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

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11 **Abstract**

12 Short-term changes in vertical distributions of copepods during the spring  
13 phytoplankton bloom were analyzed based on day and night vertically stratified  
14 sampling (9 strata between 0-1000 m) with a fine-mesh (60  $\mu\text{m}$ ) VMPS in the Oyashio  
15 region on five occasions: 8 March, 5, 11, 23 and 29 April 2007. Responses to the  
16 bloom were varied and species-specific. *Eucalanus bungii* C3-C6 were resting around  
17 400 m on 8 March. They had aroused from rest by 5 April, more completely for C6F  
18 than for C3-C4. On 29 April, newly recruited C1-C4 stayed in near surface layers (0-  
19 50 m). Both *Metridia pacifica* and *Metridia okhotensis* showed strong diel vertical  
20 migrations (DVM). When the amount of sinking flux was sufficient (23 and 29 April),  
21 juveniles ceased DVM and stayed close to 300 m throughout the day and night, while  
22 the C6F continued DVM. Continuous DVM behavior of *Metridia* spp. C6F is likely  
23 related to spawning in the surface layer at night. The growth phase of juvenile  
24 *Neocalanus* spp. occurred shallower than 250 m. Within this depth range, vertical  
25 partitioning was observed among the species: *Neocalanus flemingeri* and *Neocalanus*  
26 *plumchrus* occurred above 50 m, while *Neocalanus cristatus* was distributed from 75-  
27 250 m. The boundary between two patterns was around 50-75 m. These findings are  
28 comparable to those in the eastern subarctic Pacific.

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

30 **1. Introduction**

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

41 The most comprehensive information on diel, seasonal and ontogenetic  
42 vertical distribution came from studies of *Neocalanus* spp. and *E. bungii* (Miller et al.,  
43 1984) and *M. pacifica* (Batchelder, 1985) at Station P in the eastern subarctic Pacific.  
44 Also at Station P, vertical distribution of the whole zooplankton community (Goldblatt  
45 et al., 1999), and vertical partitioning among the species (shallower species: *N.*  
46 *flemingeri* and *N. plumchrus* and deeper species: *N. cristatus* and *E. bungii*) with  
47 boundary around 50 m were reported by Mackas et al. (1993). Vertical separation of  
48 congeners results in *N. plumchrus* and *N. flemingeri* having direct and indirect grazing  
49 effects on near-surface phytoplankton and microzooplankton, while *N. cristatus* remains  
50 below the mixed layer, feeding on aggregates sinking out of the euphotic zone (Dagg,  
51 1993).

52           Details of the responses of these copepods to phytoplankton bloom conditions  
53 were revealed by several iron-fertilization experiments in the oceanic HNLC areas of  
54 the subarctic Pacific. The responses to iron-fertilized blooms varied between  
55 experiments. Vertical distribution of these copepods did not vary between inside and  
56 outside the bloom patch in SEEDS-2001 in the western subarctic Pacific during July  
57 (Tsuda et al., 2005), whereas there were upward shifts of the vertical distributions of *E.*  
58 *bungii* and *N. cristatus* in the SERIES phytoplankton patch in the eastern HNLC area  
59 during July (Tsuda et al., 2006). The contrast suggests that the responses to  
60 phytoplankton blooms vary with location or timing.

61           In the western subarctic Pacific, time-series vertical sampling was conducted  
62 at Site H in the Oyashio region during 1996-1997. Based on those samples,  
63 information has been developed on diel, seasonal and ontogenetic vertical distributions  
64 of *Neocalanus* spp. (Kobari and Ikeda, 1999, 2001a, 2001b), *E. bungii* (Shoden et al.,  
65 2005), *M. pacifica* and *M. okhotensis* (Padmavati et al., 2004) and mesopelagic  
66 copepods (*Gaidius variabilis*, *Heterorhabdus tanneri*, *Paraeuchaeta* spp. and  
67 *Pleuromamma scutullata*) (Yamaguchi and Ikeda, 2000a, 2000b, 2002). This  
68 information is part of the support for the concept of downward flux via seasonal  
69 ontogenetic migrations of copepods (Bradford-Grieve et al., 2001). The downward  
70 export of organic matter by ontogenetic vertical migration of these copepods in the  
71 western subarctic Pacific is estimated to be 73-92% of the passive gravitational flux  
72 (Kobari et al., 2003, 2008).

73           Knowledge of development and vertical distribution of copepods in the

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

86 To overcome these problems, as the part of the OECOS project (Miller and  
87 Ikeda, 2006), the present study aimed to evaluate short-term changes in vertical  
88 distribution of copepods by high resolution sampling in the Oyashio region during the  
89 spring phytoplankton bloom. Day and night vertically stratified sampling (9 strata  
90 between 0-1000 m) with fine-mesh nets (60  $\mu\text{m}$ ) was conducted on 8 March and 5, 11,  
91 23 and 29 April 2007. The vertical resolution of the new data is comparable to that of  
92 Mackas et al. (1993) at Station P (7 strata between 0-250 m). To evaluate the arousal  
93 of *E. bungii* from rest in deep layers, our sampling depths extended down to 1000 m.  
94 Analysis is based on two species groups: those spawning near the surface, *E. bungii* and  
95 *Metridia* spp., and *Neocalanus* species that are only near the surface as grow juveniles.

96 The vertical distributions during the spring bloom of the spawning species and the  
97 growing species are discussed in comparison with the same groups in the eastern  
98 subarctic and in respect to their responses to iron-fertilized blooms.

## 99 **2. Materials and methods**

### 100 *2.1. Field sampling*

101 Zooplankton sampling was conducted at one station (A-5: 42°00'N, 145°15'E; depth  
102 4,048 m) in the Oyashio region on 8 March, 5, 11, 23 and 29 April 2007. Day and  
103 night casts were made with a Vertical Multiple Plankton Sampler (VMPS: 60  $\mu$ m mesh,  
104 0.25 m<sup>2</sup> mouth opening; Terazaki and Tomatsu 1997), collecting from nine strata  
105 between 0-1000 m (0-25, 25-50, 50-75, 75-100, 100-150, 150-250, 250-500, 500-750  
106 and 750-1000 m) (Table 1). Samples were immediately preserved with 5% borax-  
107 buffered formalin. Temperature and salinity were measured by Sea-Bird CTD casts.  
108 Water samples for chlorophyll *a* were collected from 10, 30, 50, 75, 100, 125, 150 and  
109 200 m, then filtered through Whatman GF/F filters, and measured fluorometrically after  
110 extraction with dimethyl-formamide (Suzuki and Ishimaru, 1990).

### 111 *2.2. Identification and enumeration of copepods*

112 In the land laboratory, we enumerated the biomass-dominant copepods: *E. bungii*, *M.*  
113 *pacifica*, *M. okhotensis*, *N. cristatus*, *N. flemingeri* and *N. plumchrus*. After  
114 measurement of sample volume, the samples were stirred gently and well with a wide-  
115 bore pipette (1 cm diameter), and a pipette subsample was taken (1/10- 1/35 of total

116 volume, varying with the amount of the sample). Then, species and stages of the  
117 dominant copepods were identified and enumerated in the subsample under a  
118 stereomicroscope.

119           Sexes were distinguished from copepodid stage 4 (C4) to adults (C6) for *E.*  
120 *bungii*, *M. pacifica* and *M. okhotensis* (Padmavati et al. 2004, Shoden et al., 2005).  
121 For *Neocalanus* spp., sex determination was possible only for C6 (Kobari and Ikeda,  
122 1999, 2001a, 2001b).

### 123 2.3. Analysis of data

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

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

$$134 \text{ Mean stage} = \sum (i \times N_i) / N$$

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

137 **3. Results**

138 *3.1. Hydrography*

139 Temperatures between 0 and 1000 m varied from 1.0 to 6.1°C during 8 March to 29  
140 April 2007 (Fig. 1a). In the upper 400 m temperature was higher (3-6°C) in 8 March,  
141 lower (1-3°C) in 5 April. Salinity varied from 33.0 to 34.4, increasing downward (Fig.  
142 1b). Variation in salinity was synchronized with temperature, thus high temperature  
143 corresponded high salinity (33.7) on 8 March, while low temperature matched low  
144 salinity (33.0) on 5 April. Chlorophyll *a* in the upper 200 m varied between 0.1 to 3.5  
145 mg m<sup>-3</sup>, and was high on April dates and low on 8 March (Fig. 1c). On 8 March, chl. *a*  
146 was extremely low, <0.2 mg m<sup>-3</sup> throughout the water column.

