Title	Vertical segregation within four grazing copepods in the Oyashio region during early spring
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Citation	Journal of Plankton Research, 33(8), 1230-1238 https://doi.org/10.1093/plankt/fbr018
Issue Date	2011-08
Doc URL	https://hdl.handle.net/2115/48558
Rights	This is a pre-copy-editing, author-produced PDF of an article accepted for publication in Journal of Plankton Research following peer review. The definitive publisher-authenticated version J. Plankton Res. (2011) 33 (8): 1230-1238 is available online at: http://plankt.oxfordjournals.org/content/33/8/1230
Type	journal article
File Information	JPR33-8_1230-1238.pdf

Vertical segregation within four grazing copepods in the Oyashio region during early spring

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Abstract

Fine-scale vertical distribution patterns of *Neocalanus flemingeri*, *Neocalanus cristatus, Eucalanus bungii* and *Metridia pacifica* were studied by stratified sampling (9 strata between 0 and 1000 m) with a Vertical Multiple Plankton Sampler (VMPS) every 3 h for 24 h during 21-22 March 2005 in the Oyashio region. Most C1-C5 stages of *N. flemingeri* and *N. cristatus* occurred in the 30-90 m and 70-200 m strata, respectively, both day and night. Irrespective of day and night, C3-C6 *E. bungii* were distributed broadly in the 200-430 m stratum (C5 inhabiting the shallowest layer). Thus, these three copepods exhibited vertical partitioning of their habitats in the upper layers. The C1-C6 of *M. pacifica* were distributed broadly from 140 to 400 m during daytime and migrated up to the 100-180 m layer at night (except for non-migrant C1 and C6 males). The within-species zonation of copepodid stages was less marked, but older stages tended to occupy deeper zones (*N. flemingeri*, *N. cristatus* and *M. pacifica*) or shallower zones (*E. bungii*). Gut content analyses of *N. flemingeri* and *N. cristatus* revealed predominance of diatoms in both species, but the proportion of broken cells was greater in the deep-dwelling *N. cristatus* than in the shallow-dwelling *N. flemingeri*, suggesting the importance of sinking phytoplankton aggregate as food source for the former species.

Introduction

Mesozooplankton communities in the subarctic Pacific Ocean are characterized by the predominance of a few large/medium-sized grazing copepods, including *Neocalanus cristatus*, *Neocalanus plumchrus*, *Neocalanus flemingeri*, *Eucalanus bungii* and *Metridia pacifica* (Mackas and Tsuda, 1999). These copepods altogether often constitute 80-95% of the mesozooplankton biomass in the upper layers in summer (Vinogradov, 1968), and they are major components of the prey of pelagic fishes (Odate, 1994; Beamish et al., 1999), seabirds (Hunt et al., 1998) and whales (Nemoto, 1963), thus forming a vital link between primary production and these animals at higher trophic levels.

In recent years, information about the life history and seasonal vertical migration patterns of these copepods in the Oyashio region has accumulated rapidly: *N. cristatus* and *N. plumchrus* have annual life cycles and undergo large-scale, ontogenetic vertical migrations extending to the bathypelagic zone (Kobari and Ikeda, 1999, 2001a; Tsuda et al., 2001). Life cycles of *N. flemingeri* and *E. bungii* are complex (1 or 2 year life cycles) and both exhibit large seasonal vertical migrations in each year (Kobari and Ikeda, 2001b; Tsuda et al., 2004; Shoden et al., 2005). Unlike those large copepods, medium-sized *M. pacifica* progresses through several short (2-3 months) generations in the surface zone in summer, and it has a long generation (9-10 months) at depth during winter (Padmavati et al., 2004). Common features among these copepods are rapid development and accumulation of lipids during the spring diatom bloom in the Oyashio region (Kobari et al., 2010; Yamaguchi et al., 2010).

While we have obtained general pictures of the life history patterns and ontogenetic vertical migrations of these grazing copepods, the sampling designs of the previous studies in the Oyashio regions cited above (from 5 discrete depths between the surface and 2000 m sampled monthly) have not been sufficient to resolve the mechanisms allowing the coexistence of several species with similar food habits in the surface zone of the Oyashio region. One way to avoid possible food competition among the species is partition of feeding time, which can be achieved by differentiated residence periods in the diatom-rich surface zones. For example, early copepodids of *N. cristatus* may reach the surface zone first, followed in the order of *N. flemingeri* and then *N. plumchrus* (cf. Kobari and Ikeda, 2000; Tsuda et al., 2001). Another way may be fine-scale habitat partitioning among the copepods within the upper zone, although there are many data both supporting this explanation and conflicting with it (cf. Mauchline, 1998). For *Neocalanus* spp. and *E. bungii*, vertical habitat separation within the upper layers has been reported from Station P in the eastern subarctic Pacific (Mackas et al., 1993), however generalization of the phenomenon to those living elsewhere is not currently available.

This study was made to fill the gap in our knowledge about vertical distribution patterns of *N. flemingeri*, *N. cristatus*, *E. bungii* and *M. pacifica* in the upper layer of the Oyashio region in spring, and to gain insight into possible vertical habitat partitioning by the copepods during early spring when the phytoplankton bloom has just started. The present results are compared with those at Station P in the eastern subarctic Pacific, and are discussed in light of feeding strategy differences among the species.

