covering wide geographical areas (Batten et al., 2003a ; Richardson et al., 2006). Currently, CPRs are towed in more than seven areas in the world's oceans, and these surveys are helping clarify the effect of climate change on the zooplankton community (Beaugrand et al., 2002 ; Beaugrand and Kirby, 2010).

Because CPRs are towed continually, diel changes in abundance of the dominant copepods have been reported in the North Atlantic, where the majority of CPR samples have been collected (Hays, 1995a, 1995b ; Hays et al., 1995). Such diel changes in abundance have been attributed to diel vertical

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migration (DVM) behaviour (Hays et al., 1995). In the North Pacific, similar CPR surveys began in 2000 (Lindley and Batten, 2008). Various studies have been conducted using the Pacific CPR survey data, focusing primarily on the dominant copepods (Batten et al., 2003b ; Batten and Walne, 2011 ; Yoshiki et al., 2013 ; Chiba et al., 2015). However, there are no reports on diel changes in abundance based on the Pacific CPR samples.

The large, dominant copepods in the subarctic Pacific are *Neocalanus cristatus*, *N. flemingeri*, *N. plumchrus*, *Eucalanus bungii* and *Metridia pacifica*, and they account for more than 77% of the mesozooplankton biomass in this area (Miller et al., 1984 ; Ikeda et al., 2008). Regional differences in life cycles (e.g., generation length and resting stage) have been reported for *N. flemingeri*, *E. bungii* and *M. pacifica* between the western and eastern subarctic Pacific (Kobari and Ikeda, 2001b ; Padmavati et al., 2004 ; Shoden et al., 2005). Such east-west differences in life cycles are attributed to regional differences in thermal and food conditions (Shoden et al., 2005). Since the dominant copepods have a wide distribution range throughout the subarctic Pacific, horizontal changes in the timing of their life histories have been estimated from physical oceanographic models (Tatebe et al., 2010), but there have not been any direct observations on these changes. CPR tows, which can collect zooplankton samples frequently and continuously at the sea surface, are a useful tool for evaluating the horizontal differences in the life cycles of these copepods.

In this study, we investigated the abundance and population structure of the five large, dominant copepods and evaluated the differences in (1) season, (2) region and (3) diel scales using CPR samples collected in the western subarctic Pacific between 2001 and 2015. We evaluated changes in abundance due to the three factors using Generalized Additive Models (GAMs).

Materials and methods

Sample collection and enumeration

Zooplankton samples were collected during 2001-2015 by CPR tows along transects three times annually : spring (April-May), summer (June-July) and autumn (September-October). The CPR was towed by a merchant ship between Vancouver and northern Japan. In this study, we analyzed samples collected in the western subarctic Pacific (40°-54°N, 143°E-174°E) (Fig. 1). For regional classification, we divided the sampling area into the Oyashio region (OY) west of 155°E and the Western Subarctic Gyre (WSG) east of 155°E (Yoshiki et al., 2013).

The CPR was towed horizontally at a depth of approximately 7 m and collected samples through a 1.27 cm^2 square mouth opening with 270 μm mesh. Collected samples were fixed in a formalin preservative tank inside the CPR (Batten et al., 2003a ; Richardson et al., 2006). The local time of each sample collection was recorded as field collection data, with a binary response for day and night based on sunrise and sunset times. Following collection, each continuous tow was divided into discrete samples, each representing 18.5 km (10 nautical miles) of tow. The sampling points in Fig. 1 indicate the mid-points of the discrete samples. The five dominant copepods (*N. cristatus*, *N. flemingeri*, *N. plumchrus*, *E. bungii* and *M. pacifica*) in each sample were identified and counted to species level and copepodite stage using a microscope. Abundance was represented by the number of individuals per sample (ind. $sample^{-1}$).

