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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 0-1000 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 75-250 m. The boundary between two patterns was around 50-75 m. These findings are comparable to those in the eastern subarctic Pacific.

Keywords: Copepods; Diel vertical migration; Flux; Ontogenetic vertical distribution

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 1980's: 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 SEEDS-2001 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 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 (bi-monthly) 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 0-2000 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 0-1000 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 0-250 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 grow 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 4,048 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 nine strata between 0-1000 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.

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 ith 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 to 3.5 mg m^{-3}, and was high on April dates and low on 8 March (Fig. 1c). On 8 March, chl. *a* was extremely low, <0.2 mg m^{-3} throughout the water column.

3.2. Population structure of the dominant copepods

Abundance (total of copepodid stages) of *E. bungii* varied between 3,800 and 15,000 ind. m^{-2} (0-1000 m), and was greatest on 29 April 2007 (Fig. 2a). Population structure of *E. bungii* was mostly C3-C5 during 8 March to 11 April, dominated by C6 on 23 April, and C1 and C2 were >60% of the total population on 29 April. The mean stage of *E. bungii* was around C4 during 8 March to 23 April, dropping to 2.7 on 29 April.

Abundance of *M. pacifica* varied from 3,000 to 44,000 ind. m^{-2} and gradually increased during 5-29 April (Fig. 2b). All of its copepodid stages occurred throughout the study period, but C6 dominated on 5 April and C1 dominated on 23 April, causing a decrease of the mean stage of *M. pacifica* to around C3 on 23-29 April (Fig. 2b).

Abundance of *M. okhotensis* fluctuated between 300 and 2,300 ind. m^{-2} (Fig. 2c). Throughout the study period, C5 and C6 were its dominant stages. The proportion of C6 was greater on 8 March than on the later dates (Fig. 2c). The mean stage of *M. okhotensis* was stable around C5-C6 throughout the study period.

Abundance of *N. cristatus* varied between 900 and 3,500 ind. m^{-2} (Fig. 2d). For *N. cristatus*, C1 and C2 were the dominant stages on 8 March, C2 and C3 on 5 April, with a relative increase of C4 and C5 on 23-29 April 2007. The mean stage of *N. cristatus* slightly increased during the study from C2.0 to C2.8 (Fig. 2d).

Abundance of *N. flemingeri* was 1,600-4,500 ind. m^{-2} (Fig. 2e). The dominant stages were C1 and C2 on 8 March, C2-C4 on 5 April and C4-C5 on 29 April 2007. The mean stage of *N. flemingeri* increased accordingly from C2.2 to C4.6 during the study period (Fig. 2e).

Abundance of *N. plumchrus* varied between 100 and 10,000 ind. m^{-2} and was extremely low during 8 March to 11 April. It had increased by 29 April 2007 (Fig. 2f). The dominant stages of *N. plumchrus* were C4 and C5 on 8 March and 5 April and were C1-C3 on 29 April 2007. Mean stage of *N. plumchrus* was high during 8 March-5 April and was about C2 on 23-29 April (Fig. 2f).

3.3. Diel variation of vertical distribution

Eucalanus bungii were distributed between 250-500 m both day and night on 8 March 2007 (Fig. 3). Vertical distribution of part of the population of C3-C6 extended to the surface both day and night on 5 April. On 11 April, C4-C6 were near the surface, while C3 remained in deeper layers. All C3-C6 were distributed near the surface on 23 April. On 29 April, newly recruited C1-C2 dominated, and C1-C4 were distributed near the surface. Later stages, C5 and C6 showed bimodal vertical distributions near the surface and from 150-250 m. Throughout the study period, no sexual differences in vertical distribution were detected for C4-C5, but C6M were distributed below 150 m both day and night, not occurring closer to the surface. For none of the copepodid stages were day vs. night differences observed in vertical distribution (no DVM) at any time during the sampling (Table 2).

Daytime distribution depths of *M. pacifica* on 8 March were from 150-250m for C1-C3, 150-500 m for C4 and C5, and 250-500 m for C6 (Fig. 4). All of the copepodid stages, except C6M, were distributed from surface to 150 m at night. The strongest upward migrations at night were observed on 5 and 11 April. On 23 and 29 April, the vertical distributions of C1-C5 did not vary between day and night, and the distributions were deeper with advancing stage. The C6F migrated upward at night on 23 and 29 April (Table 2). Throughout, C6M were distributed below 250 m both day and night. The magnitude of DVM by adult females, evaluated with $D_{50\%}$, was 46-359 m. Since the daytime distributions were deeper for later copepodid stages, their magnitudes of DVM were progressively greater (Table 2). It should be noted that the DVM on 23-29 April was only observed for C6F, and there was none by the other stages (Table 2).

Metridia okhotensis were distributed below 250 m both day and night and had no DVM on 8 March (Fig. 5). On 5 and 11 April, C5F/M and C6F migrated upward from 250-500 m in daytime to near the sea surface at night. On 23 and 29 April, this upward migration was observed only for C6F, from 150-500 m in daytime to the surface at night, while C4 and C5 remained between 150-500 m both day and night (Fig. 5). The C6M were distributed from 250-500 m both day and night throughout the study. The magnitude of DVM was 71-358 m for C5 and C6F (Table 2).

C1-C4 of *N. cristatus* were distributed shallower than 250 m both day and night from March through April (Fig. 6). Interestingly, their vertical depth range was wide (0-250 m) on 8 March, narrower (0-150 m) from 5 April to 29 April (Fig. 6). Throughout the study period, part of the C5 population extended below 250 m, and C6 occurred only below 500 m. No DVM of *N. cristatus* was detected for any of the stages on any date.

The C1-C4 of *N. flemingeri* were collected above 150 m both day and night on all dates (Fig. 7). Within that layer, vertical distribution was wide on 8 March and more concentrated close to the surface (0-50 m) from 5 to 29 April. Most of the C5 of *N. flemingeri* were also distributed shallower than 150 m, but some of them extended the distribution down to 1000 m. C6F/M occurred below 250 m both day and night throughout the study period (Fig. 7). DVM of *N. flemingeri* was only detected for stage C4 on 8 March, but the amplitude was small (66 m).

C1-C5 of *N. plumchrus* occurred steadily during 23-29 April, and were concentrated in the 0-50 m layer (Fig. 8). On the other dates, only small numbers of *N. plumchrus* occasionally occurred. No DVM of *N. plumchrus* was detected for any of the stages.

3.4. Ontogenetic variation in diel vertical migrations

For evaluation of ontogenetic variation in DVM, the $D_{25\%,}$ D_{50} and $D_{75\%}$ values for each copepodid stage during day and night are summarized in Figs. 9 and 10.

All copepodid stages of *E. bungii* were concentrated around 400 m on 8 March (Fig. 9a). On 5 April, the distributions of its C3-C6F stages were extensive, and their $D_{50\%}$ varied from 200-600 m, evidently a developmental ascent pattern. On 11 April, C5F/M and C6F reached the surface while C3 and C4 remained deep. On 23 April, all the stages reached the surface layer, a developmental ascent pattern. On 29 April, C1-C4 of *E. bungii* were collected above 50 m, and C5-C6 were found from 100-200 m, consistent with a developmental decent pattern (Fig. 9a).

Ontogenetic variation in vertical distribution of *M. pacifica* in daytime was C1-C3 distributed above 200 m, C4-C5 and C6F from 300-500 m and C6M from 400-800 m (Fig. 9b). Nighttime depths of C1-C6F of *M. pacifica* were around 100 m on 8 March, shifting to near the surface on 5 and 11 April, when the DVM was observed, not varying with stage. On 23 and 29 April, most of the stages of *M. pacifica,* except C6F, stayed down at the daytime depth throughout the night (Fig. 9b).

Daytime distribution of *M. okhotensis* was concentrated around 400 m, and no ontogenetic differences were evident (Fig. 9c). Nighttime depths of *M. okhotensis* for the stages engaging in DVM (C5F/M on 5 and 11 April and C6F on 5-29 April) were around 50 m with no variation among the stages. On 23 and 29 April, most of the stages of *M. okhotensis,* except C6F, stayed at the daytime depth throughout the night

(Fig. 9c).

The $D_{50\%}$ values of C1-C4 *N. cristatus* were in the range 25-200 m, the shallowest being that of C2 throughout the study period (Fig. 10a). The C5 of *N. cristatus* were distributed from 200-400 m, and diel depth differences were not observed.

The $D_{50\%}$ values for C1-C5 of *N. flemingeri* were in the range from 25-200 m, while C6 was distributed from 400-1000 m (Fig. 10b). Vertical distribution of *N. flemingeri* was shallower than that of *N. cristatus* in the same period. In common among *Neocalanus* spp., vertical distributions on 8 March were deeper than those on 5-29 April (Fig. 10a, b).