Method

Field sampling

Field samplings were conducted at Site H (41°30'N, 145°50'E) in the Oyashio region, western subarctic Pacific during 21 through 22 March 2005. Zooplankton was sampled with a

Vertical Multiple Plankton Sampler (VMPS: 0.25 m^2 opening mouth and mounted 60 μm mesh, Tsurumi Seiki Co. Ltd., cf. Terazaki and Tomatsu, 1997). A flow meter was mounted on the mouth of the net to register the volume of water passed through the net. Stratified vertical hauls, designated as 0-25, 25-50, 50-75, 75-100, 100-150, 150-250, 250-500, 500-750 and 750-1000 m were made every 3h interval for 24h (Table I). Thus, we obtained a time series of 8 consecutive sample profiles, which could be divided into four daytime casts and four nighttime casts based on the local time of sunset (17:30, 21 March) and sunrise (05:18, 22 March) (Table I). Zooplankton samples were preserved with 5% borax-buffered formaldehyde immediately after each sampling. Temperature, salinity, dissolved oxygen (DO) and fluorescence were measured with a CTD system (Sea-Bird Electronics, Inc.) in four times during the study period.

Copepods

Neocalanus flemingeri, N. cristatus, E. bungii and *M. pacifica* were sorted from the whole sample or from 1/10 aliquots, then identified with each copepodid stage under a dissecting microscope. Identification into male and females made from C4 onward for *E. bungii* and *M. pacifica*, while only C6 for *Neocalanus* spp. *Neocalanus plumchrus* did not occur in sufficient numbers for the present analysis, reflecting the later developmental timing of this species (Kobari and Ikeda, 2000), as compared with the other copepods mentioned above. Since C1 of *N. flemingeri* and *N. plumchrus* could not be distinguishable in morphology (cf. Tsuda et al., 2001), it should be noted that C1 of *N. flemingeri* in this study may inevitable including C1 of *N. plumchrus* but in limited extent. Depending on internal body condition, C5 specimens of *N. cristatus* were classified into three categories: 'transparent' type with poorly developed musculature and no lipid, 'solid' type with rigid musculature and a large amount of lipid, and 'intermediate' type with conditions between the transparent and solid types (Ikeda et al., 1990).

Gut contents of C5 *N. flemingeri* and *N. cristatus* were examined on the specimens collected from 75-100 m (*N. flemingeri*) or 250-500 m (*N. cristatus*) of the same cast (23:47-00:52, 21 March). Up to 10 individuals of which gut filled were sorted and their guts were carefully removed from the prosome with a pair of fine needles under a dissecting microscope. After removing all remains of the gut wall by means of a pair of tweezers, all gut contents were picked up with a fine pipette and mounted on a slide glass. Phytoplankton cells found in the guts were identified to species or genus level and the overall condition of the cells was classified into three categories depending on the proportion of broken cells in the total (intact [100%], fragment [50-100%] and broken [0-50%]).

Statistical analysis

To make a quantitative comparison possible, the depth above and below which 50% of population resided ($D_{50\%}$, cf. Pennak, 1943) was calculated for each copepodid stage of the four species. Differences in $D_{50\%}$ were examined by Mann-Whitney U-test for day/night or male/female in the same species and Kruskal-Wallis test for lipid deposition types in C5 *N. cristatus*.

Results

Hydrography

Water temperatures in the 0-1000 m fluctuated between 1.5 and 3.5°C (Fig. 1). Weak thermocline was around 70 to 80 m, and temperature minimum was at that depths. Salinities increased downward gradually (32.2-34.4). Dissolved oxygen (DO) was high (6-7 ml O_2 L^{-1}) in the top 100 m, decreased to 1 ml O_2 L^{-1} at 500 m and then stabilized until 1000 m depth. Chlorophyll *a* fluorescence concentrations were 1.0-2.0 mg m^{-3} in the top 50 m. Since these chlorophyll *a* were lower than the values of spring bloom in this region (up to 30 mg m^{-3}, cf. Kono and Sato, 2010), study period was considered to be before the spring bloom.

Population structure

The abundance and stage composition of the four copepods (*N. flemingeri*, *N. cristatus*, *E. bungii* and *M. pacifica*) integrated over 0-1000 m in water column are shown in Fig. 2. Common to the four species, the abundance showed irregular fluctuation throughout the day, but there was no consistent trend with time of the day. *Neocalanus flemingeri* (4,169-11,432 inds. m^{-2}) was more abundant than *N. cristatus*, and C1 and C2 were the major component of the population. The total abundance of *N. cristatus* varied from 1,317 to 3,426 inds. m^{-2}, and C1 and C2 were also the major components of the population throughout the day. Different from these *Neocalanus* spp., no C1-C2 but dominance of C3 and C6 was observed for *E. bungii* (4,589-9,064 inds. m^{-2}). *Metridia pacifica* (6,689-18,799 inds. m^{-2}) was the most abundant among the four copepods in this study. The population structure of *M. pacifica* was characterized by the predominance of C6 (mainly adult female) and C1 (Fig. 2).