147 *3.2. Population structure of the dominant copepods*

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

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

157 Abundance of *M. okhotensis* fluctuated between 300 and 2,300 ind. m<sup>-2</sup> (Fig.  
158 2c). Throughout the study period, C5 and C6 were its dominant stages. The  
159 proportion of C6 was greater on 8 March than on the later dates (Fig. 2c). The mean  
160 stage of *M. okhotensis* was stable around C5-C6 throughout the study period.

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

165 Abundance of *N. flemingeri* was 1,600-4,500 ind. m<sup>-2</sup> (Fig. 2e). The  
166 dominant stages were C1 and C2 on 8 March, C2-C4 on 5 April and C4-C5 on 29 April  
167 2007. The mean stage of *N. flemingeri* increased accordingly from C2.2 to C4.6  
168 during the study period (Fig. 2e).

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

### 174 3.3. Diel variation of vertical distribution

175 *Eucalanus bungii* were distributed between 250-500 m both day and night on 8 March  
176 2007 (Fig. 3). Vertical distribution of part of the population of C3-C6 extended to the  
177 surface both day and night on 5 April. On 11 April, C4-C6 were near the surface,

178 while C3 remained in deeper layers. All C3-C6 were distributed near the surface on 23  
179 April. On 29 April, newly recruited C1-C2 dominated, and C1-C4 were distributed  
180 near the surface. Later stages, C5 and C6 showed bimodal vertical distributions near  
181 the surface and from 150-250 m. Throughout the study period, no sexual differences  
182 in vertical distribution were detected for C4-C5, but C6M were distributed below 150 m  
183 both day and night, not occurring closer to the surface. For none of the copepodid  
184 stages were day vs. night differences observed in vertical distribution (no DVM) at any  
185 time during the sampling (Table 2).

186 Daytime distribution depths of *M. pacifica* on 8 March were from 150-250m  
187 for C1-C3, 150-500 m for C4 and C5, and 250-500 m for C6 (Fig. 4). All of the  
188 copepodid stages, except C6M, were distributed from surface to 150 m at night. The  
189 strongest upward migrations at night were observed on 5 and 11 April. On 23 and 29  
190 April, the vertical distributions of C1-C5 did not vary between day and night, and the  
191 distributions were deeper with advancing stage. The C6F migrated upward at night on  
192 23 and 29 April (Table 2). Throughout, C6M were distributed below 250 m both day  
193 and night. The magnitude of DVM by adult females, evaluated with  $D_{50\%}$ , was 46-359  
194 m. Since the daytime distributions were deeper for later copepodid stages, their  
195 magnitudes of DVM were progressively greater (Table 2). It should be noted that the  
196 DVM on 23-29 April was only observed for C6F, and there was none by the other stages  
197 (Table 2).

198 *Metridia okhotensis* were distributed below 250 m both day and night and had  
199 no DVM on 8 March (Fig. 5). On 5 and 11 April, C5F/M and C6F migrated upward

200 from 250-500 m in daytime to near the sea surface at night. On 23 and 29 April, this  
201 upward migration was observed only for C6F, from 150-500 m in daytime to the surface  
202 at night, while C4 and C5 remained between 150-500 m both day and night (Fig. 5).  
203 The C6M were distributed from 250-500 m both day and night throughout the study.  
204 The magnitude of DVM was 71-358 m for C5 and C6F (Table 2).

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

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

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

222 3.4. Ontogenetic variation in diel vertical migrations

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

225 All copepodid stages of *E. bungii* were concentrated around 400 m on 8  
226 March (Fig. 9a). On 5 April, the distributions of its C3-C6F stages were extensive, and  
227 their  $D_{50\%}$  varied from 200-600 m, evidently a developmental ascent pattern. On 11  
228 April, C5F/M and C6F reached the surface while C3 and C4 remained deep. On 23  
229 April, all the stages reached the surface layer, a developmental ascent pattern. On 29  
230 April, C1-C4 of *E. bungii* were collected above 50 m, and C5-C6 were found from 100-  
231 200 m, consistent with a developmental decent pattern (Fig. 9a).

232 Ontogenetic variation in vertical distribution of *M. pacifica* in daytime was  
233 C1-C3 distributed above 200 m, C4-C5 and C6F from 300-500 m and C6M from 400-  
234 800 m (Fig. 9b). Nighttime depths of C1-C6F of *M. pacifica* were around 100 m on 8  
235 March, shifting to near the surface on 5 and 11 April, when the DVM was observed,  
236 not varying with stage. On 23 and 29 April, most of the stages of *M. pacifica*, except  
237 C6F, stayed down at the daytime depth throughout the night (Fig. 9b).

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

243 (Fig. 9c).

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

248 The  $D_{50\%}$  values for C1-C5 of *N. flemingeri* were in the range from 25-200 m,  
249 while C6 was distributed from 400-1000 m (Fig. 10b). Vertical distribution of *N.*  
250 *flemingeri* was shallower than that of *N. cristatus* in the same period. In common  
251 among *Neocalanus* spp., vertical distributions on 8 March were deeper than those on 5-  
252 29 April (Fig. 10a, b).

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

## 257 **4. Discussion**

### 258 *4.1. Analysis of the data*

259 To evaluate DVM, we applied two-sample Kolmogorov-Smirnov (K-S) tests (Sokal and  
260 Rohlf, 1995). While the robustness of this test for evaluating DVM of zooplankton  
261 can be questioned in the case of the great differences in abundance between day and  
262 night (Venrick, 1986), we have checked those differences and found them to be less than  
263 5-fold. Given that problems with the K-S test only substantially affect differences

264 greater 10-fold (Table 1 in Venrick, 1986), we consider it appropriate for our evaluations  
265 of DVM (Table 2).

#### 266 4.2. Effect of water mass exchange

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

283 4.3. *Eucalanus bungii*

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

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

305 Campbell et al., 2004).

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

#### 315 4.4. *Metridia pacifica*

316 Diel vertical migration behavior of *M. pacifica* is well known (Tsuda and Sugisaki,  
317 1994; Takahashi et al., 2008). In our sampling on 23-29 April, C1-C4 of *M. pacifica*  
318 stayed in the same layer both day and night (Fig. 9b). However, part of the C5F/M  
319 stock migrated upward at night, while majority stayed between 150-500 m throughout  
320 the day. Consistent DVM was only observed for C6F (Fig. 4). In several locations  
321 and seasons, cessation of DVM has been reported: the eastern subarctic Pacific in winter  
322 (Batchelder, 1985) and the western subarctic Pacific in June and August (Hattori, 1989).  
323 According to Hattori (1989), staying in the 200-300 m layer throughout the day is  
324 possible for *M. pacifica* copepodids because they can obtain enough food at that depth;  
325 damaged diatoms and fecal pellet-like particles were found in their guts.

326 Individual differences in DVM behavior of *Metridia* spp. are generally  
327 considered to be related to their nutrition. According to Hays et al. (2001), the mean  
328 size of the oil sacs of migrant specimens was much smaller than for those that remained  
329 at depth. Animals with larger lipid stores need not risk coming to the surface at night  
330 to feed. In Dabob Bay, Washington, *M. pacifica* (= *M. lucens*) underwent a reverse  
331 DVM on some dates, avoiding the surface 25 m at night, while on still other dates the  
332 C3 and younger stages avoided the surface 25 m day and night (Osgood and Frost,  
333 1994). This reverse DVM behavior of *M. pacifica* was considered to be related the  
334 abundance of vertebrate and invertebrate predators (Osgood and Frost, 1994). These  
335 facts indicate that the *Metridia* spp. have flexibility in their vertical distribution and  
336 DVM behaviors. During 23-29 April in this study, *M. pacifica* could have  
337 accumulated lipids to sustain them, or they might be able to find sufficient food at that  
338 depth. In the following, we calculate whether they might meet their dietary  
339 requirements at depth.