The $D_{50\%}$ values of C1-C3 of *N. plumchrus* were around 20 m, those of C4 and C5 were 25-700 m and 25-900 m, respectively (Fig. 10c). Vertical distribution depths of *N. plumchrus* were similar to those of *N. flemingeri*, thus shallower than those of *N. cristatus*.

4. Discussion

4.1. Analysis of the data

To evaluate DVM, we applied two-sample Kolmogorov-Smirnov (K-S) tests (Sokal and Rohlf, 1995). While the robustness of this test for evaluating DVM of zooplankton can be questioned in the case of the great differences in abundance between day and night (Venrick, 1986), we have checked those differences and found them to be less than 5-fold. Given that problems with the K-S test only substantially affect differences greater 10-fold (Table 1 in Venrick, 1986), we consider it appropriate for our evaluations of DVM (Table 2).

4.2. Effect of water mass exchange

As a possible cause of changes in vertical distribution of large copepods, water mass exchanges must be addressed. Repeated water mass changes were observed during the study period; thus modified Kuroshio water was present at A-5 on 8 March characterized by high temperature (6˚C) and salinity (33.6). Coastal Oyashio water was present on 5 April characterized by low temperature (1˚C) and salinity (33.2). A mixture was present from 11 to 29 April (Fig. 1). Vertical distribution of large copepod species may be affected by the changes in water mass. However, we conclude that the effect of water mass exchange on vertical distribution of large copepods was rather small compared to causes endogenous to the population. Vertical distribution of the large copepods is limited by high temperature, such that *N. cristatus* stays below a surface layer at 12 ˚C for, *N. plumchrus* below 15˚C and *M. pacifica* below 20˚C (Morioka, 1976, 1977). Compared with those temperatures the observed temperature and salinity ranges in this study (1-6˚C and 33.0-34.4) were both narrower and well within favorable conditions for these large copepods. Thus, we assume the water mass exchanges had minimal effects on the vertical distributions of large copepod species.

4.3. Eucalanus bungii

There are several prominent findings on vertical distribution of *E. bungii*: (1) recruitment (upward migration) to the surface layer was earlier for resting C6F than for resting C3-C4; (2) newly recruited C1-C3 were distributed from 0-50 m (Fig. 9a); (3) the males of *E. bungii* remained at considerable depth and mated without subsequent feeding (see also Miller et al., 1984). For *E. bungii*, no DVM was observed, regardless of stage, throughout the sampling periods, while seasonal ontogenetic migration was evident. Reports by Shoden et al. (2005) and Takahashi et al. (2008) agree with the present results.

In the present study, *E. bungii* was in diapause at depth on 8 March, while apparently arousing and migrating upward on 5 April (Fig. 9a). What is the proximal cue that arouses *E. bungii* from rest at depth? While there are no studies concerning this for *E. bungii*, several factors are reported to be the cue for other copepods. Particle flux to the resting depth is argued for *Calanus finmarchicus* (Heath et al., 2000). Seasonal changes in day length are supposed to initiate DVM behavior of *Chiridius armatus* (Falkenhaug et al., 1997). Direct changes in temperature or salinity (thus turbulence and mixing) are not likely, because those parameters are stable at the *E. bungii* resting depth (250-500 m) (Fig. 1). Signals from other seasonal organisms (upward migration of nauplii of *Neocalanus* spp.) might also be considered. For *N. plumchrus*, the timing of molting from C5 to C6 involves an interaction between an endogenous clock or an unknown cue that stimulates the termination of dormancy and the onset of reproductive development and maturation (Miller and Clemons, 1988;

Campbell et al., 2004).

Upward migration of *E. bungii* was also reported for the SERIES iron-fertilization experiment in the eastern subarctic Pacific during summer (Sastri and Dower, 2006; Tsuda et al., 2006). Tsuda et al. (2006) suggested that the increases of *E. bungii* in the fertilized patch were likely due to lowered mortality during the egg and naupliar stages. Eggs and nauplii would have been of less import in the diets of suspension-feeding omnivores due to increased diatom abundance. However, that would not likely have been the case in our study, because the distributions of late copepodid stages of suspension feeding copepods (for instance *N. cristatus* C5) were well below 0-50 m (Fig. 6).

4.4. Metridia pacifica

Diel vertical migration behavior of *M. pacifica* is well known (Tsuda and Sugisaki, 1994; Takahashi et al., 2008). In our sampling on 23-29 April, C1-C4 of *M. pacifica* stayed in the same layer both day and night (Fig. 9b). However, part of the C5F/M stock migrated upward at night, while majority stayed between 150-500 m throughout the day. Consistent DVM was only observed for C6F (Fig. 4). In several locations and seasons, cessation of DVM has been reported: the eastern subarctic Pacific in winter (Batchelder, 1985) and the western subarctic Pacific in June and August (Hattori, 1989). According to Hattori (1989), staying in the 200-300 m layer throughout the day is possible for *M. pacifica* copepodids because they can obtain enough food at that depth; damaged diatoms and fecal pellet-like particles were found in their guts.

Individual differences in DVM behavior of *Metridia* spp. are generally considered to be related to their nutrition. According to Hays et al. (2001), the mean size of the oil sacs of migrant specimens was much smaller than for those that remained at depth. Animals with larger lipid stores need not risk coming to the surface at night to feed. In Dabob Bay, Washington, *M. pacifica* (=*M. lucens*) underwent a reverse DVM on some dates, avoiding the surface 25 m at night, while on still other dates the C3 and younger stages avoided the surface 25 m day and night (Osgood and Frost, 1994). This reverse DVM behavior of *M. pacifica* was considered to be related the abundance of vertebrate and invertebrate predators (Osgood and Frost, 1994). These facts indicate that the *Metridia* spp. have flexibility in their vertical distribution and DVM behaviors. During 23-29 April in this study, *M. pacifica* could have accumulated lipids to sustain them, or they might be able to find sufficient food at that depth. In the following, we calculate whether they might meet their dietary requirements at depth.

Since primary production was measured during 7-30 April (Isada et al., this issue), the downward particle flux to 300 m was estimated from an equation suggested by Suess (1980); $C_{flux}= C_{prod}/(0.0238Z+ 0.212)$, where C_{prod} is primary production (mg C m^{-2} day^{-1}), and C_{flux} is carbon flux (mg C m^{-2} day^{-1}) at a given depth (Z: m). We can take the dry mass (DM: mg ind.$^{-1}$) of each copepodid stage of *M. pacifica* from Padmavati (2002). Respiration rate (R: μl O_2 ind.$^{-1}$ h^{-1}) can be estimated from $\ln (R)= -0.399+ 0.801 \ln (DM) + 0.069T$ (Ikeda et al., 2001), where temperature (T) at 300 m was 3°C (Fig. 1). Metabolism was converted to units of carbon (M) from R by assuming a respiratory quotient ($[CO_2]/[O_2]$) of 0.97 (for protein metabolism, see Gnaiger, 1983). Carbon budgets of living copepods may be expressed as: Ingestion (*I*) = Metabolism (*M*)+ Growth (*G*)+ Egestion (*E*). Assuming assimilation efficiency ([*M*+*G*]/*I*, or [*I*-*E*]/I) to be 70% and gross growth efficiency (*G*/*I*) to be 30% (for detail accounts, see Ikeda and Motoda, 1978), ingestion rates (*I*: μg C ind.$^{-1}$ h^{-1}) can be calculated as *I*=*M*/(0.7-0.3). Values for *I* were computed, expressed on a daily basis (x 24 hours) and summed for all individuals (mg C m^{-2} day^{-1}). The resulting estimates (Table 3) show that *M. pacifica* could likely meet its energetic requirements at 300 m in April without DVM, as was suggested by Hattori (1989). The *M. pacifica* stock ingestion rate was probably less than the likely carbon flux to 300 m, about 4-40% of the supply rate.

4.5. Metridia okhotensis

Metridia okhotensis showed short-term changes in DVM behavior. They stayed around 400 m both day and night on 8 March. The C5 and C6F migrated to the surface at night on 5-11 April, while on 23-29 April only C6F migrated upward (Fig. 9c). Several authors have reported no DVM by *M. okhotensis* (Hattori, 1989; Padmavati et al., 2004), while Vinogradov and Arashkevich (1969) reported DVM ascents of 500-700 m in the Okhotsk Sea, where it is abundant. More recently, Takahashi et al. (2008) have reported that DVM by *M. okhotensis* in the Oyashio region was only observed in April. April is the only season that the C6F have been observed in the surface layer in the Oyashio region (Padmavati et al., 2004).