Vertical distribution

Neocalanus flemingeri: C1-C6 stages of *N. flemingeri* were found, but C6 data were excluded because of their deeper distribution (>1000 m) (Kobari and Ikeda, 2001b). Throughout the entire sampling period, C1-C3 stages occurred consistently from 0-50 m and C4-C5 from 50-150 m (Fig. 3). No significant day/night effects on $D_{50\%}$ were detected for C1-C5 stages (U-test, $p > 0.05$, Table II).

Neocalanus cristatus: While all copepodid stages (C1-C6) were found, C6s were few and possibly underestimated because of their occurrence from 500-2000 m (Vinogradov and Arashkevich, 1969; Kobari and Ikeda, 1999), deeper than the sampling depth of this study (0-1000 m). For that reason, the C6 data were omitted in the present analysis. The $D_{50\%}$s of the three types of C5 specimens (transparent, intermediate and solid) differed some but not significantly (Kruskal-Wallis test, $p > 0.05$, Fig. 3). From this result, the $D_{50\%}$ data of the three types of C5 were pooled in the following analysis. The $D_{50\%}$s of C1 through C5 stages were stable during the study period, and no day/night effects were detectable (U-test, $p > 0.05$). C1-C3 stages occurred largely from 50-150 m, and C4-C5 stages from 100-250 m (Fig. 3, Table II).

Eucalanus bungii: Male-female differences in $D_{50\%}$s were not seen in C4 and C5, but C6 males resided much deeper than C6 females (U-test, $p < 0.001$) (Fig. 3). Most C3, C4 and C6 males inhabited 300-500 m, and C5 and C6 females inhabited shallower than them (Fig. 3). Within the depth range of each stage, day/night differences in $D_{50\%}$ values were not significant (U-test, $p > 0.05$) (Table II).

Metridia pacifica: Differences in $D_{50\%}$s between males and females were not significant for the C4-C5. In C6 the males resided deeper than females during nighttime (U-test, $p < 0.001$) (Fig. 3). During daytime, C1-C3 were concentrated in 100-200 m, C4 in 200-400 m and C5-C6 in 250-500 m (Fig. 3). During nighttime, C1 and C6 males remained at the same depths where they were abundant during daytime. The C2-C3, C4-C5 males and females and C6 females ascended to shallower depths at night (Fig. 3, Table II). The results of samplings made just after sunset (Cast No. 3) and just before sunrise (Cast No. 6) indicated that they were shifting their depth distributions (Fig. 3).

Gut contents of *Neocalanus flemingeri* and *N. cristatus*

Gut contents of C5 *N. flemingeri* and *N. cristatus* were largely composed of diatoms, in which the proportion of intact/broken cells was different between the two copepods (Fig. 4). The proportion of intact cells was greater in *N. flemingeri* than in *N. cristatus.* Common to these two copepods, *Thalassiosira* spp. were the most dominant diatoms (ca. 60%), followed by *Neodenticula seminae* (20%) or unidentified pennate diatoms (20%). As minor components, *Fragilariopsis* spp., *Chaetoceros* spp., *Pseudo-nitzschia* spp. and *Coscinodiscus* spp. were identified (Fig. 4).

Discussion

Neocalanus flemingeri, *N. cristatus* and *E. bungii* did not perform diel vertical migrations, and the distribution depths of these three copepods were well separated from each other. For example, *N. flemingeri* occurred the shallowest ($D_{50\%}$: 29-90 m, Table II) and *E. bungii* the deepest (194-435 m), with *N. cristatus* intermediate (67-213 m). At present, the only comparably fine-scale data on vertical habitat separation among *Neocalanus* spp. and *E. bungii* are those from Station P in the eastern subarctic Pacific on three occasions (May 1984, 1988, and June 1987) by Mackas et al. (1993). According to their results, which were consistent on all three occasions, most *N. flemingeri* and *N. plumchrus* at Station P were concentrated at 35-45 m while *N. cristatus* and *E. bungii* were at 50-150 m. For the other three copepods, the present results for the order of depth of occurrence (*N. flemingeri* < *N. cristatus* < *E. bungii*) at Site H are nearly comparable to those (*N. flemingeri* < *N. cristatus* = *E. bungii*) at Station P. However, the actual distribution depth ranges of *N. flemingeri* (29-90 m, Table II), *N. cristatus* (67-213 m, Table II) and *E. bungii* (194-435 m, Table II), respectively, at Site H were much wider than those observed at Station P. For *E. bungii*, it is partly because of the C5s and C6s just emerge from dormancy but the C3 and C4 seem to be still dormant due to the samplings in early spring (Fig. 3). This would make the wider distribution at Site H than Station P for *E. bungii* and thus not be niche segregation of feeding habit.

These regional differences in habitat depth ranges of copepods may result from species-specific responses of each copepod to the dissimilar physical conditions of Site H and Station P. For example, the halocline in our sampling at Site H in March was weaker than that in Mackas et al. (1993), and temperature profiles had weak thermocline around 70 and 80 m (Fig. 1) during our sampling in contrast to the development of strong thermocline in Mackas et al. Mackas et al. (1993) suggested that the shallow habitat depth of *N. flemingeri* - *N. plumchrus* pairs is characterized by strong turbulence, while the deep habitat of *N. cristatus* - *E. bungii* is less turbulent, and the boundary between the two habitat depths often corresponds to a thermocline, pycnocline or the bottom of the surface mixed layer.