340 Since primary production was measured during 7-30 April (Isada et al., this  
341 issue), the downward particle flux to 300 m was estimated from an equation suggested  
342 by Suess (1980);  $C_{flux} = C_{prod} / (0.0238Z + 0.212)$ , where  $C_{prod}$  is primary production (mg C  
343  $m^{-2} day^{-1}$ ), and  $C_{flux}$  is carbon flux (mg C  $m^{-2} day^{-1}$ ) at a given depth ( $Z$ : m). We can  
344 take the dry mass ( $DM$ : mg  $ind.^{-1}$ ) of each copepodid stage of *M. pacifica* from  
345 Padmavati (2002). Respiration rate ( $R$ :  $\mu l O_2 ind.^{-1} h^{-1}$ ) can be estimated from  $\ln(R) = -$   
346  $0.399 + 0.801 \ln(DM) + 0.069T$  (Ikeda et al., 2001), where temperature ( $T$ ) at 300 m  
347 was 3°C (Fig. 1). Metabolism was converted to units of carbon ( $M$ ) from  $R$  by

348 assuming a respiratory quotient ( $[CO_2]/[O_2]$ ) of 0.97 (for protein metabolism, see  
349 Gnaiger, 1983). Carbon budgets of living copepods may be expressed as: Ingestion ( $I$ )  
350 = Metabolism ( $M$ ) + Growth ( $G$ ) + Egestion ( $E$ ). Assuming assimilation efficiency  
351 ( $[M+G]/I$ , or  $[I-E]/I$ ) to be 70% and gross growth efficiency ( $G/I$ ) to be 30% (for detail  
352 accounts, see Ikeda and Motoda, 1978), ingestion rates ( $I$ :  $\mu\text{g C ind.}^{-1} \text{ h}^{-1}$ ) can be  
353 calculated as  $I=M/(0.7-0.3)$ . Values for  $I$  were computed, expressed on a daily basis (x  
354 24 hours) and summed for all individuals ( $\text{mg C m}^{-2} \text{ day}^{-1}$ ). The resulting estimates  
355 (Table 3) show that *M. pacifica* could likely meet its energetic requirements at 300 m in  
356 April without DVM, as was suggested by Hattori (1989). The *M. pacifica* stock  
357 ingestion rate was probably less than the likely carbon flux to 300 m, about 4-40% of  
358 the supply rate.

#### 359 4.5. *Metridia okhotensis*

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

369           As sympatric congeners, *M. pacifica* and *M. okhotensis* in the subarctic  
370 Pacific are comparable to the *M. lucens*-*M. longa* pair in the subarctic Atlantic. At the  
371 same stations, the larger *M. longa* is distributed deeper than the smaller *M. lucens*  
372 (Falkenhaus et al., 1997). Deeper occurrence of the larger form, *M. okhotensis*, than  
373 of the smaller form, *M. pacifica*, was also observed in the Pacific. Bollens et al.  
374 (1993) hypothesized that the smaller, less fecund species would have to maintain  
375 exceptionally effective avoidance behavior, including remaining migratory at all times  
376 and avoiding the surface layer except during total darkness. However, according to  
377 Hays et al. (1994), larger taxa among copepods generally show significantly stronger  
378 DVM, with body size explaining 47% of inter-taxon variation in DVM. Both  
379 explanations fit with the larger *M. okhotensis* living deeper than the smaller *M. pacifica*  
380 in the subarctic Pacific (Fig. 9b, c).

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

391 4.6. *Neocalanus cristatus*

392 Vertical distributions of *N. cristatus* C1-C3 were extensive on 8 March, between 0-250  
393 m. Distribution of C1-C3 was shifted upward to 0-150 m on 5-23 April, when C4 and  
394 C5 were dispersed from 75-250 m (Fig. 6). On 29 April, C1 and C2 were at 0-25 m,  
395 C3 and C4 were at 50-100 m. An upward shift by *N. cristatus* during an induced  
396 phytoplankton bloom was reported for the SERIES experiment (Sastri and Dower,  
397 2006; Tsuda et al., 2006).

398 The C2 of *N. cristatus* were located above the C1 (Fig. 10a). Since *N.*  
399 *cristatus* do not feed in the naupliar stage, C1 is the first feeding stage (Saito and Tsuda,  
400 2000). Spawning occurs >1000 m (Miller et al., 1984; Kobari and Ikeda, 1999), and  
401 low density eggs and nauplii float and swim upward (Nakai, 1969). Thus, deeper  
402 occurrence of younger C1 than older C2 (Fig. 10a) is reasonable; the C1 would have  
403 started upward as eggs and nauplii after the C2.

404 The two largest contributors to mesozooplankton biomass, *N. cristatus* and *E.*  
405 *bungii*, remain deeper than 50 m in the eastern subarctic Pacific during spring, while the  
406 smaller species of *Neocalanus* (*N. flemingeri* and *N. plumchrus*) remain shallower than  
407 50 m (Mackas et al., 1993). The vertical separation of congeners results in *N.*  
408 *plumchrus* and *N. flemingeri* having direct and indirect grazing effects on mixed layer  
409 phytoplankton, while *N. cristatus* remains below the mixed layer, most likely feeding on  
410 aggregates sinking out of the euphotic zone (Dagg, 1993). Exploitation of sinking  
411 particles as a food source by late *N. cristatus* copepodids likely also occurs in the

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

414

#### 415 4.7. *Neocalanus flemingeri*

416 Vertical distribution of C1-C4 *N. flemingeri* extended from 25 to 150 m on 8 March.

417 They were concentrated at 0-50 m both day and night on 5-29 April (Fig. 7). A similar

418 upward migration from residence in a subsurface layer before a bloom to the surface

419 layer during the bloom was reported for *E. bungii* (C3-C5) and *N. cristatus* (C2-C4)

420 during a summer iron fertilization experiment in the eastern subarctic Pacific (SERIES:

421 Tsuda et al., 2006). No changes in vertical distribution of copepods were observed

422 after iron fertilization in the western subarctic Pacific (SEEDS2001), but increase in

423 abundance of early copepodid stages of *N. plumchrus* and *E. bungii* was reported (Tsuda

424 et al., 2005). The cause of apparent upward migration and increase of early copepodid

425 stages during iron fertilization experiments was postulated to be reduced mortality

426 during the egg and naupliar stages. Apparently suspension-feeding omnivores ate

427 fewer of them due to increased diatom availability (Tsuda et al., 2006). The same

428 explanation may fit the shifts in this study. *Metridia pacifica* was deeper before the

429 bloom (8 March) than after its onset (5 April) (Fig. 9b). The upward shift of the C1-

430 C4 distributions of *N. cristatus* and *N. flemingeri* occurred in the same interval (Fig. 10a,

431 b). On the other hand, the shallower distribution patterns could have been a response

432 to changes in water column structure. Temperature and salinity profiles were

433 homogenous around 6°C and 33.6 throughout 0-200 m on 8 March, while a thermocline

434 was present in the upper 100 m during 5-29 April (Fig. 1a). Thus the wider vertical  
435 distribution of C1-C4 of *N. flemingeri* and *N. cristatus* on 8 March (Figs. 6 and 7)  
436 corresponded to a period of strong vertical mixing down to 200 m, while the more  
437 concentrated vertical distribution on 5 April corresponded to a period of significant  
438 upper water column stratification.

#### 439 4.8. *Neocalanus plumchrus*

440 C1-C4 of *N. plumchrus* were in the 0-50 m stratum both day and night (Fig. 8).  
441 Differences in depth of distribution between the congeneric *N. cristatus* and *N.*  
442 *plumchrus* were evident; *N. plumchrus* shallower than *N. cristatus*. No difference was  
443 observed for the active growth phases of *N. plumchrus* and *N. flemingeri*. No  
444 differences in vertical distribution pattern of similar-sized *N. plumchrus* and *N.*  
445 *flemingeri* were reported in May-June from the eastern subarctic Pacific (Mackas et al.,  
446 1993). Since temporal timing of surface occurrence of early copepodid stages of these  
447 two species is known to be sequential, i.e. first *N. flemingeri* and later *N. plumchrus*  
448 dominating (Miller and Clemons, 1988; Tsuda et al., 1999; Kobari and Ikeda, 2001b), *N.*  
449 *flemingeri* and *N. plumchrus* separate their distribution temporally, but not by spatially.