As sympatric congeners, *M. pacifica* and *M. okhotensis* in the subarctic Pacific are comparable to the *M. lucens*-*M. longa* pair in the subarctic Atlantic. At the same stations, the larger *M. longa* is distributed deeper than the smaller *M. lucens* (Falkenhaug et al., 1997). Deeper occurrence of the larger form, *M. okhotensis,* than of the smaller form, *M. pacifica,* was also observed in the Pacific. Bollens et al. (1993) hypothesized that the smaller, less fecund species would have to maintain exceptionally effective avoidance behavior, including remaining migratory at all times and avoiding the surface layer except during total darkness. However, according to Hays et al. (1994), larger taxa among copepods generally show significantly stronger DVM, with body size explaining 47% of inter-taxon variation in DVM. Both explanations fit with the larger *M. okhotensis* living deeper than the smaller *M. pacifica* in the subarctic Pacific (Fig. 9b, c).

Cessation of DVM, except for that of C6F on 23-29 April, was common to both *M. pacifica* and *M. okhotensis* (Fig. 9b, c). During this period, both species were actively spawning (Yamaguchi et al., this issue). Since the survival rate of larvae and juveniles would likely be greater in the surface layer, where phytoplankton are abundant (Fig. 1), near-surface spawning at night places the young with their food source and continuing DVM may improve survival chances for females. Other stages with sufficient food at depth would gain little from upward migration and increase their risk of predation (Table 3). As Hays et al. (2001) have pointed out, individual variability in DVM can be influenced by body condition; those with larger lipid stores need not risk coming to the surface to feed.

4.6. Neocalanus cristatus

Vertical distributions of *N. cristatus* C1-C3 were extensive on 8 March, between 0-250 m. Distribution of C1-C3 was shifted upward to 0-150 m on 5-23 April, when C4 and C5 were dispersed from 75-250 m (Fig. 6). On 29 April, C1 and C2 were at 0-25 m, C3 and C4 were at 50-100 m. An upward shift by *N. cristatus* during an induced phytoplankton bloom was reported for the SERIES experiment (Sastri and Dower, 2006; Tsuda et al., 2006).

The C2 of *N. cristatus* were located above the C1 (Fig. 10a). Since *N. cristatus* do not feed in the naupliar stage, C1 is the first feeding stage (Saito and Tsuda, 2000). Spawning occurs >1000 m (Miller et al., 1984; Kobari and Ikeda, 1999), and low density eggs and nauplii float and swim upward (Nakai, 1969). Thus, deeper occurrence of younger C1 than older C2 (Fig. 10a) is reasonable; the C1 would have started upward as eggs and nauplii after the C2.

The two largest contributors to mesozooplankton biomass, *N. cristatus* and *E. bungii*, remain deeper than 50 m in the eastern subarctic Pacific during spring, while the smaller species of *Neocalanus* (*N. flemingeri* and *N. plumchrus*) remain shallower than 50 m (Mackas et al., 1993). The vertical separation of congeners results in *N. plumchrus* and *N. flemingeri* having direct and indirect grazing effects on mixed layer phytoplankton, while *N. cristatus* remains below the mixed layer, most likely feeding on aggregates sinking out of the euphotic zone (Dagg, 1993). Exploitation of sinking particles as a food source by late *N. cristatus* copepodids likely also occurs in the

Oyashio region. *Neocalanus cristatus* C4-C5 were spread vertically between 75-250 m, and no DVM was detected (Fig. 6).

4.7. Neocalanus flemingeri

Vertical distribution of C1-C4 *N. flemingeri* extended from 25 to 150 m on 8 March. They were concentrated at 0-50 m both day and night on 5-29 April (Fig. 7). A similar upward migration from residence in a subsurface layer before a bloom to the surface layer during the bloom was reported for *E. bungii* (C3-C5) and *N. cristatus* (C2-C4) during a summer iron fertilization experiment in the eastern subarctic Pacific (SERIES: Tsuda et al., 2006). No changes in vertical distribution of copepods were observed after iron fertilization in the western subarctic Pacific (SEEDS2001), but increase in abundance of early copepodid stages of *N. plumchrus* and *E. bungii* was reported (Tsuda et al., 2005). The cause of apparent upward migration and increase of early copepodid stages during iron fertilization experiments was postulated to be reduced mortality during the egg and naupliar stages. Apparently suspension-feeding omnivores ate fewer of them due to increased diatom availability (Tsuda et al., 2006). The same explanation may fit the shifts in this study. *Metridia pacifica* was deeper before the bloom (8 March) than after its onset (5 April) (Fig. 9b). The upward shift of the C1-C4 distributions of *N. cristatus* and *N. flemingeri* occurred in the same interval (Fig. 10a, b). On the other hand, the shallower distribution patterns could have been a response to changes in water column structure. Temperature and salinity profiles were homogenous around 6˚C and 33.6 throughout 0-200 m on 8 March, while a thermocline was present in the upper 100 m during 5-29 April (Fig. 1a). Thus the wider vertical distribution of C1-C4 of *N. flemingeri* and *N. cristatus* on 8 March (Figs. 6 and 7) corresponded to a period of strong vertical mixing down to 200 m, while the more concentrated vertical distribution on 5 April corresponded to a period of significant upper water column stratification.

4.8. Neocalanus plumchrus

C1-C4 of *N. plumchrus* were in the 0-50 m stratum both day and night (Fig. 8). Differences in depth of distribution between the congeneric *N. cristatus* and *N. plumchrus* were evident; *N. plumchrus* shallower than *N. cristatus*. No difference was observed for the active growth phases of *N. plumchrus* and *N. flemingeri*. No differences in vertical distribution pattern of similar-sized *N. plumchrus* and *N. flemingeri* were reported in May-June from the eastern subarctic Pacific (Mackas et al., 1993). Since temporal timing of surface occurrence of early copepodid stages of these two species is known to be sequential, i.e. first *N. flemingeri* and later *N. plumchrus* dominating (Miller and Clemons, 1988; Tsuda et al., 1999; Kobari and Ikeda, 2001b), *N. flemingeri* and *N. plumchrus* separate their distribution temporally, but not by spatially.

The strong vertical species zonation in the eastern subarctic Pacific in May and June (Mackas et al., 1993), a near surface pair (*N. plumchrus* and *N. flemingeri*) and a subsurface pair (*N. cristatus* and *E. bungii*), was confirmed at least for the late copepodid stages of *Neocalanus* spp. in this study. However, since newly spawned *E. bungii* were distributed in the surface layer (Fig. 9a), this species did not fit the eastern subarctic pattern. For all *Neocalanus* spp., the C1 and C2 were distributed near the surface (but somewhat deeper for C1 *N. cristatus*, as mentioned before). Clear differences were observed between the C3-C5 of *N. flemingeri/plumchrus* (shallower) and C3-C5 of *N. cristatus* (deeper) (Fig. 10). The boundary between these groups shifted vertically, but was sharply defined and was often coincident with a weak and transient thermocline marking the base of the layer actively mixed by surface wind and wave energy (similarly to results of Mackas et al., 1993).

4.9. Conclusion

Patterns of diel and ontogenetic vertical distribution of large grazing copepods during the spring phytoplankton bloom in the Oyashio region were evaluated by VMPS sampling. Features common to all of the species was absence of DVM in late winter, certainly connected to a diapause at depth, and of feeding by C6M, which stayed in deep layers throughout the day, as previously observed across the region (Miller et al., 1984; Batchelder, 1985; Padmavati et al., 2004; Shoden et al., 2005). Vertical distribution of C6F of large grazing copepods had different patterns in different species: female *E. bungii, M. pacifica* and *M. okhotensis* migrated to the surface layer to spawn, while *Neocalanus* spp. remained deep and reproduced there, also without feeding (Kobari and Ikeda, 1999, 2001a, 2001b). Responses to the spring phytoplankton bloom varied among species. *Eucalanus bungii* C6F aroused from rest sooner than the C3-C4. Young of the year C1-C4 stayed near surface layer (Fig. 3). Both *M. pacifica* and *M. okhotensis* exhibited some DVM behavior. When the sinking flux provides sufficient food at depth, the *Metridia* juveniles cease DVM and stay at daytime depths throughout the night, while C6F continue DVM (Fig. 4), likely to place their eggs very close to the surface. Growth of *Neocalanus* spp. occurred above 250 m, and some vertical partitioning was observed between the species. Growth of *N. flemingeri* and *N. plumchrus* occurred above 50 m, while at least older copepodids of *N. cristatus* finished their growth in the 50-250 m stratum (Fig. 10). Their upper boundary moved up and down between 50 and 75 m, which corresponds to the pattern in the eastern subarctic Pacific.

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Figure captions

Fig. 1. Vertical distribution of temperature (a), salinity (b) and chlorophyll *a* (c) in the Oyashio region (St. A-5) on 8 March, 5, 11, 23 and 29 April 2007. Note that the depth scale of (c) differs from that of (a) and (b).