While we did not measure turbulence of the water column in our study, the absence of a marked halocline and a seasonal thermocline (Fig. 1) may be one reason why *N. flemingeri, N. cristatus* and *E. bungii* extended their vertical distribution range greater at Site H than at Station P. Figure 5 shows buoyancy frequency (N, cycles/hour) profiles at Site H derived from temperature and salinity profiles as Mackas et al. (1993) did at Station P.

During our sampling, buoyancy frequency was often near zero in the surface mixed layer (0-50 m), where turbulence was supposed to be strong. Below the mixed layer, buoyancy frequency showed two maxima, a small peak just below 50 m, and a large peak at 100-150 m depth. The general vertical pattern of buoyancy frequency characterized by one small peak followed by one large peak observed at Site H is similar to that at Station P, but these two study sites are different in the magnitude of the large peaks (N= 3-4 at Site H versus N>10 at Station P). Lower buoyancy frequency at Site H is considered to be due to weak halocline and seasonal thermocline as compared with those at Station P. At Site H, *N. cristatus* and *E. bungii* distributed below the surface mixed layer which is similar to those at Station P though the relationships between the buoyancy frequency and their habitat depths were not clear. At Station P, All stages of *N. flemingeri* were found in the same depth stratum at Station P. At Site H, C1-C3 *N. flemingeri* were observed in the highly turbulent surface mixed layer but C4 and C5 stages mostly below the mixed layer where characterized by week turbulence (Fig. 3).

Food competition between species with similar feeding habits may also be considered between stages of the same species, and ontogenetic vertical migration is a possible mechanism for niche separation among stages (Mauchline, 1998). At Station P, Mackas et al. (1993) noted that the within species zonation among copepodid stages overlapped largely without consistent vertical sequence. While the present results of depth distribution of each copepodid stage of the four copepods showed large overlap also, older stages tended to occupy deeper zones (*N. flemingeri, N. cristatus* and *M. pacifica*) or shallower zones (*E. bungii*).

While the four copepods studied are categorized as grazers, the depths where the major populations resided (Fig. 3) and that where phytoplankton was abundant (0-50 m, cf.

Fig. 1) were not the same. As the exceptions, C1-C3 *N. flemingeri* distributed at 30-50 m and C2-C6F *M. pacifica* migrated to the phytoplankton-rich upper layers at night (Fig. 3). DVM of *M. pacifica* has been reported for the populations at two stations in the Oyashio region (Hattori, 1989) and that at Station P (Batchelder, 1985). In the mixed layers of the upper water column at Station P, where phytoplankton concentrations are generally low throughout the year (<0.7 mg chl. *a* m^{-3}, Miller et al., 1984), *N. flemingeri* and *N. plumchrus* in shallow layers are considered to be feeding on rapidly growing protozoans, while *N. cristatus* and *E. bungii* inhabiting deeper layers are feeding on particle aggregates sinking from above (Mackas et al., 1993).

Dagg (1993) and Liu et al. (2005) noted also that large aggregates (such as "marine snow") were an important food resource for *N. cristatus* in the field. Our gut content analysis revealed that while diatoms are the main diet components of *N. cristatu*s and *N. flemingeri,* the proportion of broken cells was greater in the former than the latter (Fig. 4), suggesting that *N. cristatus* may also be feeding on sinking phytoplankton aggregates (which proportion of broken cell is considered to be large) at Site H. While the nutritional conditions are known to be affect within-stage differences in vertical distribution of copepods (cf. Hays et al., 2001), the depth distribution of 'solid', 'intermediate' and 'transparent' C5 *N. cristatus* did not differ significantly in this study (Fig. 3). It suggests that the food supply in the form of sinking phytoplankton aggregate is similar for the whole specimens of C5 *N. cristatus.*

In conclusion, we have confirmed a stable vertical segregation pattern over one 24 h diel cycle among the four grazing copepods in the Oyashio region in early spring (March). The patterns are in some respects similar (the order of depth distribution among species, feeding strategy) and in respects dissimilar (vertical distribution ranges among species, within-species zonations of different stages) to those reported from Station P in spring (May-June). In light of possible alternation of vertical separation patterns among grazing copepods, depending on the changes in abiotic and biotic environmental parameters (cf. Mauchline, 1998), more sampling in other seasons are needed.

Acknowledgements

We thank Prof. C. B. Miller for his critical reading and constructive comments on earlier draft of the manuscript. We acknowledge captain, officers and crews of T/S *Oshoro-Maru* for their help in the sea. We also thank Mr. R. Fukui for identification of phytoplankton species observed in the gut of copepods.

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Table and Figure legends

Table I. Sampling data of stratified vertical hauls of VMPS down to 1000 m depth at Site H in the Oyashio region, western subarctic Pacific during 21-22 March 2005.

Table II. Day and night vertical distribution ($D_{50\%}$) of copepodid stages of *Neocalanus flemingeri, N. cristatus, Eucalanus bungii* and *Metridia pacifica* at Site H in the Oyashio region, western subarctic Pacific during 21-22 March 2005. *: $p < 0.05$, **: $p < 0.01$, ns: not significant.

Fig. 1. Vertical profiles of temperature, salinity, sigma-T, fluorescence and dissolved oxygen (DO) at Site H measured in four times during the study period. Note that the split of depth scales are varied at 250 m (horizontal dashed lines).

