Impacts of ontogenetically migrating copepods on downward carbon flux in the western subarctic Pacific Ocean

Toru Kobari[a*], Deborah K. Steinberg[b], Ai Ueda[a], Atsushi Tsuda[c], Mary W. Silver[d] and Minoru Kitamura[e]

[a]Fisheries Biology and Ocanography Section, Faculty of Fisheries, Kagoshima University
4-50-20 Shimoarata, Kagoshima 890-0056, Japan

[b]Virginia Institute of Marine Science, College of William and Mary

[c]Ocean Research Institute, University of Tokyo

[d]University of California, Santa Cruz

[e]Extremobiosphere Research Center, Japan Agency for Marine-Earth Science and Technology

[*] Corresponding author
Present address: Fisheries Biology and Oceanography Section, Faculty of Fisheries, Kagoshima University
4-50-20 Shimoarata, Kagoshima 890-0056, Japan
email: kobari@fish.kagoshima-u.ac.jp

Abstract

To evaluate the impacts of ontogenetically (seasonally) migrating copepods on carbon transport to the mesopelagic zone, we investigated depth distribution, population structure, and feeding activity of the ontogentic copepod community in the western subarctic Pacific Ocean from day-night pairs of zooplankton samples down to 1000 m during the VERTIGO (VERtical Transport In the Global Ocean) program. Over the 31 July to August 16 2005 study period, the biomass of *Neocalanus cristatus* and *N. plumchrus* predominated in the near surface waters, while *N. flemingeri* was already dormant at depth. We observed a strong diel migration for *Metridia pacifica*, and a seasonal downward migration for *E. bungii*. Based on gut pigment analysis, ingestion rate of the copepod community was 214-375 mgC m^{-2} day^{-1}, which was equal to 26-37% of the concurrent primary production. However, comparison of grazing estimated from gut pigments to calculated carbon demand of the copepod community indicates that phytoplankton comprised 37-59% of the ingested carbon. Thus, the copepod community appears to have also relied on detritus and microzooplankton for their nutrition, likely because primary production during this time was dominated by picophytoplankton too small to be grazed by these large copepods. Fecal pellet flux by the copepod community was estimated to account for 141-223% of the sedimentary particulate organic carbon (POC) flux at 150 m, suggesting considerable fragmentation and consumption of pellets in the upper layers. Fecal pellets alone were adequate to meet copepod carbon demand in the surface 0-150m layer. Active carbon flux by diel migration of *M. pacifica* (respiration, egestion, and mortality) was 4-17 mg C m^{-2} day^{-1}, equal to 6-44% of sedimentary POC flux at 150 m. Active carbon flux by *N. flemingeri* ontogenetic migration (i.e., respiration and mortality at depth) contributed 246 mg C m^{-2} $year^{-1}$, equal to 9% of sedimentary POC flux at 1000 m. The imminent downward migration of *N. cristatus* and *N. plumchrus* would lead to an additional ontogenetic carbon flux on the order of 1719 mg C m^{-2} $year^{-1}$. Copepod fecal pellet transport and active transport by diel and ontogenetic migration are thus important carbon fluxes during a season dominated by small phytoplankton, and ontogenetic migrants in the subarctic Pacific Ocean play a

relatively more important role in active carbon flux compared with other open-ocean regions.

Keywords: zooplankton, copepods, vertical migration, carbon flux, subarctic Pacific Ocean

1. Introduction

It has been long accepted that carbon export into the ocean interior is channeled through passive sinking of phytoplankton, fecal pellets of zooplankton, and aggregates of both, and that this exported carbon supports mesopelagic carbon demand (Fowler and Knauer, 1986; Zhang and Dam, 1997, Aristegui et al. 2002). In the past decade, a number of studies have also shown that diel vertical migrants significantly contribute to carbon flux by consuming POC in surface waters and respiring and excreting the metabolized POC at depth. This "active" flux of carbon is equivalent to 3-127%, of the sinking POC flux in tropical to subarctic waters (Al-Mutairi and Landry, 2001; Dam et al., 1995; Longhurst et al., 1990; Le Borgne and Rodier, 1997; Steinberg et al., 2000, in press; Zhang and Dam, 1997). Seasonal or "ontogenetic" migrants also play an important role in carbon flux. Although carbon flux due to zooplankton mortality loss at depth during overwintering was once considered negligible compared to passive POC flux in the subarctic Atlantic Ocean (Longhurst and Williams, 1992), more recently it has been estimated to be similar to or even 3-fold greater than POC flux measured by sediment traps in the subarctic North Pacific Ocean (Kobari et al., 2003) and in the Southern Ocean (Bradford-Grieve et al., 2001), respectively.