Fig. 2. Abundance and mean stage (upper panel) and stage composition (lower panel) of *Eucalanus bungii* (a), *Metridia pacifica* (b), *M. okhotensis* (c), *Neocalanus cristatus* (d), *N. flemingeri* (e) and *N. plumchrus* (f) in the Oyashio region (St. A-5) during 8 March, 5, 11, 23 and 29 April 2007.

Fig. 3. Day (D) and night (N) vertical distribution of C1 to C6 of *Eucalanus bungii* in the Oyashio region (St. A-5) on 8 March, 5, 11, 23 and 29 April 2007. Separation between females (solid) and males (dotted) was done for C4-C6.

Fig. 4. Same as Fig. 3, but for *Metridia pacifica*.

Fig. 5. Same as Fig. 3, but for *Metridia okhotensis*.

Fig. 6. Day (D) and night (N) vertical distribution of C1 to C6 of *Neocalanus cristatus* in the Oyashio region (St. A-5) during 8 March, 5, 11, 23 and 29 April 2007. Separation of females (solid) and males (dotted) was made for C6.

Fig. 7. Same as Fig. 6, but for *Neocalanus flemingeri*.

Fig. 8. Same as Fig. 6, but for *Neocalanus plumchrus*.

Fig. 9. Ontogenetic changes in the depths above and below which 50% of the population resided ($D_{50\%}$) in day (open circle) and night (solid circle) for (a) *Eucalanus bungii*, (b) *Metridia pacifica* and (c) *M. okhotensis* in the Oyashio region during 8 March, 5, 11, 23 and 29 April 2007. Vertical bars indicate

depth range from $D_{25\%}$ to $D_{75\%}$.

Fig. 10. Ontogenetic changes in the depths above and below which 50% of the population resided ($D_{50\%}$) in day (open circle) and night (solid circle) for (a) *Neocalanus cristatus*, (b) *N. flemingeri* and (c) *N. plumchrus* in the Oyashio region during 8 March, 5, 11, 23 and 29 April 2007. Vertical bars indicate depth range of $D_{25\%}$ to $D_{75\%}$.

Table 1. Sampling data of VMPS in the Oyashio region during 8 March, 5, 11, 23 and 29 April 2007. (A) Local time of each cast. (B) Sampling layer and their filtered water volume (mean ± 1sd). (D): day, (N): night.

(A) Sampling date	Local time	(B) Sampling layer (m)	Filtered water volume (m^3)
8 Mar. (D)	12:17-13:23	0-25	4.3 ±0.9
8 Mar. (N)	23:42-0:51	25-50	4.6 ±0.7
5 Apr. (D)	13:48-15:12	50-75	5.9 ±0.7
5 Apr. (N)	1:57-3:15	75-100	4.9 ±0.9
11 Apr. (D)	13:35-14:57	100-150	9.3 ±2.6
11 Apr. (N)	22:28-0:01	150-250	24.5 ±2.8
23 Apr. (D)	7:51-9:19	250-500	58.9 ±4.6
23 Apr. (N)	22:41-0:13	500-750	55.3 ±5.4
29 Apr. (D)	12:45-14:17	750-1000	56.6 ±5.4
29 Apr. (N)	2:33-3:59		

Table 2. Results of Kolmogorov-Smirnov test on day and night vertical distribution of *Eucalanus bungii, Metridia pacifica* and *M. okhotensis* in the Oyashio region during March to April 2007. For significant stage, the magnitude of diel vertical migration (daytime $D_{50\%}$ - nighttime $D_{50\%}$, m) are shown. *: $p < 0.05$, **: $p < 0.01$, ns: not significant. -: no occurrence or because of low abundance (<40 ind. m^{-2}), no statistical test was carried out for the stage.

	Eucalanus bungii					*Metridia pacifica*					*Metridia okhotensis*				
Stage	8 Mar.	5 Apr.	11 Apr.	23 Apr.	29 Apr.	8 Mar.	5 Apr.	11 Apr.	23 Apr.	29 Apr.	8 Mar.	5 Apr.	11 Apr.	23 Apr.	29 Apr.
C1	-	-	-	-	ns	104^{**}	97^{*}	75^{**}	ns	ns	-	-	-	ns	-
C2	-	-	-	-	ns	96^{**}	87^{*}	88^{**}	ns	ns	-	-	-	ns	-
C3	ns	ns	ns	ns	ns	83^{**}	86^{*}	116^{**}	ns	ns	-	-	ns	ns	-
C4F	ns	ns	ns	ns	ns	97^{*}	194^{**}	183^{*}	ns	ns	-	-	ns	ns	-
C4M	ns	ns	ns	ns	ns	ns	196^{*}	194^{*}	ns	ns	-	-	ns	ns	-
C5F	ns	ns	ns	ns	ns	177^{*}	415^{**}	ns	ns	ns	-	336^{**}	178^{**}	ns	ns
C5M	ns	ns	ns	ns	ns	ns	677^{*}	158^{*}	ns	ns	-	336^{**}	358^{**}	ns	ns
C6F	ns	ns	ns	ns	ns	240^{**}	359^{**}	176^{**}	46^{*}	164^{*}	ns	-	282^{**}	71^{*}	213^{*}
C6M	ns	-	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns

Table 3. Temporal changes in primary production (*PP*), estimated carbon flux at 300 m (C_{flux} at 300 m), abundance (whole copepodid stages) and estimated ingestion of *Metridia pacifica* during 7-29 April 2007. Data on *PP* are from Isada et al. (this issue) and abundance data are from Yamaguchi et al. (this issue).

			Metridia pacifica	
Date	*PP* (mg C m^{-2} day^{-1})	C_{flux} at 300 m (mg C m^{-2} day^{-1})	Abundance (ind. m^{-2})	Ingestion (mg C m^{-2} day^{-1})
7 Apr.	2,586	352	4,879	15.5
8 Apr.	541	74	11,844	29.6
10 Apr.	1,067	145	10,076	14.8
12 Apr.	808	110	9,907	27.6
17 Apr.	988	134	9,993	22.9
20 Apr.	924	126	15,174	37.0
25 Apr.	980	133	12,863	25.4
29 Apr.	1,214	165	16,310	21.7

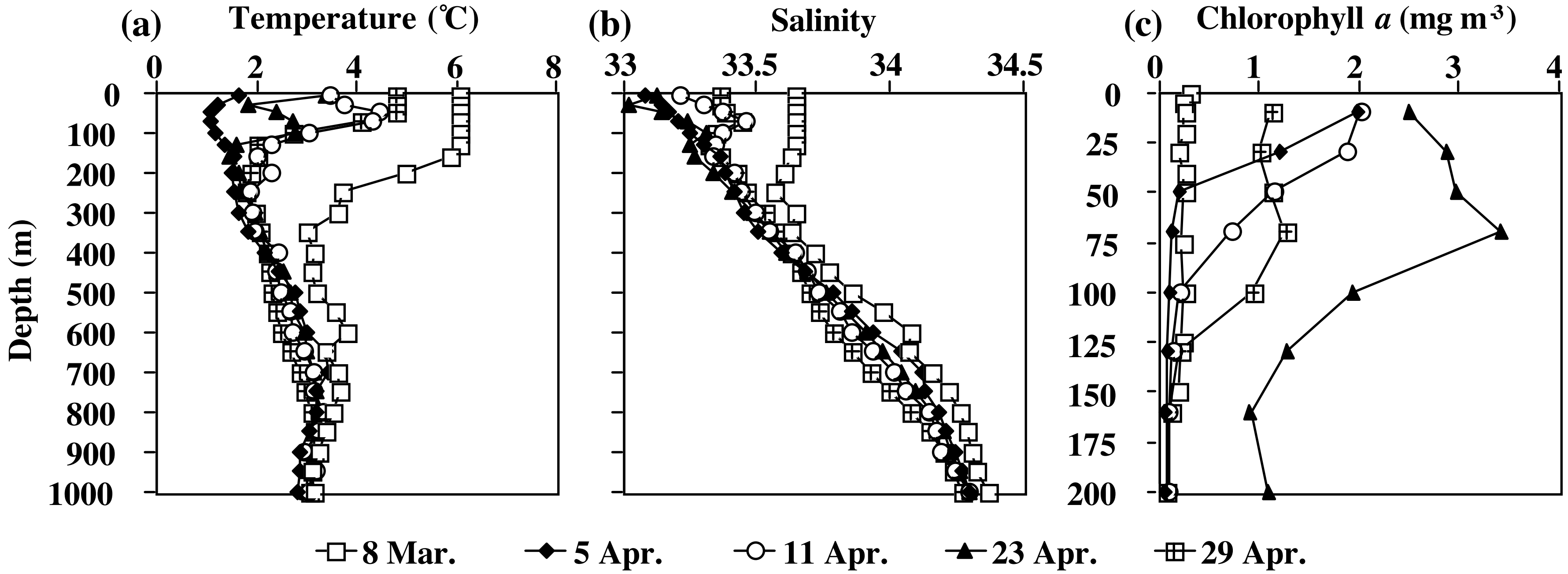

Fig. 1 (Yamaguchi et al.)