Fig. 2. Sequential changes in abundance and stage composition of *Neocalanus flemingeri*, *Neocalanus cristatus*, *Eucalanus bungii* and *Metridia pacifica* at Site H in the Oyashio region during 21-22 March 2005. For details of cast series no. see Table I.

Fig. 3. Sequential changes in vertical distribution of each copepodid stage of *Neocalanus flemingeri*, *Neocalanus cristatus*, *Eucalanus bungii* and *Metridia pacifica* at Site H during 21-22 March 2005. Symbols and vertical bars indicate depths where the 50% of the population resided ($D_{50\%}$) and depth ranges of $D_{25\%}$-$D_{75\%}$, respectively. Solid horizontal bars indicate periods of nighttime. For *N. cristatus*, based on the amount of lipid accumulation, C5 categorized into three: transparent (C5-T), intermediate (C5-I) and solid (C5-S). Sexes were distinguishable from C4 onward for *E. bungii* and *M. pacifica*. Note that C1 and C2 stages of *E. bungii* did not occur throughout the day. For details of cast series no. see Table I.

Fig. 4. Phytoplankton observed in the gut of C5 *Neocalanus flemingeri* and *Neocalanus*

cristatus as viewed from taxonomic composition (left) and condition of cells (broken or intact) (right). For each panel, the figures in parentheses are the number of specimens examined (left) or the number of cells observed (right).

Fig. 5. As in Fig. 1, but for buoyancy frequency. The ranges of $D_{50\%}$s of *N. flemingeri, N. cristatus* and *E. bungii* are superimposed by vertical arrows (cf. Table II).

Table I (Sato et al.)

Cast No.	Date	Time
1	21 March	12:02 - 13:09
2		14:50 - 15:58
Sunset		*17:30*
3		18:05 - 19:14
4		20:58 - 22:14
5		23:47 - 00:52
6	22 March	03:34 - 05:03
Sunrise		*05:18*
7		05:58 - 07:06
8		09:00 - 10:35

Table II (Sato et al.)

Species	Copepodid stage	$D_{50\%}$ (mean±1sd) Day	 Night	Day-night difference tested by U-test
Neocalanus flemingeri	C1	33 ± 4	29 ± 6	ns
	C2	36 ± 4	35 ± 11	ns
	C3	38 ± 15	49 ± 7	ns
	C4	80 ± 30	85 ± 20	ns
	C5	77 ± 30	90 ± 26	ns
Neocalanus cristatus	C1	103 ± 27	104 ± 29	ns
	C2	67 ± 19	72 ± 10	ns
	C3	82 ± 13	101 ± 26	ns
	C4	195 ± 123	114 ± 60	ns
	C5	213 ± 24	193 ± 17	ns
Eucalanus bungii	C3	405 ± 35	398 ± 21	ns
	C4	434 ± 70	399 ± 31	ns
	C5	194 ± 59	201 ± 68	ns
	C6F	257 ± 55	258 ± 63	ns
	C6M	384 ± 18	435 ± 119	ns
Metridia pacifica	C1	138 ± 5	124 ± 9	ns
	C2	144 ± 20	107 ± 32	*
	C3	182 ± 23	110 ± 65	**
	C4	297 ± 78	155 ± 126	**
	C5	358 ± 45	178 ± 96	**
	C6F	385 ± 29	142 ± 79	**
	C6M	411 ± 28	433 ± 121	ns