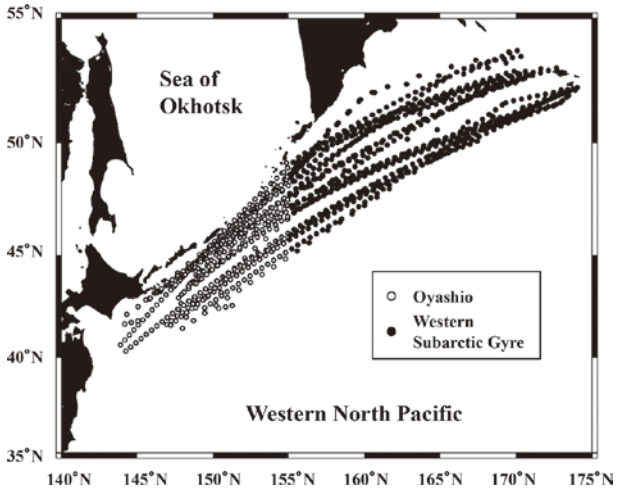

Fig. 1. Sampling locations of the CPR surveys in the western North Pacific during three seasons (spring [April-May], summer [June-July], and autumn [September-October]) for 2001-2015. Sampling points were separated into two sectors based on longitude (155°E) : the Oyashio region and the Western Subarctic Gyre.

Environmental data and statistical analyses

We used satellite-derived sea surface temperature (SST) data for 2000-2011 from Chiba et al. (2015) and chlorophyll *a* (chl *a*) concentration data for 2000-2009 from Chiba et al. (2012) to represent environmental data for each region and season. SST was summarized by season and region, and chl *a* was classified into month and region. Regional differences in SST and chl *a* between each season or month were evaluated using the Mann-Whitney *U*-test.

Using GAMs, we evaluated the effects of season, region and local time on the abundance of the five large dominant copepods. Within the analysis, the abundance of the five copepods was used as a response variable, and seasons (spring, summer and autumn), regions (OY and WSG), and collection time (local time) were included as explanatory variables. A smoothing spline approximation based on local time was performed. Because the abundance data contained many zeros, the scale was converted to $\log_{10}(X+1)$, where X is abundance (ind. $sample^{-1}$) to reduce bias, and used as a

response variable. All statistical analyses were carried out in R software with the package "mgcv" (version 3.6.2, R Development Core Team, 2017).

Results

Hydrography

Seasonal changes in SST and chl *a* in the OY and WSG based on satellite data are shown in Fig. 2. There were significant regional differences in SST between each season and in chl *a* between each month ($p<0.001$, Mann-Whitney *U*-test). SST ranged from 0.5 to 16.9°C and continuously increased from spring to autumn in both the OY and WSG. SST was lower in the OY than the WSG in spring. In contrast, SST was higher in the OY than in the WSG during summer and autumn. Chl *a* ranged from 0.04 to 64.6, and peaked in May for both regions. Chl *a* was 1.4-2.4 times higher in the OY than in the WSG from February to April. However, chl *a* was higher in the WSG in May and had a pulse-like peak.