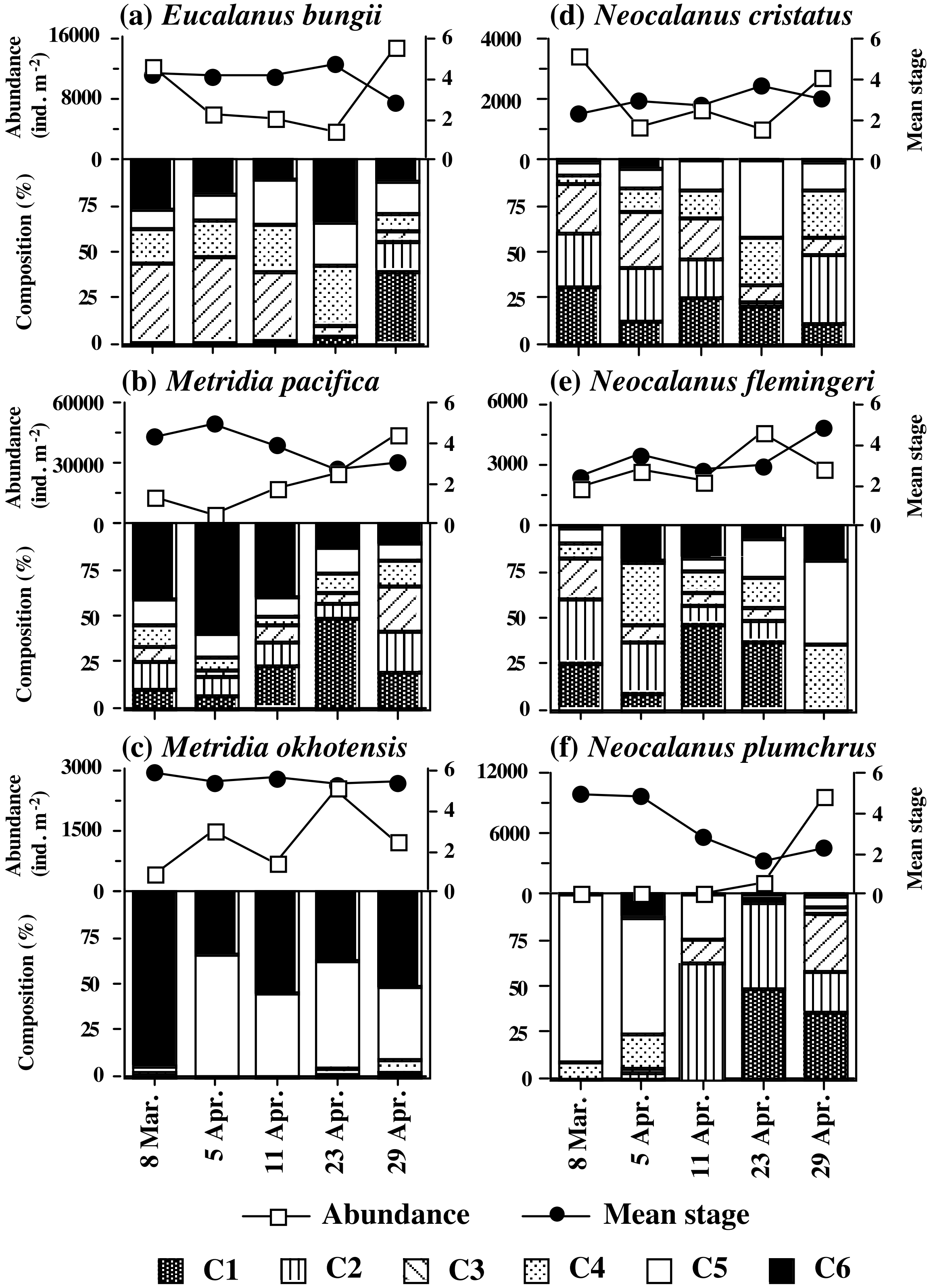

Fig. 2 (Yamaguchi et al.)

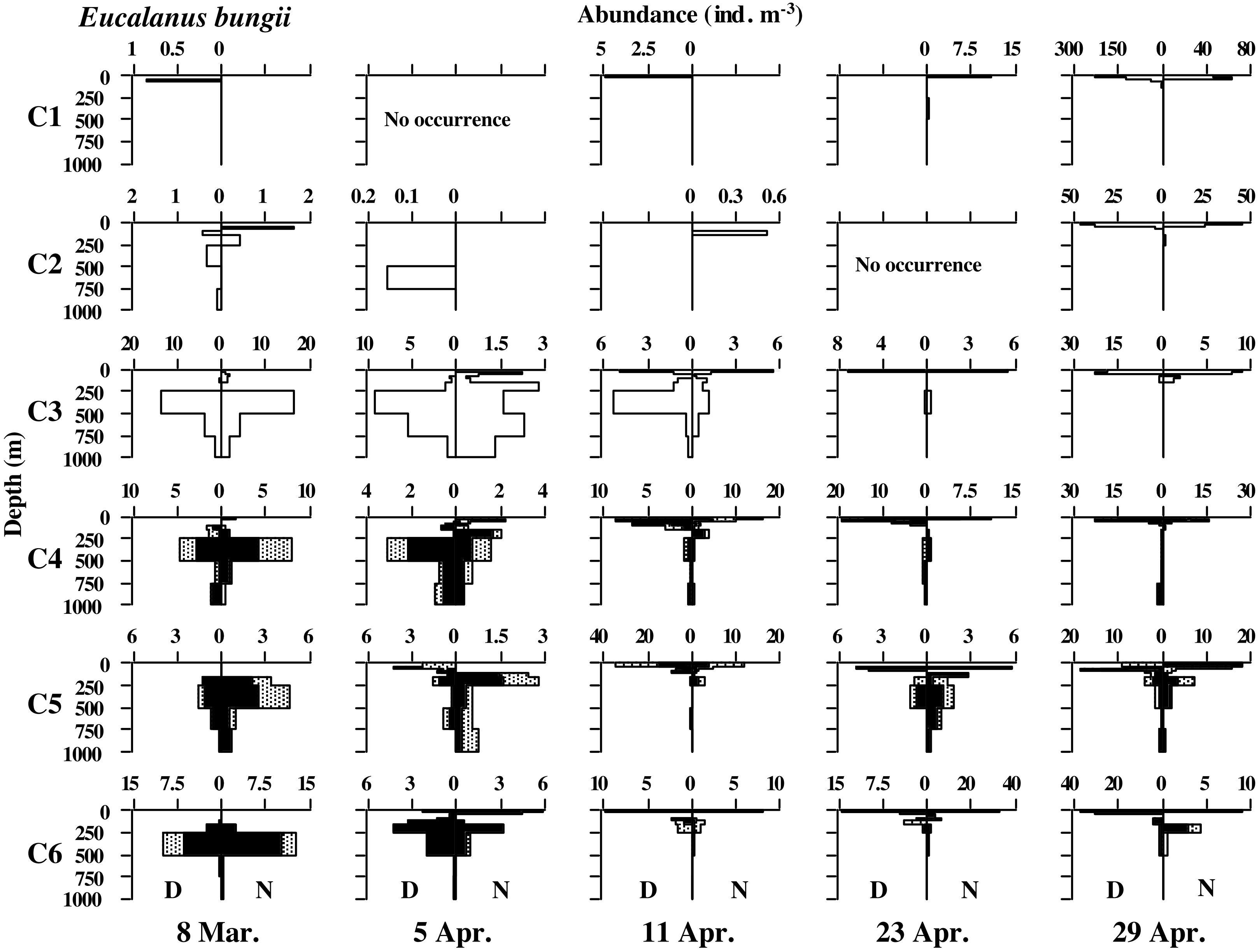

Fig. 3 (Yamaguchi et al.)