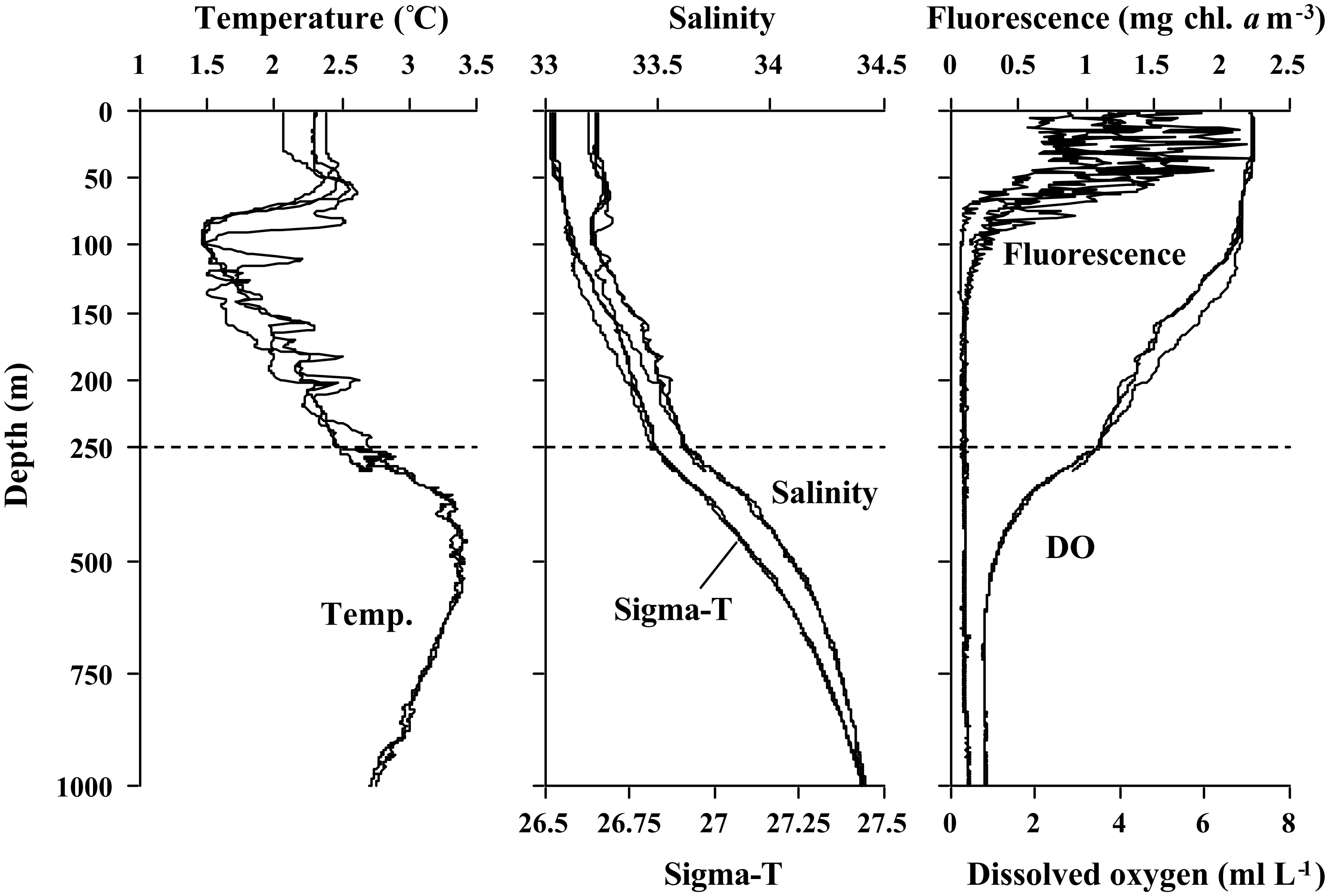

Fig. 1 (Sato et al.)