450 The strong vertical species zonation in the eastern subarctic Pacific in May  
451 and June (Mackas et al., 1993), a near surface pair (*N. plumchrus* and *N. flemingeri*) and  
452 a subsurface pair (*N. cristatus* and *E. bungii*), was confirmed at least for the late  
453 copepodid stages of *Neocalanus* spp. in this study. However, since newly spawned *E.*  
454 *bungii* were distributed in the surface layer (Fig. 9a), this species did not fit the eastern

455 subarctic pattern. For all *Neocalanus* spp., the C1 and C2 were distributed near the  
456 surface (but somewhat deeper for C1 *N. cristatus*, as mentioned before). Clear  
457 differences were observed between the C3-C5 of *N. flemingeri/plumchrus* (shallower)  
458 and C3-C5 of *N. cristatus* (deeper) (Fig. 10). The boundary between these groups  
459 shifted vertically, but was sharply defined and was often coincident with a weak and  
460 transient thermocline marking the base of the layer actively mixed by surface wind and  
461 wave energy (similarly to results of Mackas et al., 1993).

#### 462 4.9. Conclusion

463 Patterns of diel and ontogenetic vertical distribution of large grazing copepods during  
464 the spring phytoplankton bloom in the Oyashio region were evaluated by VMPS  
465 sampling. Features common to all of the species was absence of DVM in late winter,  
466 certainly connected to a diapause at depth, and of feeding by C6M, which stayed in  
467 deep layers throughout the day, as previously observed across the region (Miller et al.,  
468 1984; Batchelder, 1985; Padmavati et al., 2004; Shoden et al., 2005). Vertical  
469 distribution of C6F of large grazing copepods had different patterns in different species:  
470 female *E. bungii*, *M. pacifica* and *M. okhotensis* migrated to the surface layer to spawn,  
471 while *Neocalanus* spp. remained deep and reproduced there, also without feeding  
472 (Kobari and Ikeda, 1999, 2001a, 2001b). Responses to the spring phytoplankton  
473 bloom varied among species. *Eucalanus bungii* C6F aroused from rest sooner than the  
474 C3-C4. Young of the year C1-C4 stayed near surface layer (Fig. 3). Both *M. pacifica*  
475 and *M. okhotensis* exhibited some DVM behavior. When the sinking flux provides

476 sufficient food at depth, the *Metridia* juveniles cease DVM and stay at daytime depths  
477 throughout the night, while C6F continue DVM (Fig. 4), likely to place their eggs very  
478 close to the surface. Growth of *Neocalanus* spp. occurred above 250 m, and some  
479 vertical partitioning was observed between the species. Growth of *N. flemingeri* and *N.*  
480 *plumchrus* occurred above 50 m, while at least older copepodids of *N. cristatus* finished  
481 their growth in the 50-250 m stratum (Fig. 10). Their upper boundary moved up and  
482 down between 50 and 75 m, which corresponds to the pattern in the eastern subarctic  
483 Pacific.

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659 Population structure, egg production and gut content pigment of large grazing  
660 copepods during the spring phytoplankton bloom in the Oyashio region. Deep-  
661 Sea Research II, this issue.

662 **Figure captions**

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

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

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

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

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

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

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

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

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

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

685 Fig. 10. Ontogenetic changes in the depths above and below which 50% of the  
686 population resided ( $D_{50\%}$ ) in day (open circle) and night (solid circle) for (a)  
687 *Neocalanus cristatus*, (b) *N. flemingeri* and (c) *N. plumchrus* in the Oyashio  
688 region during 8 March, 5, 11, 23 and 29 April 2007. Vertical bars indicate  
689 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  $\pm$  1sd). (D): day, (N): night.

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

Stage	<i>Eucalanus bungii</i>					<i>Metridia pacifica</i>					<i>Metridia okhotensis</i>				
	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).

Date	$PP$ (mg C m <sup>-2</sup> day <sup>-1</sup> )	$C_{flux}$ at 300 m (mg C m <sup>-2</sup> day <sup>-1</sup> )	<i>Metridia pacifica</i>	
			Abundance (ind. m <sup>-2</sup> )	Ingestion (mg C m <sup>-2</sup> day <sup>-1</sup> )
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

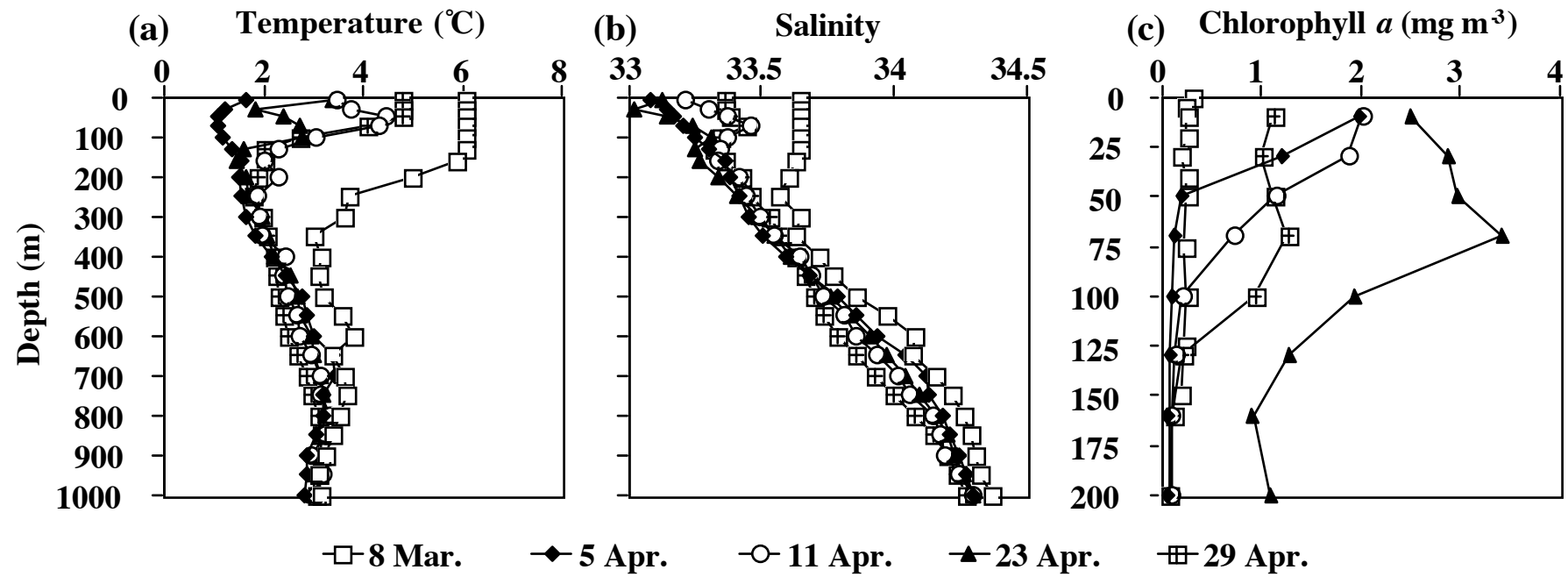


Fig. 1 (Yamaguchi et al.)