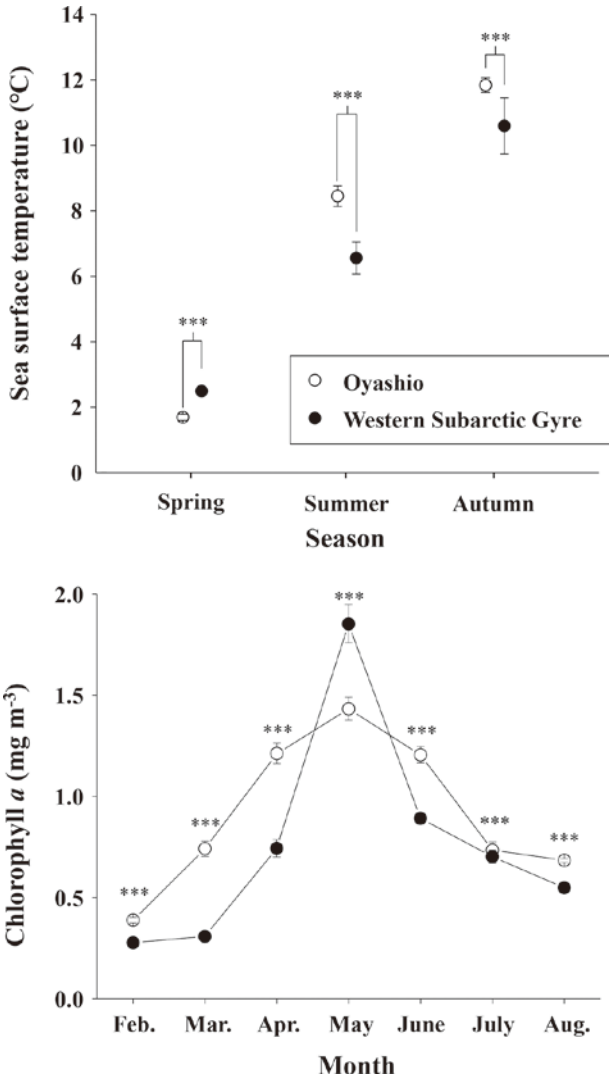

Fig. 2. Seasonal changes in sea surface temperature (upper) and chlorophyll *a* (lower) in the Oyashio region and Western Subarctic Gyre of the western North Pacific Ocean. Temperature and chlorophyll *a* data were derived from satellite data (cf. Chiba et al., 2012, 2015). Symbols and bars represent means and standard errors, respectively. *** : $p<0.001$, Mann-Whitney *U*-test.

Abundance and population structure

The mean seasonal abundance of each copepodid stage (C1-C6) of the five dominant copepods at each local time during 2001-2015 was calculated for the OY (Fig. 3) and WSG (Fig. 4). *N. cristatus* was abundant in both regions during spring and summer, and its population structure was dominated by C5. In every season, the abundance was higher in the WSG than in the OY. *N. flemingeri* was abundant in both regions during spring, declined in summer, and rarely appeared in autumn. The population structure in spring was mainly composed of C2, with abundance higher in the WSG than in the OY. *N. plumchrus* was abundant in both regions during summer, and its population structure was dominated by C2. *E. bungii* was abundant in both regions during summer and comprised mainly early copepodid stages such as C1. *M. pacifica* was abundant in both regions during summer and autumn, and all copepodid stages were present evenly. It should be noted that *N. plumchrus*, *E. bungii* and *M. pacifica* occurred in the OY in spring but were rare in the WSG (Figs. 3, 4).

GAM analysis

The results of the GAM analysis that evaluated seasonal and regional differences in the abundance of the five large dominant copepods are shown in Table 1. *N. cristatus*, *N. flemingeri* and *E. bungii* had large seasonal differences, and they were more abundant in spring and summer than in autumn. *N. plumchrus* showed no difference between spring and autumn and was most abundant in summer. *M. pacifica* was the only species that was least abundant in spring. Significant regional differences were observed for the three *Neocalanus* species (Table 1). *N. cristatus* and *N. flemingeri* were more abundant in the WSG, while *N. plumchrus* was more abundant in the OY. The results of the smoothing spline regression on the relationship between the abundance of the five large dominant copepods and local time are shown in Fig. 5. Abundances of *N. cristatus* and *M. pacifica* had significant relationships with local time, with both species more abundant at night. *N. cristatus*, *N. flemingeri*, *N. plumchrus* and *M. pacifica* had seasonal differences in diel change. Additionally, regional differences were observed for the diel changes of *N. flemingeri*, *E. bungii* and *M. pacifica* (Fig. 5).