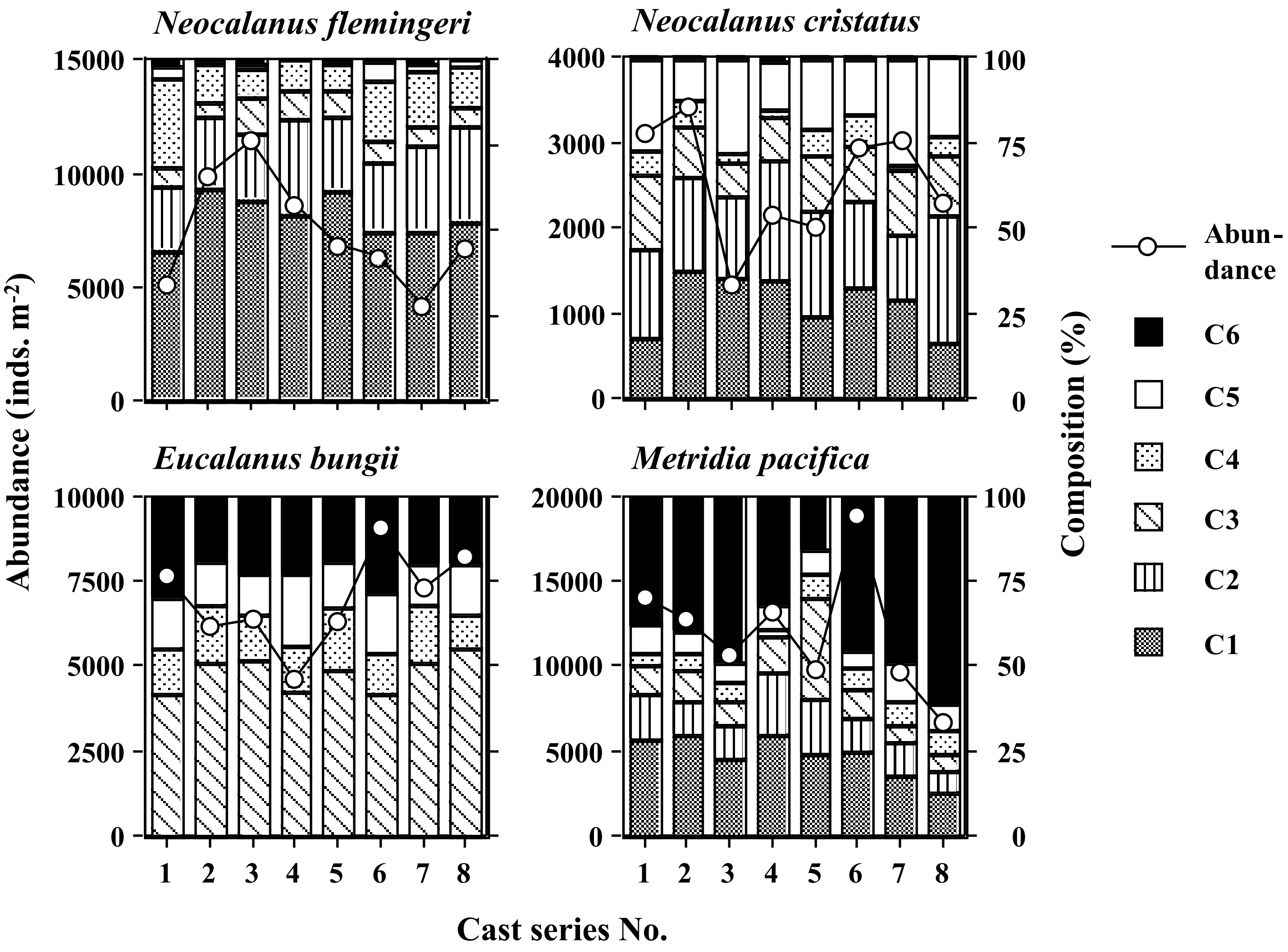

Fig. 2 (Sato et al.)

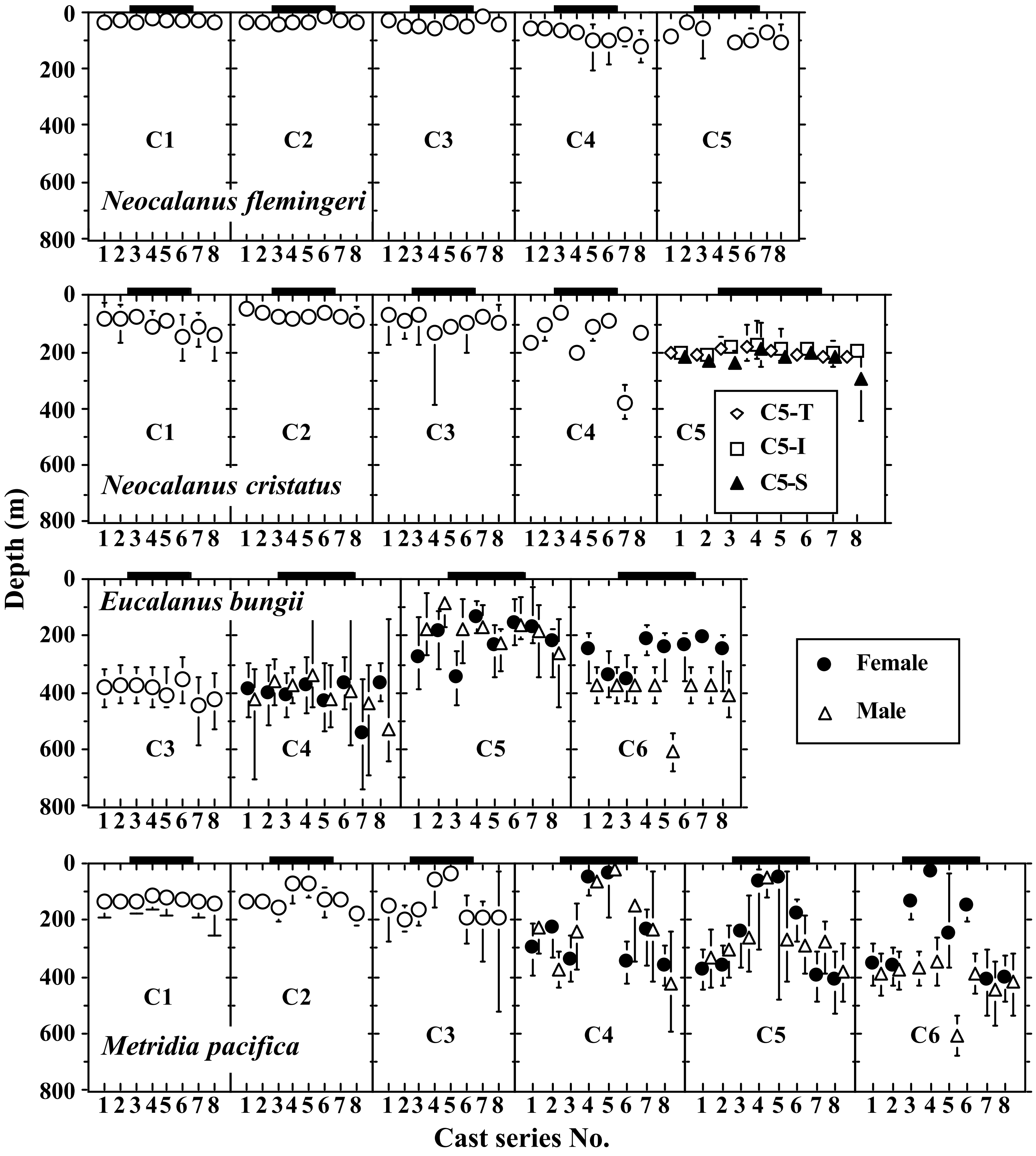

Fig. 3 (Sato et al.)