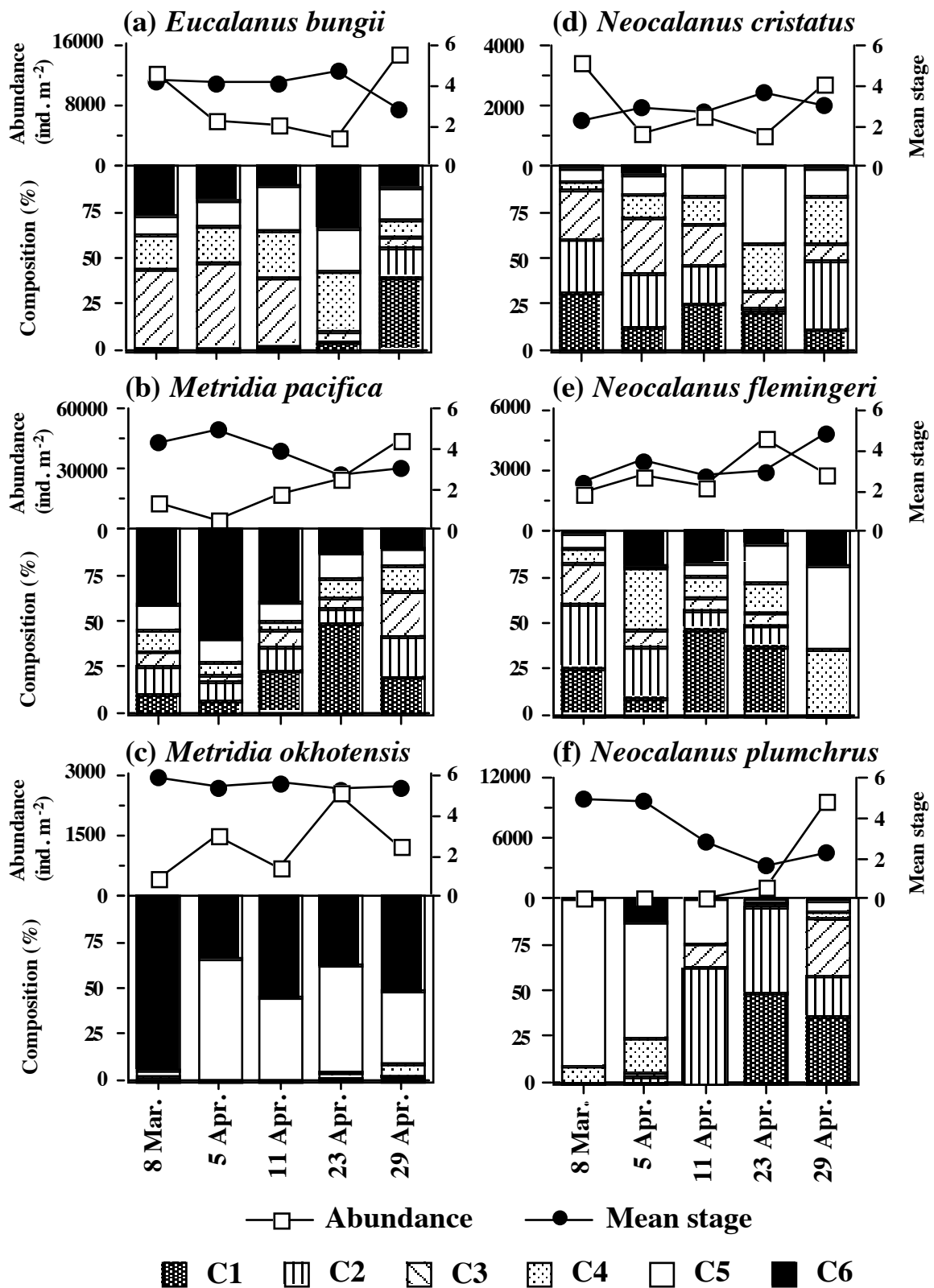


Fig. 2 (Yamaguchi et al.)

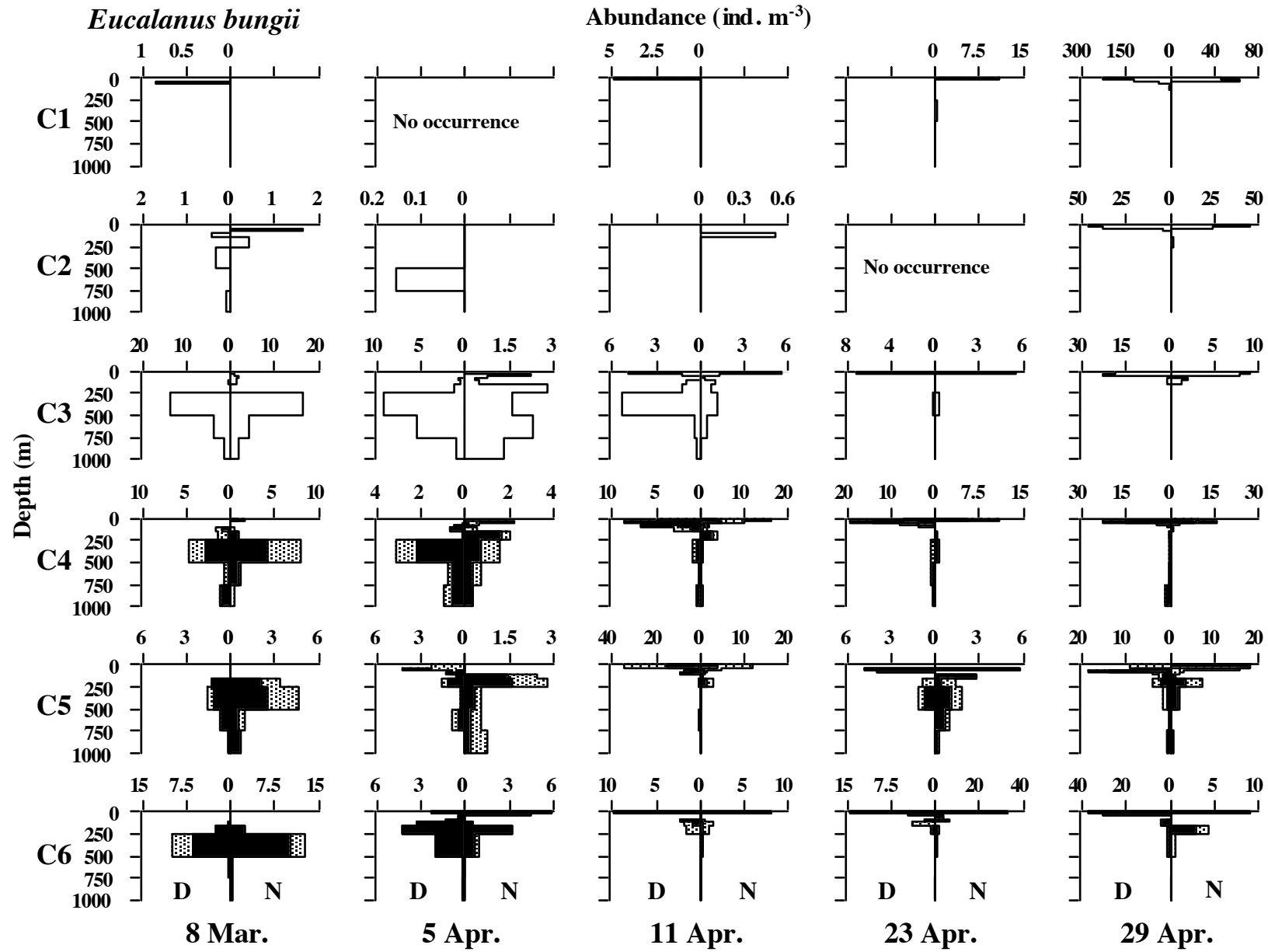


Fig. 3 (Yamaguchi et al.)