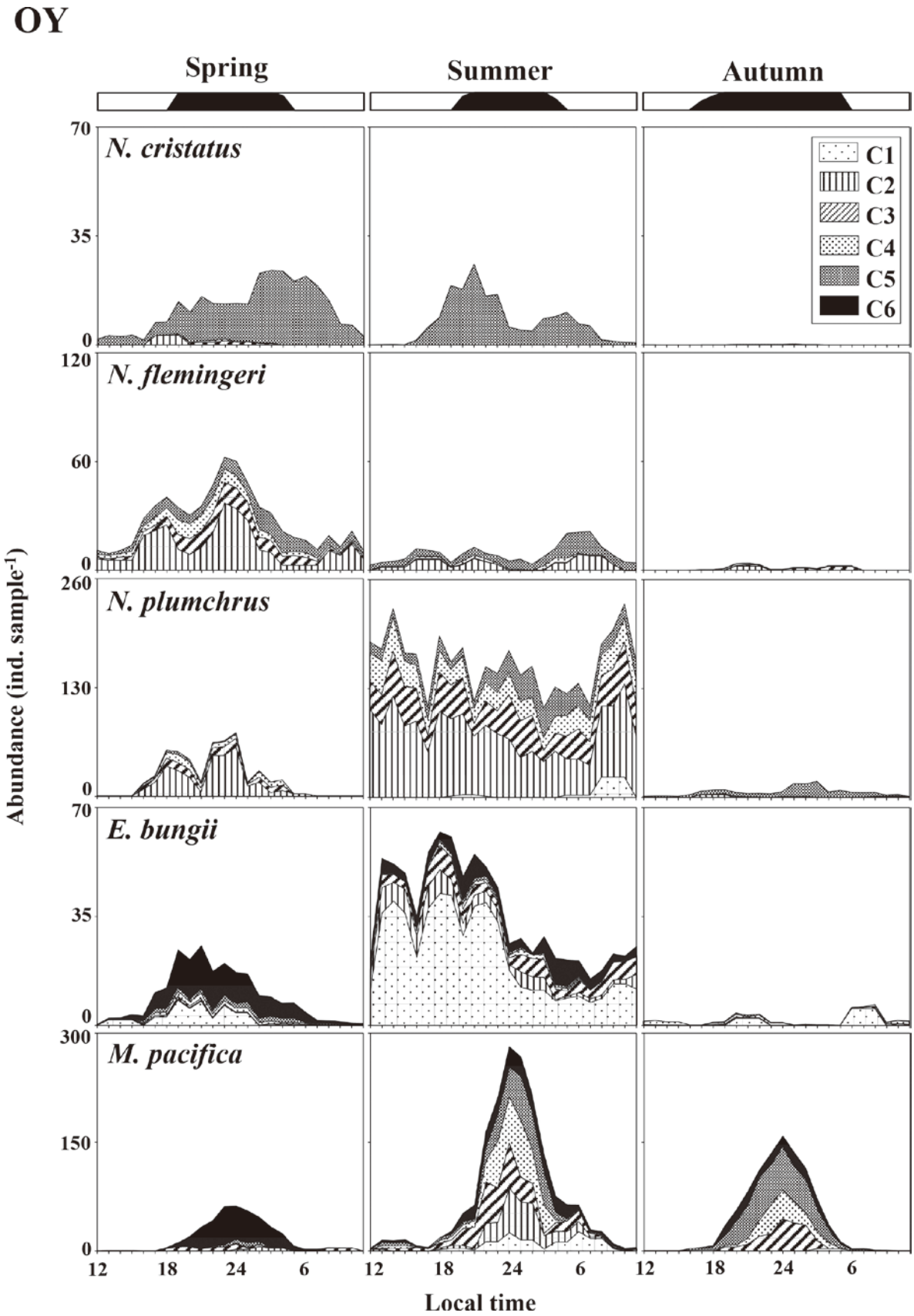

Fig. 3. Mean seasonal abundance of each copepodid stage of *Neocalanus cristatus*, *N. flemingeri*, *N. plumchrus*, *Eucalanus bungii*, and *Metridia pacifica* along with local time in the Oyashio region during 2001–2015. Panels are separated by season. Daylight and dark hours are indicated in top row.

