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Diel and ontogenetic variations in vertical distributions of large grazing copepods during the spring phytoplankton bloom in the Oyashio region

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ABSTRACT

Short-term changes in vertical distributions of copepods during the spring phytoplankton bloom were analyzed based on day and night vertically stratified sampling (9 strata between 0 and 1000 m) with a fine-mesh (60 μm) VMPS in the Oyashio region on five occasions: 8 March, 5, 11, 23 and 29 April 2007. Responses to the bloom were varied and species-specific. *Eucalanus bungii* C3–C6 were resting around 400 m on 8 March. They had aroused from rest by 5 April, more completely for C6F than for C3–C4. On 29 April, newly recruited C1–C4 stayed in near-surface layers (0–50 m). Both *Metridia pacifica* and *Metridia okhotensis* showed strong diel vertical migrations (DVM). When the amount of sinking flux was sufficient (23 and 29 April), juveniles ceased DVM and stayed close to 300 m throughout the day and night, while the C6F continued DVM. Continuous DVM behavior of *Metridia* spp. C6F is likely related to spawning in the surface layer at night. The growth phase of juvenile *Neocalanus* spp. occurred shallower than 250 m. Within this depth range, vertical partitioning was observed among the species: *Neocalanus flemingeri* and *Neocalanus plumchrus* occurred above 50 m, while *Neocalanus cristatus* was distributed from 75 to 250 m. The boundary between two patterns was around 50–75 m. These findings are comparable to those in the eastern subarctic Pacific.

1. Introduction

Throughout the oceanic subarctic Pacific, the zooplankton fauna is characterized by the predominance of a few large grazing copepods: *Neocalanus cristatus*, *Neocalanus flemingeri*, *Neocalanus plumchrus*, *Eucalanus bungii*, *Metridia pacifica* and *Metridia okhotensis* (Mackas and Tsuda, 1999). Several aspects of their vertical distributions had been evaluated before the 1980s: ontogenetic vertical migration (developmental descent) of *N. cristatus* and *N. plumchrus* (Minoda, 1971; Sekiguchi, 1975), seasonal ontogenetic vertical migration of *N. plumchrus* in the Strait of Georgia (Fulton, 1973), diel vertical migration (DVM) of *M. pacifica* and lack of DVM in its adult males (C6M) (Morioka, 1972; Marlowe and Miller, 1975), diapause of *E. bungii* and transportation of its resting stocks along the lengths of fjords (Krause and Lewis, 1979).

The most comprehensive information on diel, seasonal and ontogenetic vertical distribution came from studies of *Neocalanus* spp. and *E. bungii* (Miller et al., 1984) and *M. pacifica* (Batchelder, 1985) at Station P in the eastern subarctic Pacific. Also at Station P, vertical distribution of the whole zooplankton community (Goldblatt et al., 1999), and vertical partitioning among the species (shallower species: *N. flemingeri* and *N. plumchrus* and deeper species: *N. cristatus* and *E. bungii*) with boundary around 50 m were reported by Mackas et al. (1993). Vertical separation of congeners results in *N. plumchrus* and *N. flemingeri* having direct and indirect grazing effects on near-surface phytoplankton and microzooplankton, while *N. cristatus* remains below the mixed layer, feeding on aggregates sinking out of the euphotic zone (Dagg, 1993).

Details of the responses of these copepods to phytoplankton bloom conditions were revealed by several iron-fertilization experiments in the oceanic HNLC areas of the subarctic Pacific. The responses to iron-fertilized blooms varied between experiments. Vertical distribution of these copepods did not vary between inside and outside the bloom patch in SEEDS2001 in the western subarctic Pacific during July (Tsuda et al., 2005), whereas there were upward shifts of the vertical distributions of *E. bungii* and *N. cristatus* in the SERIES phytoplankton patch in the eastern HNLC area during July (Tsuda et al., 2006). The contrast suggests that the responses to phytoplankton blooms vary with location or timing.

In the western subarctic Pacific, time-series vertical sampling was conducted at Site H in the Oyashio region during 1996–1997. Based on those samples, information has been developed on diel, seasonal and ontogenetic vertical distributions of *Neocalanus* spp. (Kobari and Ikeda, 1999, 2001a, 2001b), *E. bungii* (Shoden et al., 2005), *M. pacifica* and *M. okhotensis* (Padmavati et al., 2004) and mesopelagic copepods (*Gaidius variabilis*, *Heterorhabdus tanneri*, *Paraeuchaeta* spp. and *Pleuromamma scutullata*) (Yamaguchi and

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Ikeda, 2000a, 2000b, 2002). This information is part of the support for the concept of downward flux via seasonal ontogenetic migrations of copepods (Bradford-Grieve et al., 2001). The downward export of organic matter by ontogenetic vertical migration of these copepods in the western subarctic Pacific is estimated to be 73–92% of the passive gravitational flux (Kobari et al., 2003, 2008).

Knowledge of development and vertical distribution of copepods in the western subarctic Pacific has come mainly from low-resolution spatial (vertical separation) and temporal (bimonthly) sampling. In the Oyashio region, the large copepods utilize the production of the phytoplankton bloom during April–June (Ikeda et al., 2008). There are two types of phenology in respect to this bloom exploitation: *E. bungii* and *Metridia* spp. utilize the pulse of nutrition for reproduction by adults (Padmavati et al., 2004; Shoden et al., 2005), while the *Neocalanus* spp. utilize it for growth of new generations of copepodids (Kobari and Ikeda, 1999, 2001a, 2001b). Because of the coarse temporal resolution (bi-monthly) of the previous time series, the cue for upward migration of resting *E. bungii* from deep layers for surface reproduction remains unknown. Also the low vertical resolution (5 layers between 0 and 2000 m) of the older data prevented evaluation of the fine-scale vertical separations among *Neocalanus* copepods (Mackas et al., 1993) in the Oyashio region.