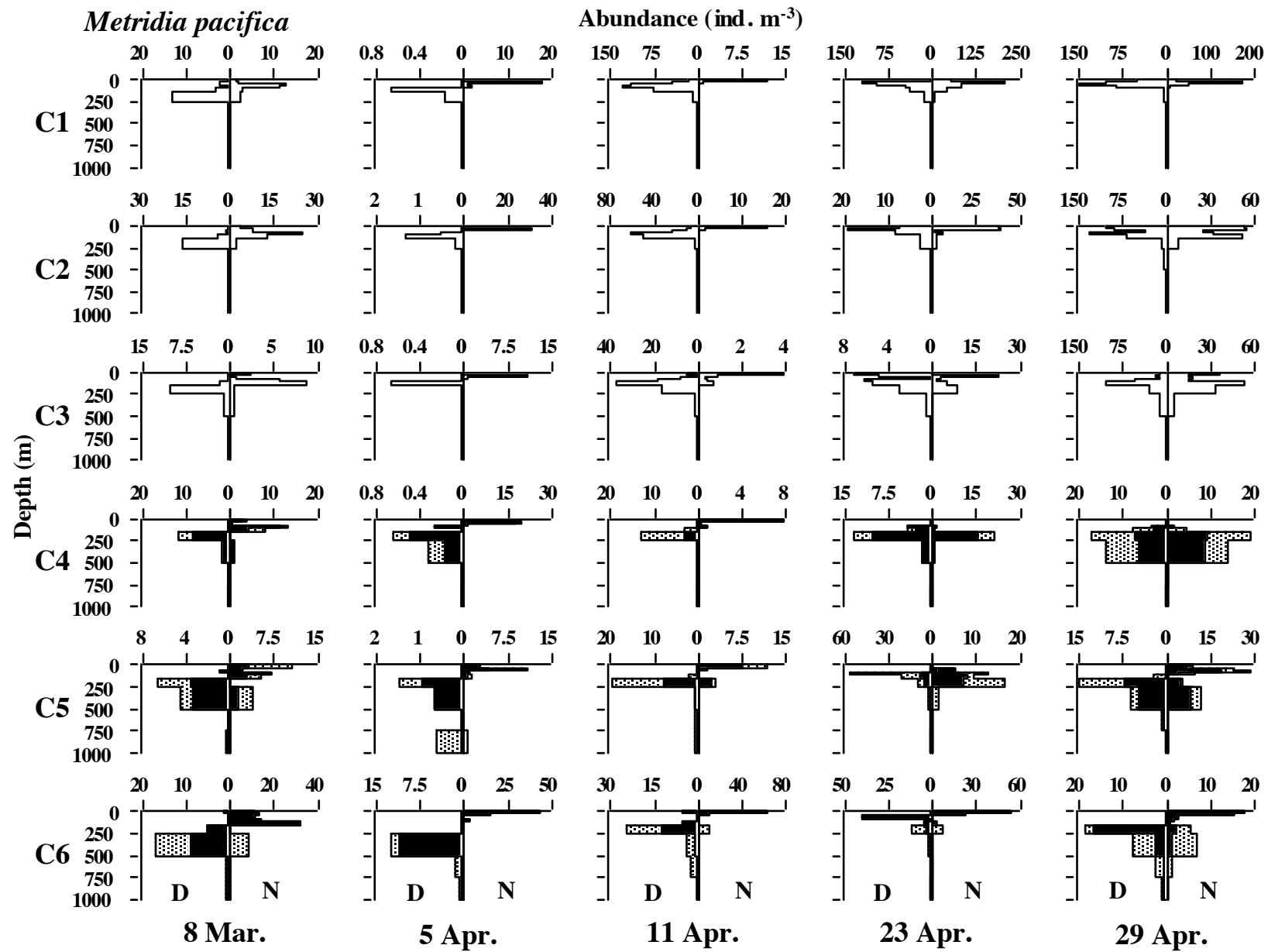


Fig. 4 (Yamaguchi et al.)

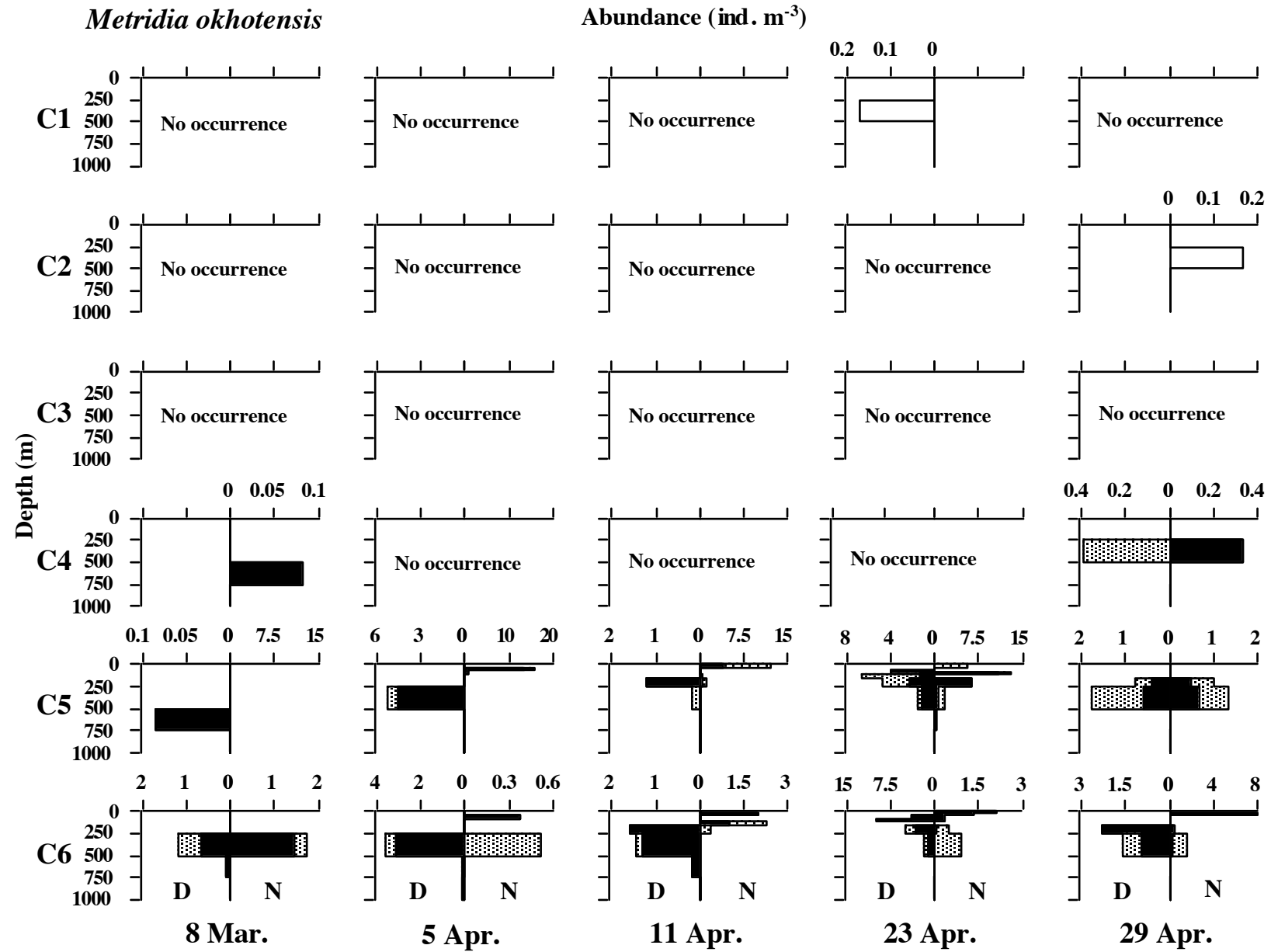


Fig. 5 (Yamaguchi et al.)

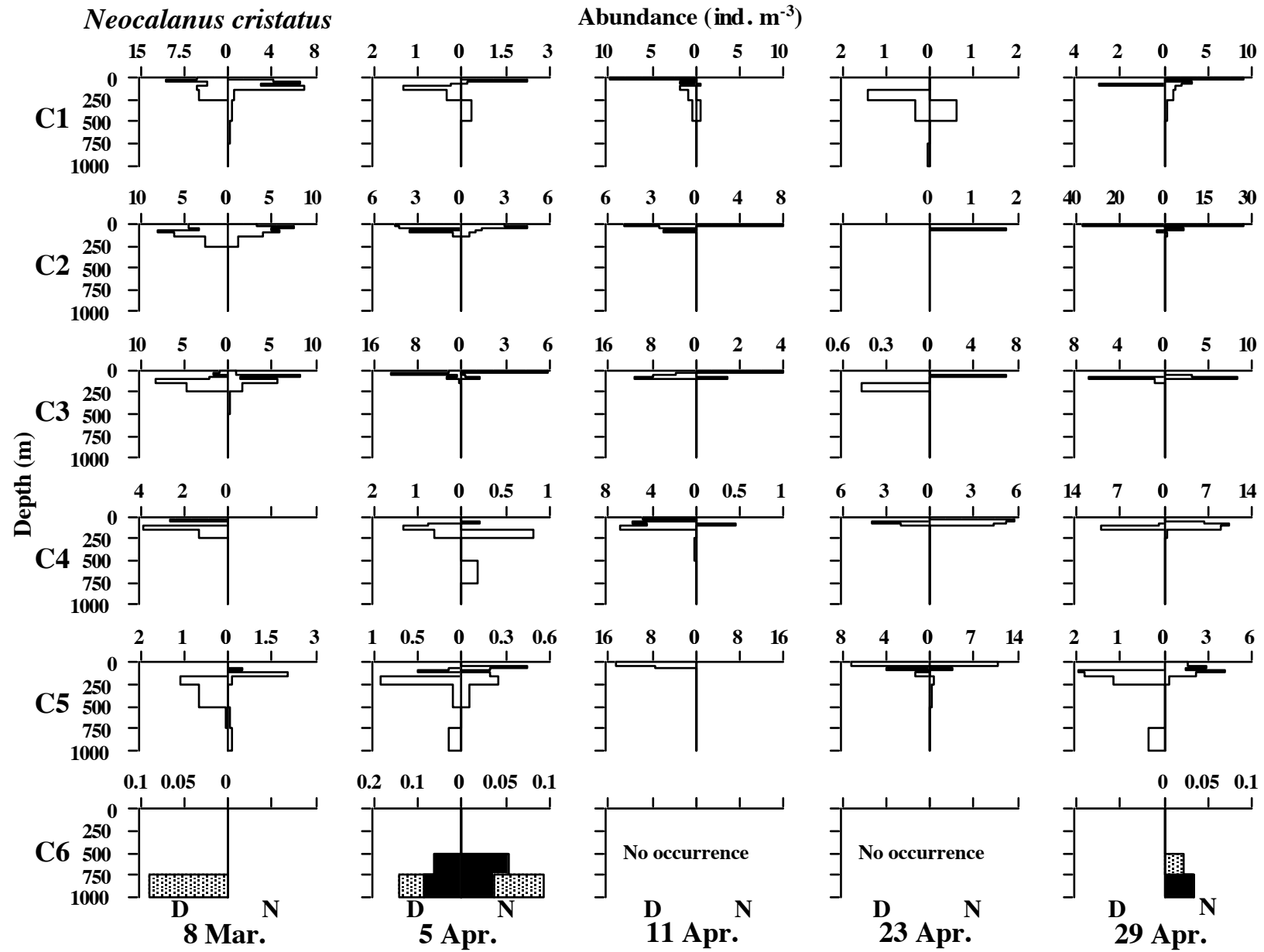


Fig. 6 (Yamaguchi et al.)