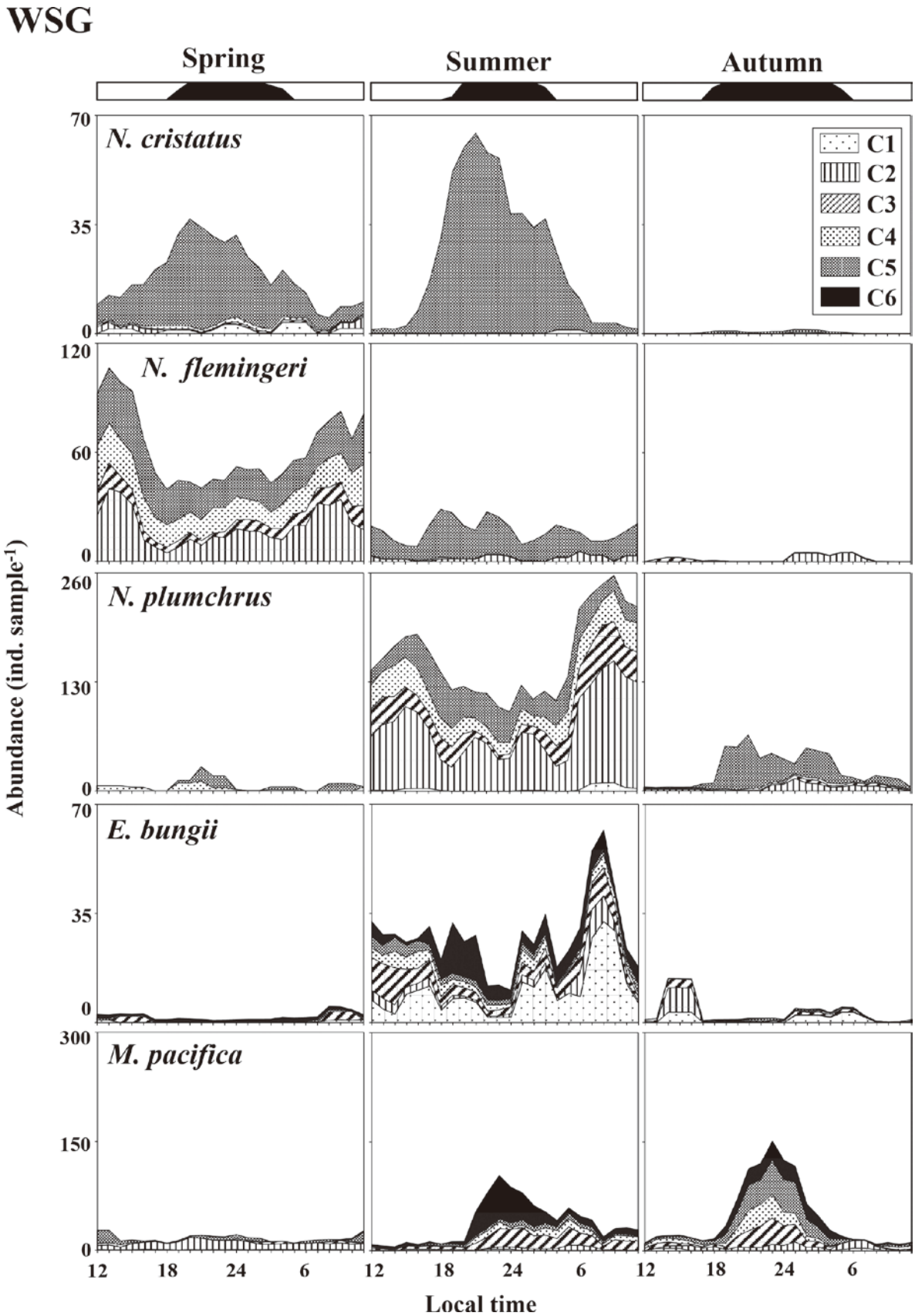

Fig. 4. Mean seasonal abundance of each copepodid stage of *Neocalanus cristatus*, *N. flemingeri*, *N. plumchrus*, *Eucalanus bungii*, and *Metridia pacifica* along with local time in the Western Subarctic Gyre during 2001–2015. Panels are separated by season. Daylight and dark hours are indicated in top row.

Table 1. Results of the GAMs based on the total abundance of *Neocalanus cristatus*, *N. flemingeri*, *N. plumchrus*, *Eucalanus bungii*, and *Metridia pacifica* within the season and region. +: positive, −: negative, +/−: $p<0.05$, ++/−−: $p<0.01$, +++/−−−: $p<0.001$, ns: not significant. The estimated smooths for each level of factor are shown in Fig. 5.

Species	Season		Region	
N. cristatus	+++	(spring)	+++	(WSG)
	+++	(summer)		
N. flemingeri	+++	(spring)	+++	(WSG)
	+++	(summer)		
N. plumchrus	+++	(summer)	−−	(WSG)
E. bungii	+++	(spring)	ns	
	+++	(summer)		
M. pacifica	−−	(spring)	ns	