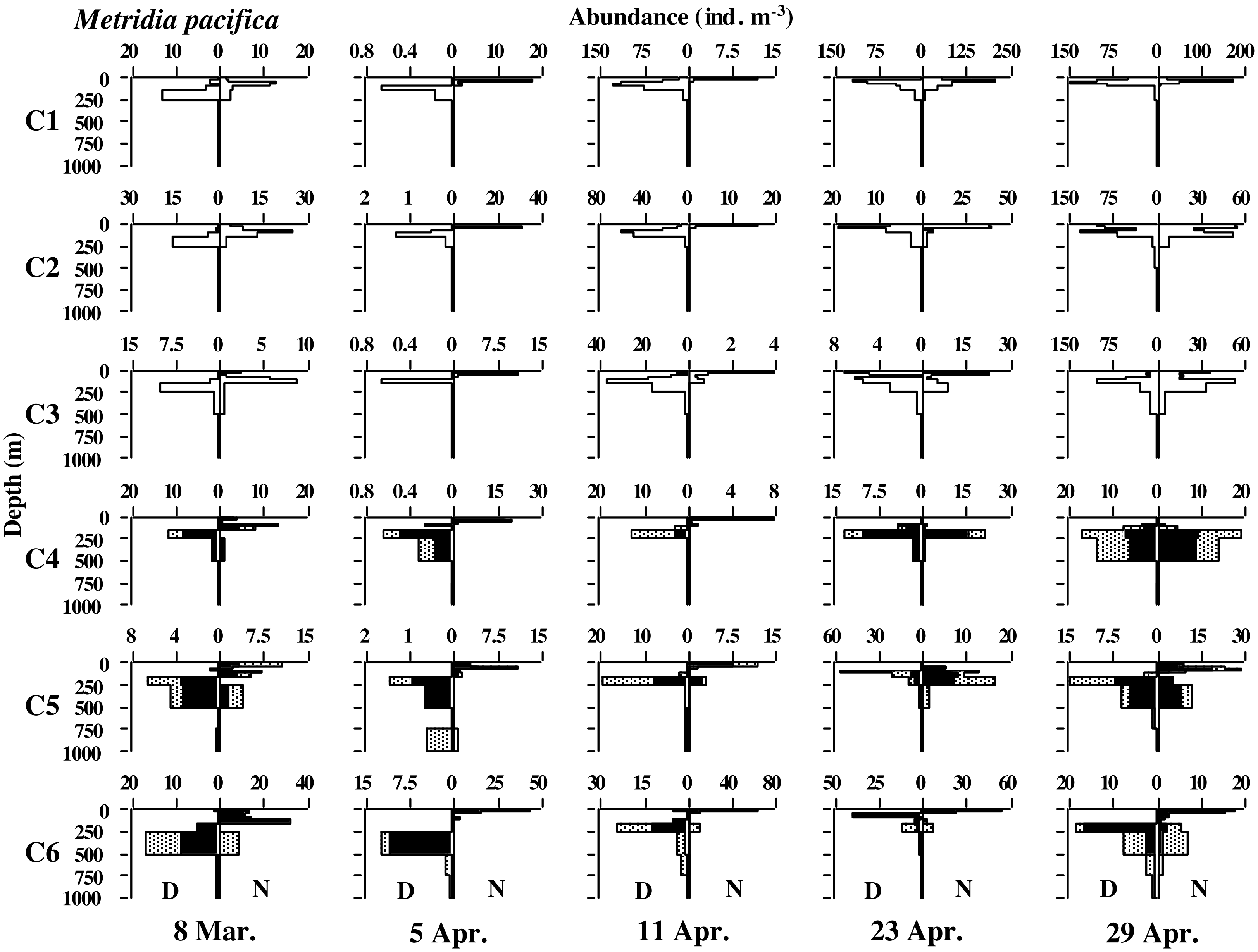

Fig. 4 (Yamaguchi et al.)

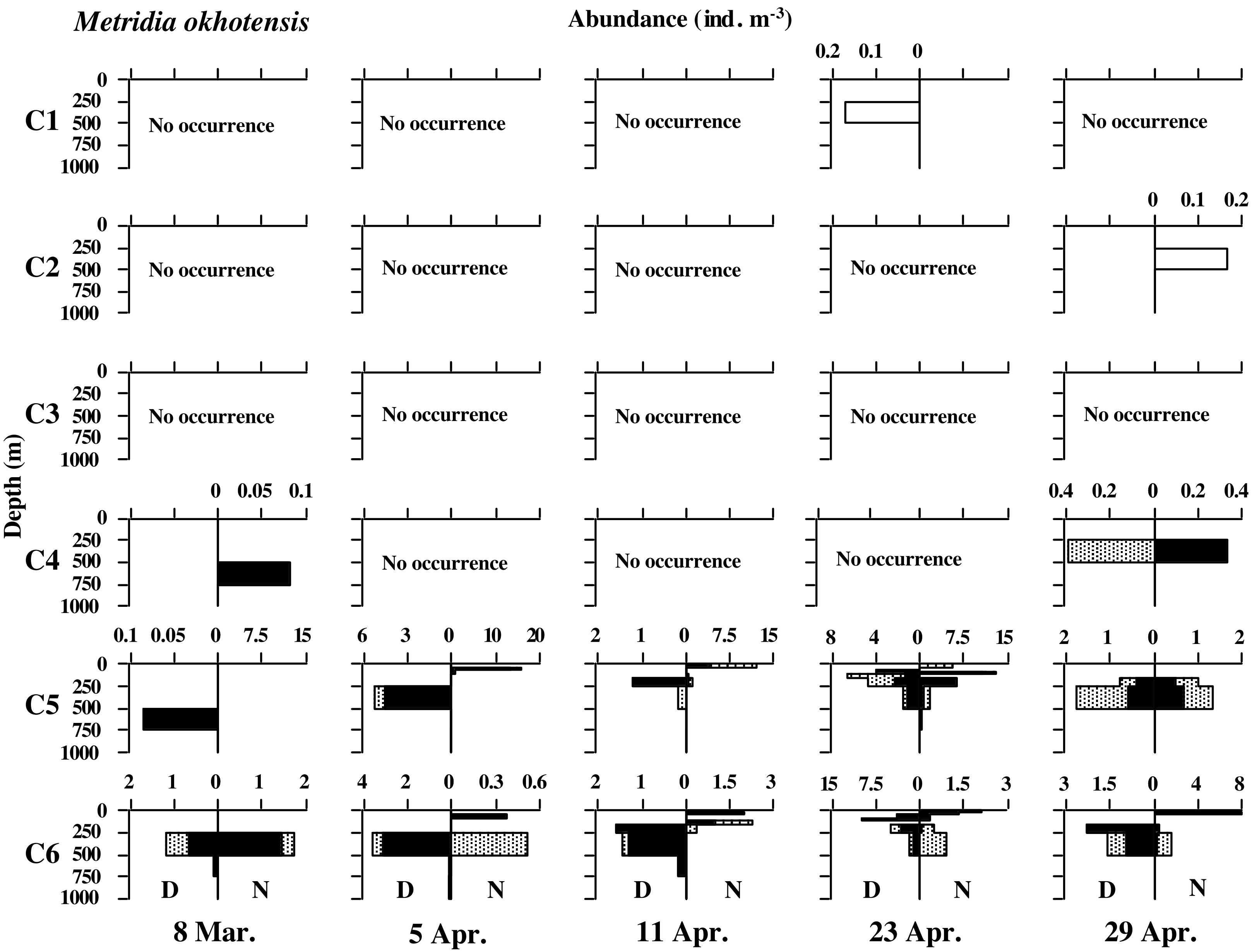

Fig. 5 (Yamaguchi et al.)