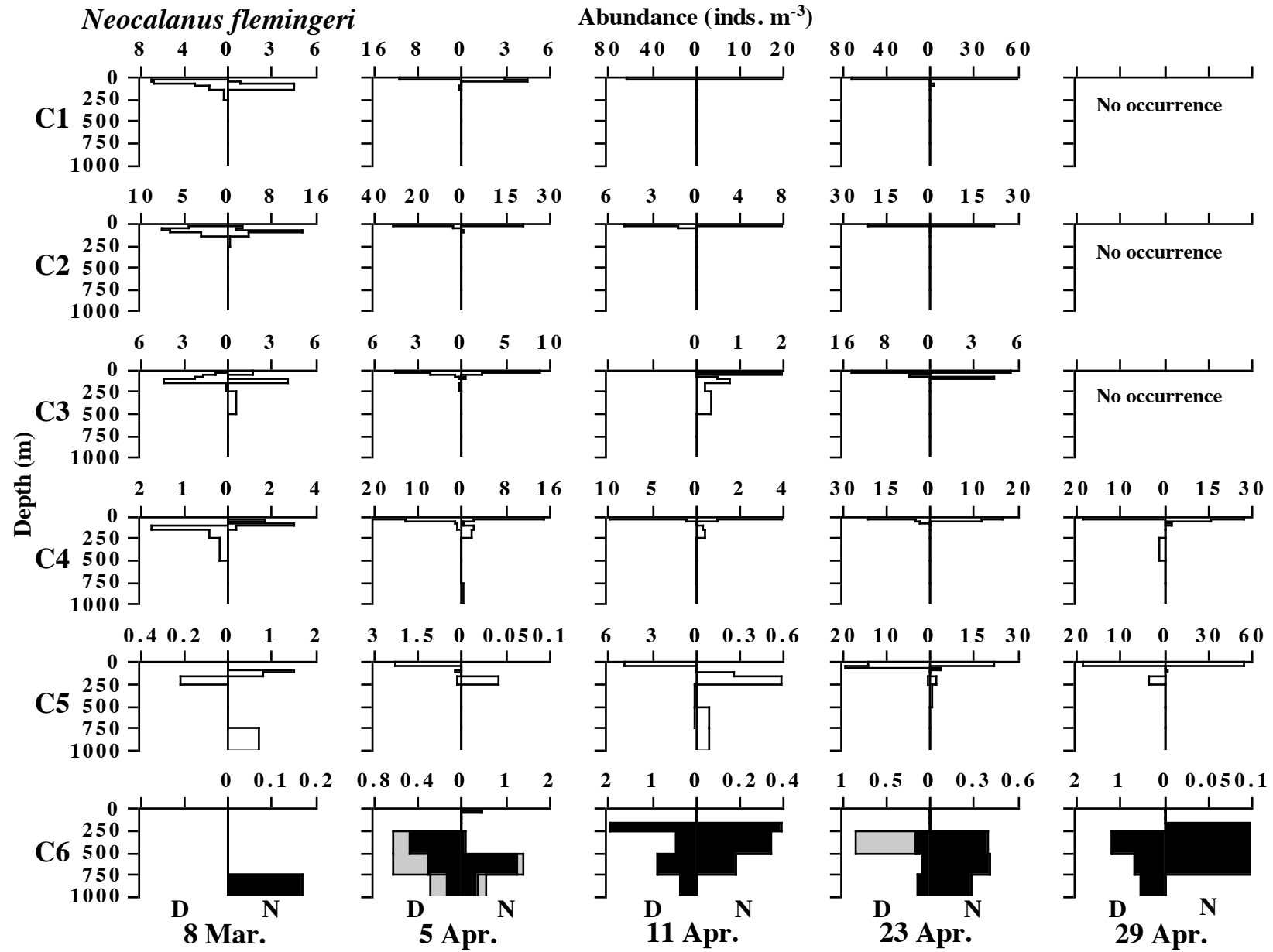


Fig. 7 (Yamaguchi et al.)

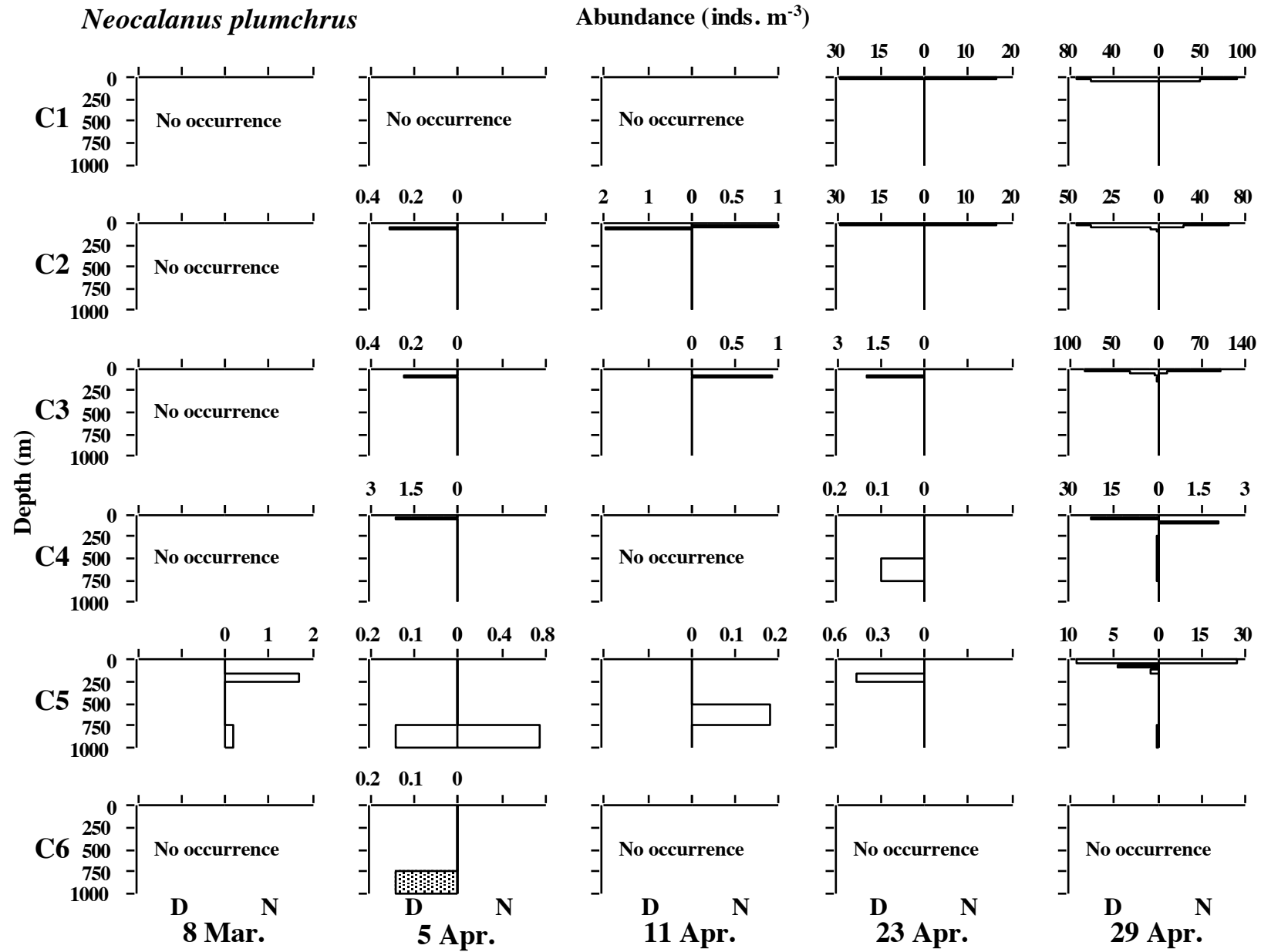


Fig. 8 (Yamaguchi et al.)