Discussion

Seasonality of abundance and population structure

Seasonal changes in abundance and population structure of the five large dominant species could be interpreted as a reflection of the life cycle of each species. It is well known that *Neocalanus* species reproduce in the deep sea, and only stages C1–C5 appear at the surface (Miller et al., 1984; Miller and Clemons, 1988). The growth of *N. cristatus* and *N. flemingeri* at shallow depths occurs from winter to spring (Kobari and Ikeda, 1999, 2001b). In contrast, the growth of *N. plumchrus* at the epipelagic layer occurs later than that of *N. flemingeri* (Tsuda et al., 1999; Kobari and Ikeda, 2001a). The results of the present study agree with these findings for the three *Neocalanus* species. Thus, C6 did not occur in the *Neocalanus* species, and *N. cristatus* and *N. flemingeri* were abundant in spring, while *N. plumchrus* was more common in summer (Figs. 3, 4). Unlike the *Neocalanus* species, *E. bungii* and *M. pacifica* are known to reproduce at the surface layer (Miller et al., 1984; Batchelder, 1985). In this study, adults (C6) of *E. bungii* and *M. pacifica* were common at the surface layer (Figs. 3, 4).

Three species, including *N. plumchrus*, *E. bungii* and *M. pacifica*, which were more abundant in summer than in spring, occurred in the OY during spring, and the adults (C6) of *E. bungii* and *M. pacifica* were dominant, especially in spring (Figs. 3, 4). In the western subarctic Pacific, it is well known that *E. bungii* and *M. pacifica* undergo diapause, with diapause ending and reproduction occurring during phytoplankton blooms in the spring (Padmavati et al., 2004; Shoden et al., 2005). Since the magnitude of the spring bloom is larger in the OY than in the WSG (Okamoto et al., 2010; Fujiki et al., 2014), the C6s of both species awakened from diapause are considered to occur at the surface layer in spring (Fig. 3). Actually, chl *a* from February to April was constantly higher in the OY than in the WSG (Fig. 2). However, since these species in the WSG are in a diapause phase at depth during spring, they may be less abundant in the WSG than in the OY (Fig. 4).

Seasonally, abundances of the three *Neocalanus* species and *E. bungii* were high in spring–summer (Table 1). All of these species undergo diapause in the deep ocean (Miller et al., 1984). In autumn, since the main populations descend to the deep ocean, abundances of these species were extremely low (Figs. 3, 4). In contrast, *M. pacifica* was abundant in summer and autumn (Table 1). *M. pacifica* has been reported to have three generations in a year in the Gulf of Alaska, reproducing in late winter, summer, and autumn (Batchelder, 1985), and two generations per year in the Oyashio region, reproducing in April–May and June–July (Padmavati et al., 2004). The results of the present study indicate that *M. pacifica* occupies the surface layer after the *Neocalanus* species, then has a diapause phase, and finally descends to the deep ocean.

Regional differences in abundance

Regional differences were detected for the three *Neocalanus* species; *N. cristatus* and *N. flemingeri* were more abundant in the WSG, while *N. plumchrus* was more common in the OY (Table 1). Notably, the species showing regional differences in abundance were all *Neocalanus* spp. In the subarctic Pacific, *Neocalanus* copepods are preyed upon by pelagic fishes such as salmon and sardines (Odate, 1994), and are the primary prey for the Pacific saury (*Cololabis saira*), which performs a large-scale feeding migration to the subarctic region during summer (Taka et al., 1982). Within the *Neocalanus* species, *N. flemingeri*, the abundant species in spring, showed high abundance in the WSG (Fig. 4). This might be because the other competitive species (*N. plumchrus*, *E. bungii* and *M. pacifica*) occurred less frequently in the WSG during spring (Fig. 4).

Meanwhile, the abundance of *N. cristatus* in the WSG was high, especially during summer (Fig. 4). This might be a reflection of the fact that *N. cristatus* can feed effectively on sporadic phytoplankton blooms that occurred in the WSG during May (Fig. 2). Since the chl *a* values of these sporadic phytoplankton bloom were the highest throughout the region and season (Fig. 2), and large-sized chain-forming diatoms are considered to be major taxonomic components (Tsuda et al., 2005a; Suzuki et al., 2011). *N. cristatus* is the largest copepod in the epipelagic zone of the subarctic Pacific and primarily feeds on large (>20 μm) particles (Liu et al., 2005). These facts suggest that *N. cristatus* can respond quickly and feed on the pulse-like phytoplankton blooms observed in the WSG (Fig. 2). As a result of effective grazing on these blooms, the growth and survival rates of *N. cristatus* may be higher, and their abundance in the WSG has the potential to become much higher than in the OY (Figs. 3,