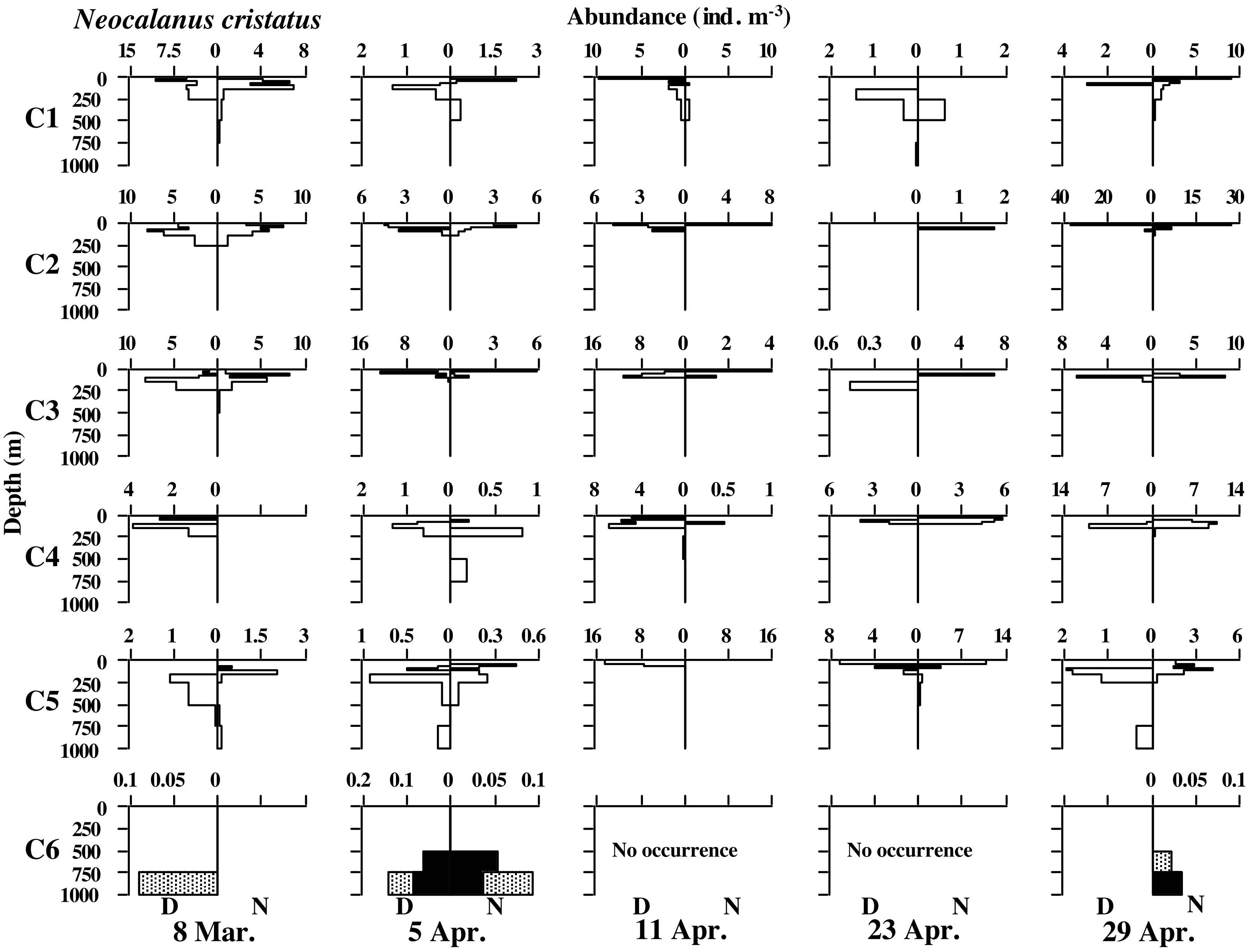

Fig. 6 (Yamaguchi et al.)

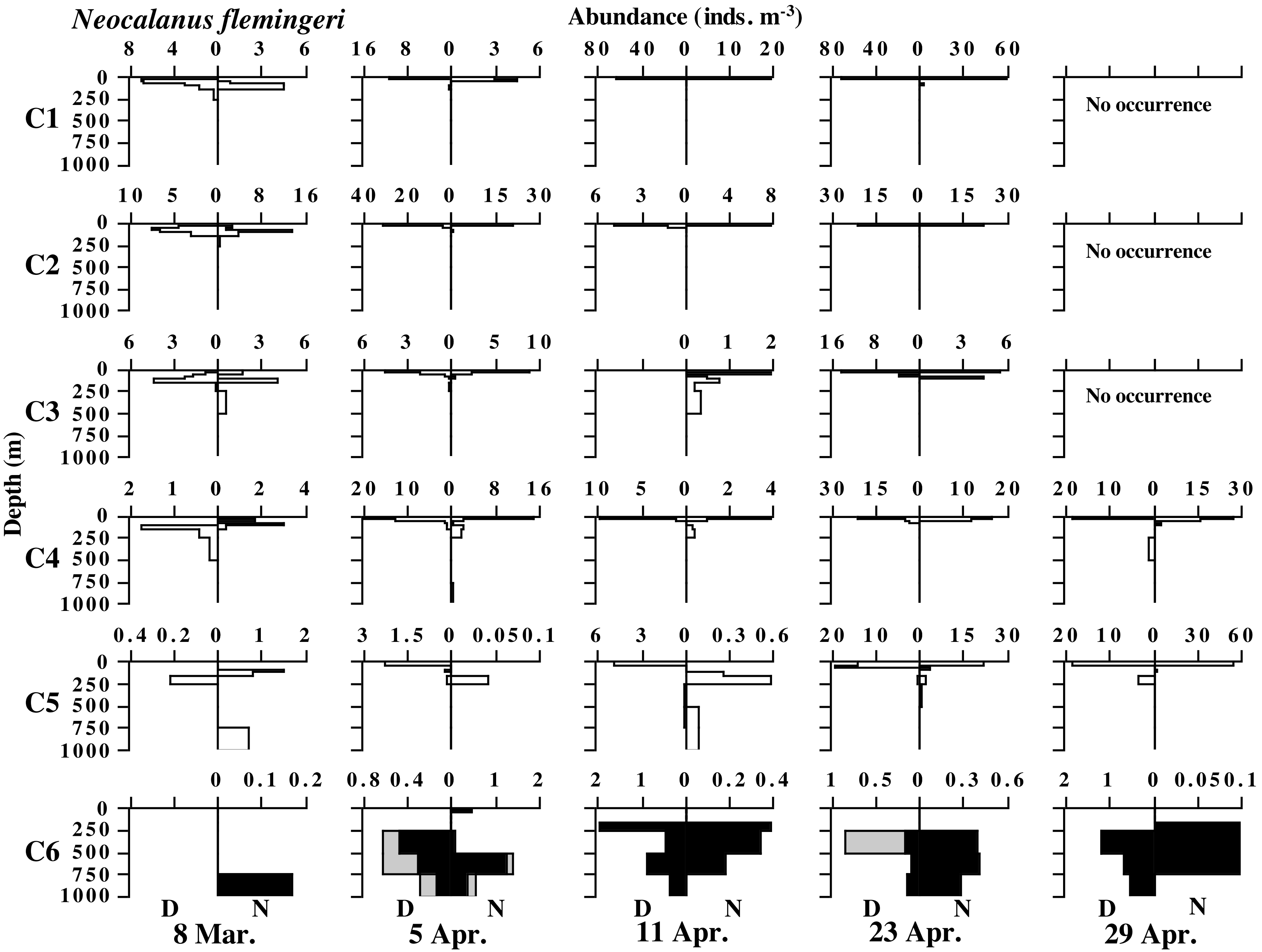

Fig. 7 (Yamaguchi et al.)

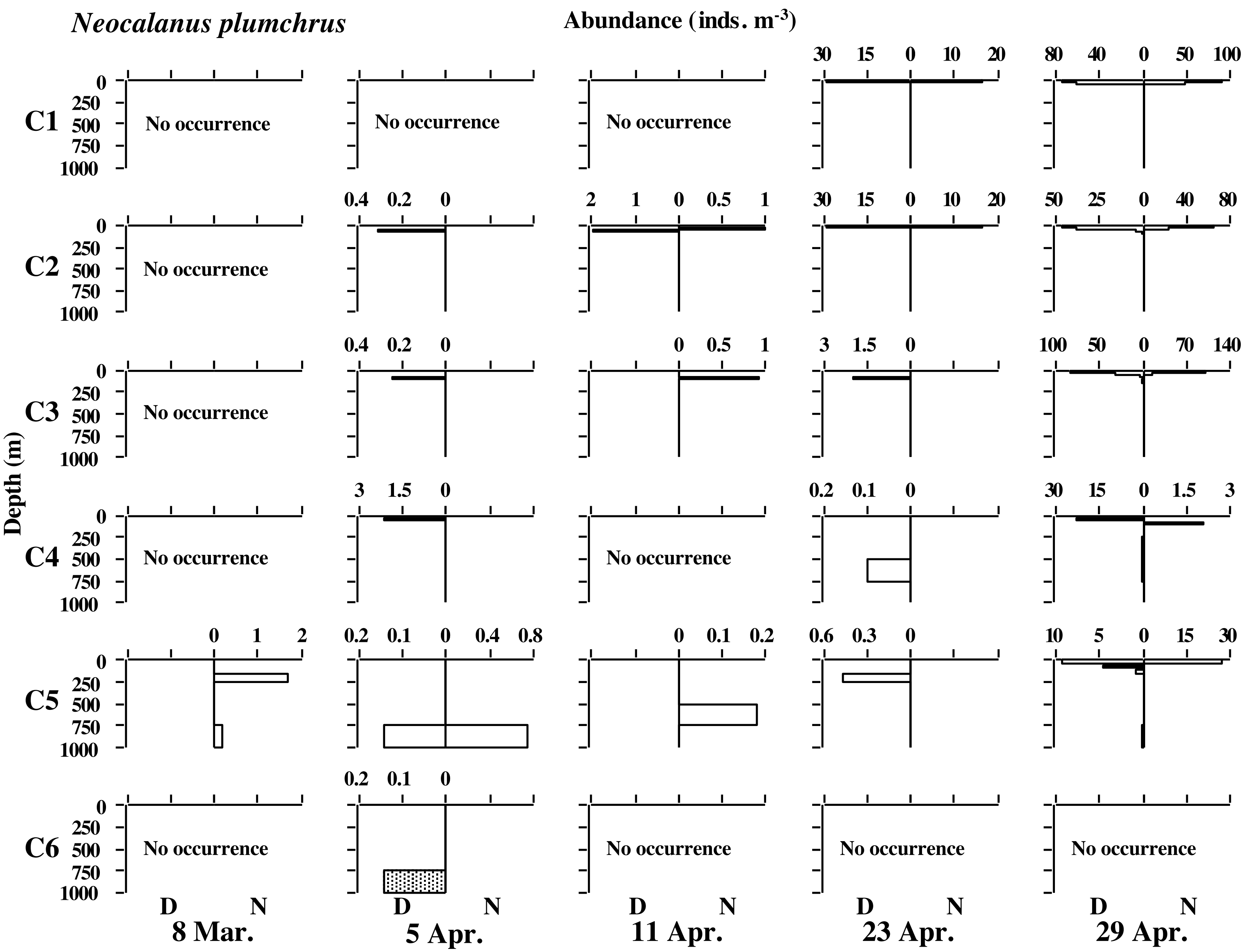

Fig. 8 (Yamaguchi et al.)