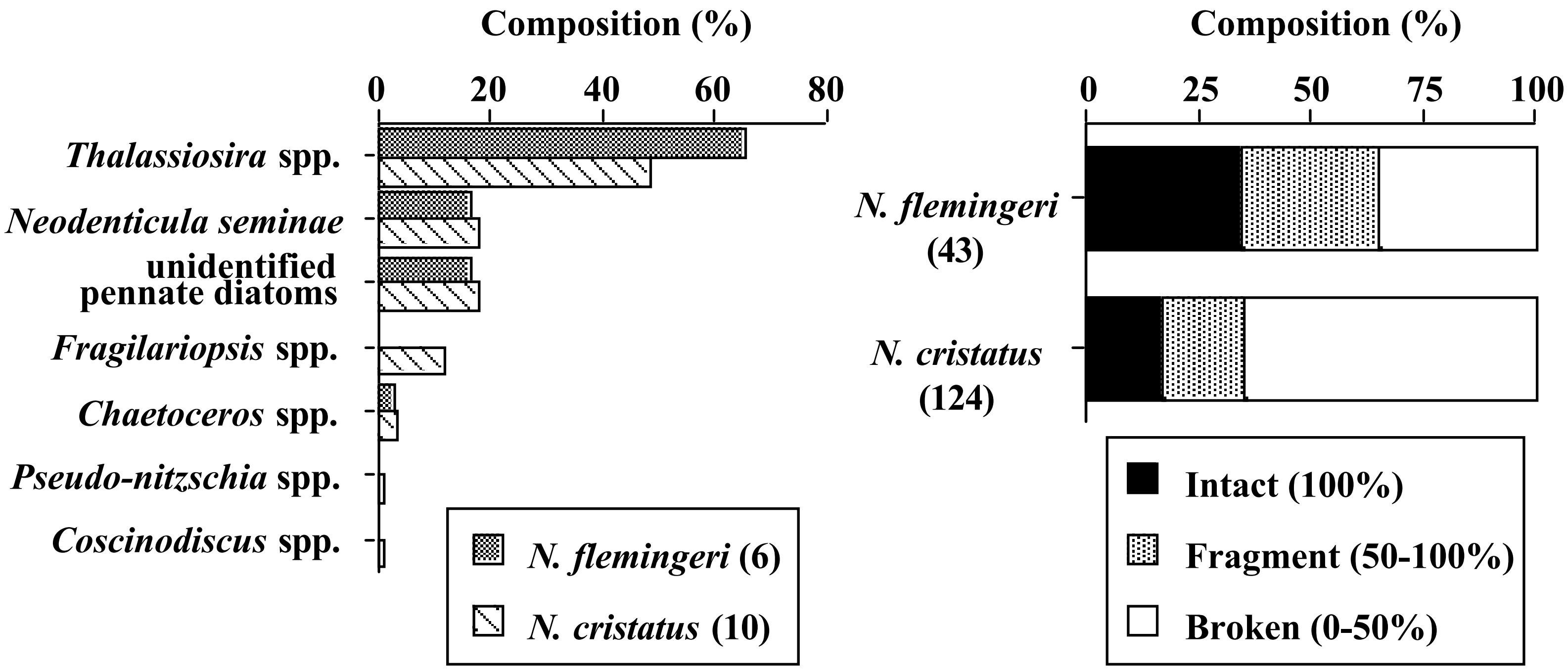

Fig. 4 (Sato et al.)

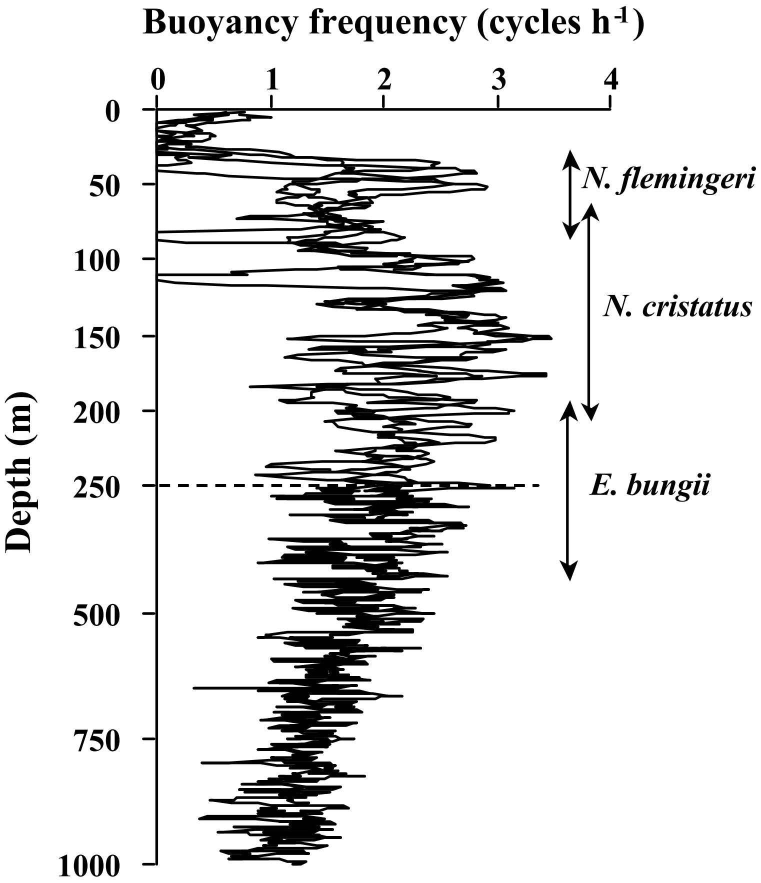

Fig. 5 (Sato et al.)