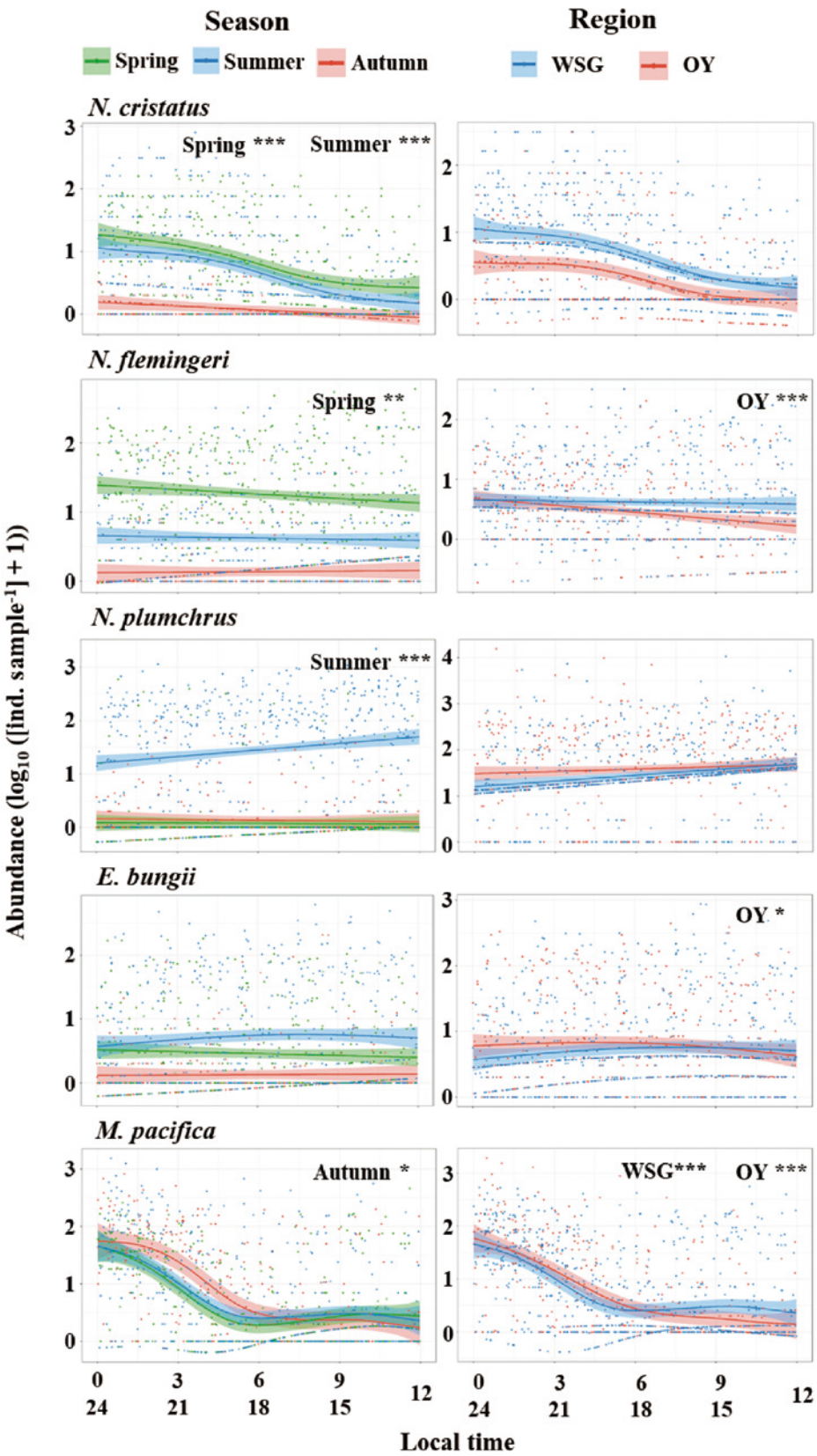

Fig. 5. GAM smooths for the effects on the abundance of local time in each season (left) and region (right) for five dominant copepods (*Neocalanus cristatus*, *N. flemingeri*, *N. plumchrus*, *Eucalanus bungii*, and *Metridia pacifica*) in the western subarctic Pacific. Asterisks represent significant seasonal and regional differences in the abundance of each species changing with local time. The shaded area marks the 95% CL around the mean prediction. WSG : Western Subarctic Gyre, OY : Oyashio.