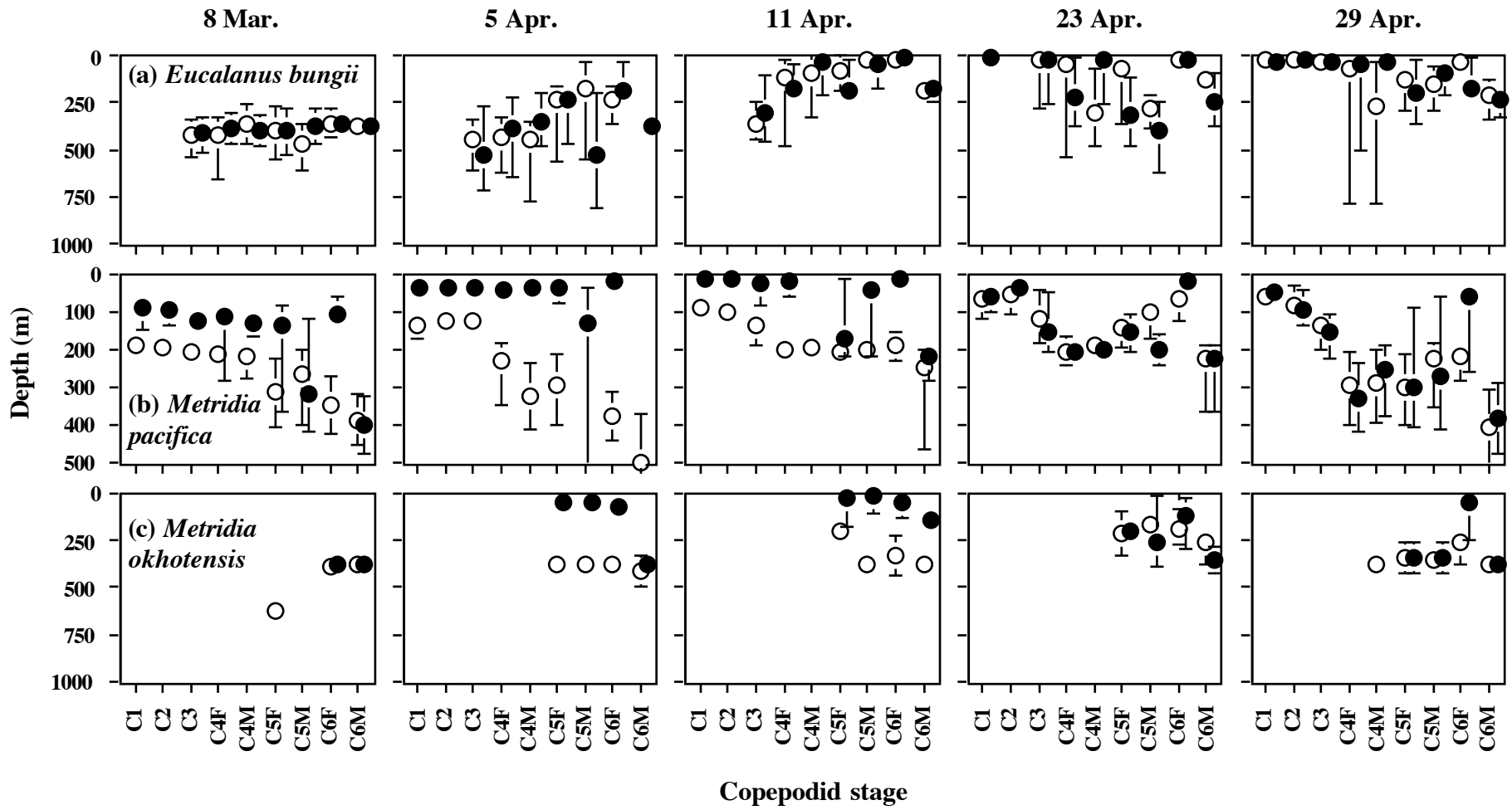


Fig. 9 (Yamaguchi et al.)

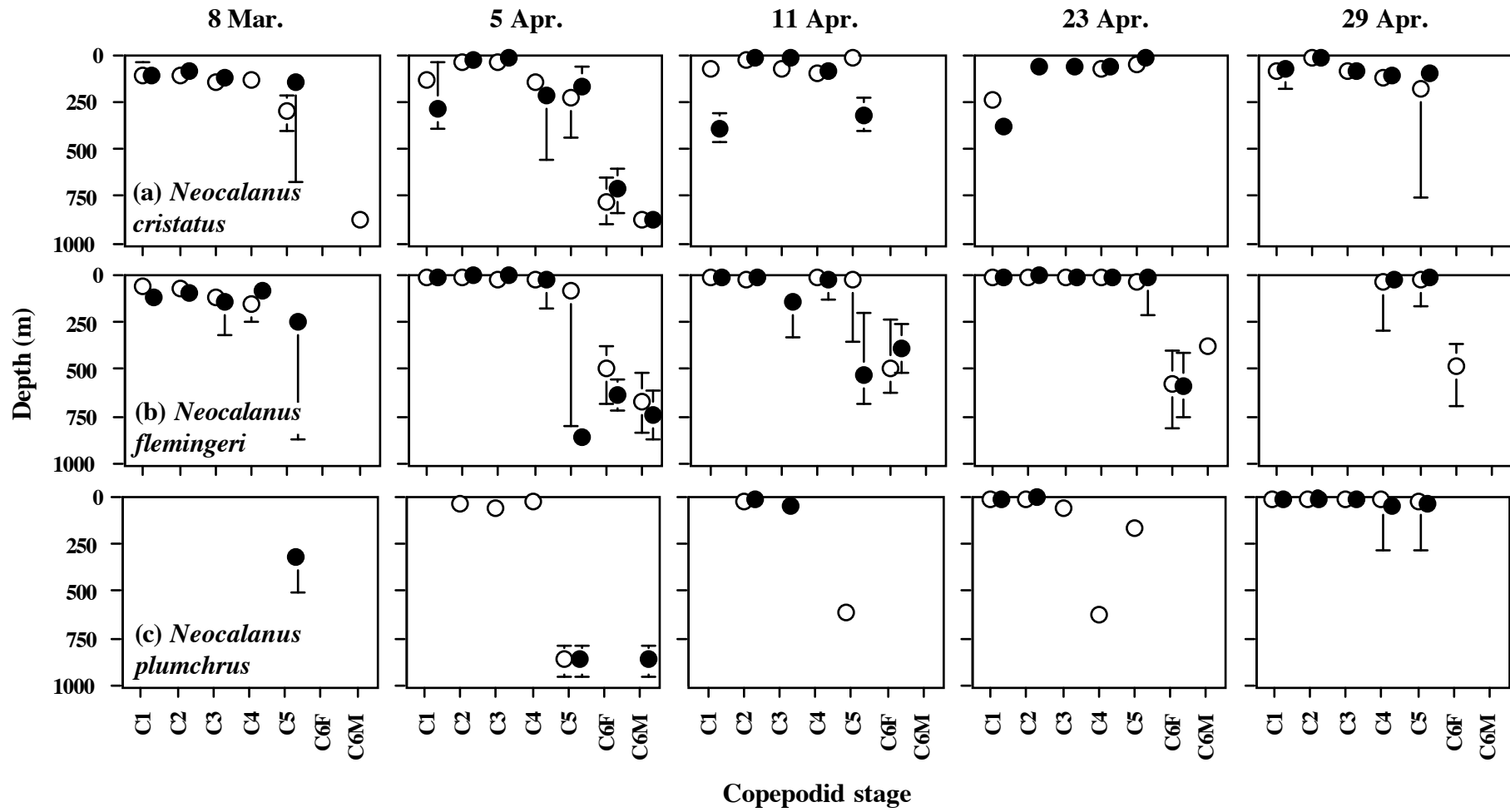


Fig. 10 (Yamaguchi et al.)