To overcome these problems, as the part of the OECOS project (Miller and Ikeda, 2006), the present study aimed to evaluate short-term changes in vertical distribution of copepods by high resolution sampling in the Oyashio region during the spring phytoplankton bloom. Day and night vertically stratified sampling (9 strata between 0 and 1000 m) with fine-mesh nets (60 μm) was conducted on 8 March and 5, 11, 23 and 29 April 2007. The vertical resolution of the new data is comparable to that of Mackas et al. (1993) at Station P (7 strata between 0 and 250 m). To evaluate the arousal of *E. bungii* from rest in deep layers, our sampling depths extended down to 1000 m. Analysis is based on two species groups: those spawning near the surface, *E. bungii* and *Metridia* spp., and *Neocalanus* species that are only near the surface as grown juveniles. The vertical distributions during the spring bloom of the spawning species and the growing species are discussed in comparison with the same groups in the eastern subarctic and in respect to their responses to iron-fertilized blooms.

2. Materials and methods

2.1. Field sampling

Zooplankton sampling was conducted at one station (A-5: 42°00′N, 145°15′E; depth 4048 m) in the Oyashio region on 8 March, 5, 11, 23 and 29 April 2007. Day and night casts were made with a Vertical Multiple Plankton Sampler (VMPS: 60 μm mesh, 0.25 m^2 mouth opening; Terazaki and Tomatsu 1997), collecting from 9 strata between 0 and 1000 m (0–25, 25–50, 50–75, 75–100, 100–150, 150–250, 250–500, 500–750 and 750–1000 m) (Table 1). Samples were immediately preserved with 5% borax-buffered formalin. Temperature and salinity were measured by Sea-Bird CTD casts. Water samples for chlorophyll *a* were collected from 10, 30, 50, 75, 100, 125, 150 and 200 m, then filtered through Whatman GF/F filters, and measured fluorometrically after extraction with dimethyl-formamide (Suzuki and Ishimaru, 1990).

2.2. Identification and enumeration of copepods

In the land laboratory, we enumerated the biomass-dominant copepods: *E. bungii*, *M. pacifica*, *M. okhotensis*, *N. cristatus*, *N. flemingeri* and *N. plumchrus*. After measurement of sample volume, the samples were stirred gently and well with a wide-bore pipette (1 cm diameter), and a pipette subsample was taken (1/10–1/35 of total volume, varying with the amount of the sample). Then, species and stages of the dominant copepods were identified and enumerated in the subsample under a stereomicroscope.

Table 1
Sampling data for VMPS hauls in the Oyashio region during 8 March, 5, 11, 23 and 29 April 2007. (A)—local time of each cast, (B)—sampling layers and the mean volumes of water filtered, (D)—day and (N)—night.

(A) Sampling		(B) Sampling layer (m)	Filtered water volume (m^3)
Date	Local time		
8 Mar. (D)	12:17–13:23	0–25	4.3
8 Mar. (N)	23:42–0:51	25–50	4.6
5 Apr. (D)	13:48–15:12	50–75	5.9
5 Apr. (N)	1:57–3:15	75–100	4.9
11 Apr. (D)	13:35–14:57	100–150	9.3
11 Apr. (N)	22:28–0:01	150–250	24.5
23 Apr. (D)	7:51–9:19	250–500	58.9
23 Apr. (N)	22:41–0:13	500–750	55.3
29 Apr. (D)	12:45–14:17	750–1000	56.6
29 Apr. (N)	2:33–3:59		

Sexes were distinguished from copepodid stage 4 (C4) to adults (C6) for *E. bungii*, *M. pacifica* and *M. okhotensis* (Padmavati et al., 2004; Shoden et al., 2005). For *Neocalanus* spp., sex determination was possible only for C6 (Kobari and Ikeda, 1999, 2001a, 2001b).

2.3. Analysis of data

To make a quantitative comparison possible, the depth above and below which 50% of the population resided ($D_{50\%}$) was calculated for each copepod species (Pennak, 1943). Additional calculations were made of quartile depths above which 25% ($D_{25\%}$) and 75% ($D_{75\%}$) of the population occurred. Day vs. night differences in vertical distributions of each copepodid stage were evaluated by two-sample Kolmogorov–Smirnov tests (Sokal and Rohlf, 1995). To avoid errors due to small sample sizes in this DVM analysis, comparisons were done only for stages with >40 individuals m^{-2} (ind. m^{-2}).

For evaluation of population structure of the species, estimates of the mean stage were calculated based on the abundance data for the 0–1000 m water column. Mean stage is defined as

$$\text{Mean stage} = \sum (i \times N_i)/N$$

where N_i is the abundance (ind. m^{-2}) of *i*th copepodid stage ($i=1$ to 6) and N is the total copepodid abundance of the species.

3. Results

3.1. Hydrography

Temperatures between 0 and 1000 m varied from 1.0 to 6.1 °C during 8 March to 29 April 2007 (Fig. 1A). In the upper 400 m temperature was higher (3–6 °C) in 8 March, lower (1–3 °C) in 5 April. Salinity varied from 33.0 to 34.4, increasing downward (Fig. 1B). Variation in salinity was synchronized with temperature, thus high temperature corresponded high salinity (33.7) on 8 March, while low temperature matched low salinity (33.0) on 5 April. Chlorophyll *a* in the upper 200 m varied between 0.1 and 3.5 mg m^{-3}, and was high on April dates and low