4). It has also been reported that the vertical distribution of *N. cristatus* changes quickly in response to artificial phytoplankton blooms induced by *in situ* iron enrichment experiments (Tsuda et al., 2006).

Among the three *Neocalanus* species, *N. plumchrus* occurs at the surface layer later than the other two species and adapts to higher temperatures during summer (Tsuda et al., 1999 ; Kobari et al., 2001a). The seasonal increase in SST in the OY was more remarkable than in the WSG (Fig. 2). To avoid higher temperatures, the two other *Neocalanus* species are expected to descend to the deep layer much earlier in the OY. In fact, the abundances of the two other *Neocalanus* species in the OY were low in summer (Fig. 3). Because of the lower abundance of congener species that compete for feeding, *N. plumchrus* may have a higher abundance in the OY during summer. *N. plumchrus* composes >90% of the prey biomass of the Pacific saury, which performs a feeding migration around the Kuril Islands during summer (Taka et al., 1982). Thus, the regional differences in the abundance of the three *Neocalanus* species can be interpreted as reflections of the thermal and feeding environments of each region.

Diel changes in abundance

Diel changes in abundance were observed for *N. cristatus* and *M. pacifica* (Fig. 5). Both species were commonly more abundant at night (Fig. 5). These facts suggest that DVM is a major factor in their diel changes in abundance. The occurrence of DVM is well reported for *M. pacifica* (Batchelder, 1985 ; Padmavati et al., 2004 ; Takahashi et al., 2009 ; Sato et al., 2011). In contrast, DVM has not been reported for *N. cristatus* (Miller et al., 1984 ; Kobari and Ikeda, 1999 ; Sato et al., 2011). However, several studies have reported that *N. cristatus* performs small-scale DVM within the 0-40 m depth range (Tsuda et al., 1993) and small DVM during iron fertilization experiments (Tsuda et al., 2005b). Since *N. cristatus* is the largest copepod that occurs at the surface layer in the subarctic Pacific (Brodsky, 1950), it is thought that large *N. cristatus* perform DVM to avoid predation by visual predators (e.g., pelagic fishes). However, because the magnitude of DVM behaviour is expected to be small, it might be difficult to evaluate this behaviour using ordinary plankton net samplings, which usually sample through wide depth ranges. Thus, the small-scale DVM behaviour of *N. cristatus* could be detected by diel-scale continuous samplings from the sea surface (5-7 m depth), such as pump-up sampling (from 5 m depth, Tsuda et al., 1993) or the CPR tows used in this study.

Among the two species with diel changes in abundance, *N. cristatus* showed seasonal differences characterized by a large-scale diel change in spring and summer (Fig. 5). These seasonal differences may be because *N. cristatus* occurs at the surface in spring and summer and descends to undergo diapause in autumn (Miller et al., 1984). Since *N. cristatus* migrates to the deep ocean, there would be no diel differences in abundance in autumn. For *M. pacifica*, diel changes in abundance were observed in autumn and in the OY and WSG regions. These facts suggest that *M. pacifica* performs a more prominent DVM in autumn when the other large-sized dominant copepods descend to the deep ocean, and its DVM behaviour is common in both regions.

Summary

In this study, we used CPR samples collected in the western subarctic Pacific to evaluate the differences in abundance and population structure at seasonal, regional and diel scales. Large species-specific, seasonal changes in abundance and population structure were detected for the dominant copepods, and these changes were considered to be reflections of the life history of each species. Regional differences were detected for the three *Neocalanus* species and were considered to be related to SST and food availability. Diel changes in abundance were observed for *N. cristatus* and *M. pacifica*. Since their abundances was commonly higher at night, these changes were thought to be due to DVM. DVM has been well reported in *M. pacifica*, but is not well known in *N. cristatus*. Several studies have reported that *N. cristatus* performs small-scale DVM, which makes it difficult to evaluate using ordinary net sampling. Since the magnitude of the DVM behaviour of *N. cristatus* is small (within 0-40 m), its DVM would be detectable based on continuous samplings from the sea surface (5-7 m), such as by pump-up collection or CPR samplings.

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