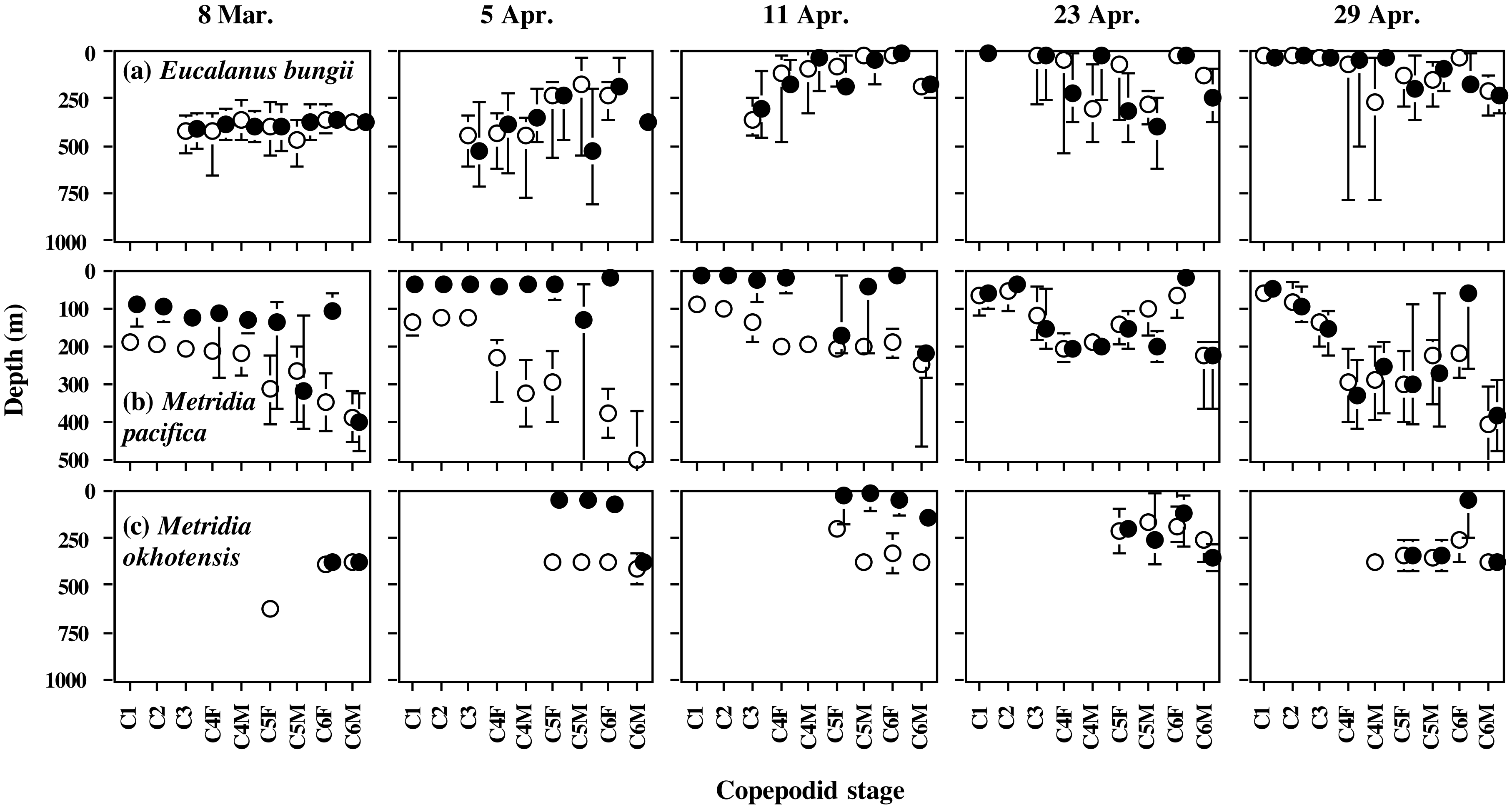

Fig. 9 (Yamaguchi et al.)

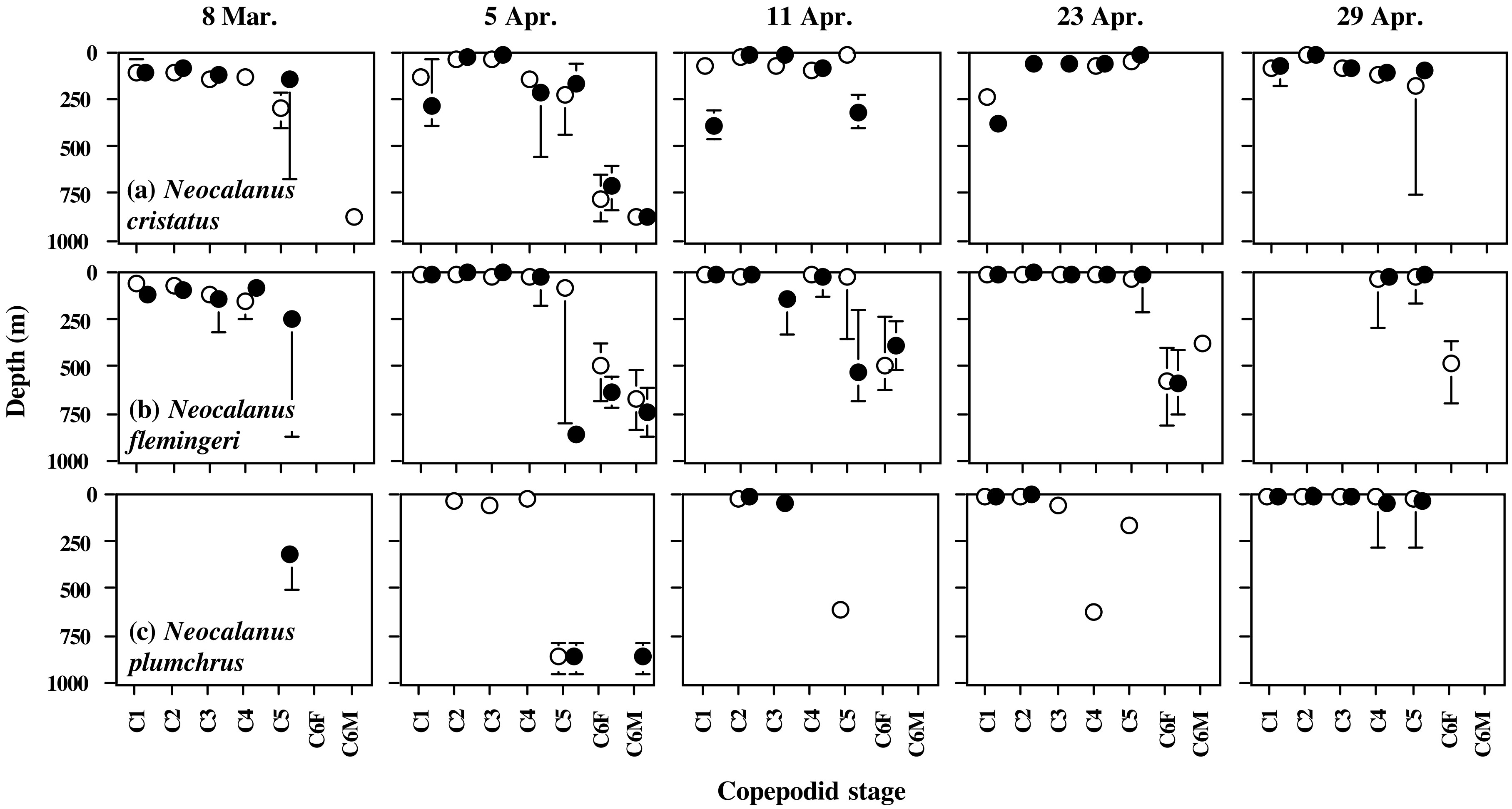

Fig. 10 (Yamaguchi et al.)