Copepods within the genera *Neocalanus, Eucalanus, Calanus* and *Metridia,* dominate the zooplankton community in abundance and biomass in the subarctic Pacific Ocean and its neighboring waters (Mackas and Tsuda, 1999). These large-sized copepods actively feed on various particulate materials, including not only phytoplankton, but also microzooplankton, sinking aggregates, and faecal pellets (Dagg, 1993b; Gifford, 1993; Kobari et al., 2003) and accumulate large lipid reserves in their bodies (Kobari and Ikeda, 1999; 2001b). Thus, they have significant impacts on suspended and sinking POC. Moreover, these copepods have life histories that include diel and seasonal vertical migration down to meso- and bathypelagic waters (Kobari and Ikeda, 1999, 2001a, b; Tsuda et al., 1999, 2004; Kobari et al. 2004; Padomavati et al., 2004; Shoden et al., 2005). Because these abundant copepods have a large body size, the respiratory and mortality loss at depth should be significant components of active carbon flux. However, there is no direct

89 comparison between the actively transported and sedimentary carbon flux in the subarctic Pacific
90 Ocean.

91 Therefore, we investigated the depth distribution, population structure, and feeding activity of
92 ontogenetic migrating copepods in the western subarctic Pacific Ocean to evaluate the impacts of
93 these migrants on POC flux to the mesopelagic zone.

94

95 **2. Materials and methods**

96 *2.1 Zooplankton collections and enumeration*

97 The present analyses are based on depth-stratified zooplankton samples collected at station K2
98 in the western subarctic Pacific Ocean (47˚N, 161˚00'E) during 31 July to 16 August 2005.
99 Zooplankton were collected at discrete depth intervals with an Intelligent Operative Net Sampling
100 System (IONESS: mesh size 335μm, mouth opening 1.0 m^2) from 0-50, 50-100, 100-150, 150-200,
101 200-300, 300-400, 400-500, 500-750, and 750-1000 m. A flowmeter was mounted in the mouth
102 of the frame to register the volume of water passed through the net. Day and night tows were
103 made between 11:00-15:00 and 22:30-03:00 (local time), respectively. Zooplankton samples were
104 split on board and aliquots were stored at -80˚C for enumeration. Zooplankton samples for gut
105 pigment and dry weight were collected with vertical tows from 150 m with a North Pacific standard
106 net (NORPAC: mesh size 100μm, mouth opening 0.16 m^2) at each IONESS deployment. The
107 samples were immediately frozen in liquid nitrogen after absorbing remaining seawater on paper
108 towels, and stored at -80˚C for measurement of gut pigments. Vertical profiles of water
109 temperature, salinity and chlorophyll *a* concentration were determined with a CTD-RMS system on
110 each IONESS deployment. Water samples for chlorophyll measurement were taken from 11
111 discrete depths (0, 5, 10, 20, 40, 50, 75, 100, 125, 150 and 200 m) using a Niskin bottle and filtered
112 through a Whatman GF/F filter. Chlorophyll *a* concentration was extracted with *N,*
113 *N*-dymethylformamide (Suzuki and Ishimaru, 1990) and determined with the method of
114 Holm-Hansen et al. (1965).

We identified (post-cruise) the ontogenetically migrating copepods from all samples, including 2 *Calanus* (*C. pacificus* and *C. jashinovi*), 1 *Eucalanus* (*E. bungii*), 2 *Metridia* (*M. pacifica* and *M. okhotensis*) and 3 *Neocalanus* (*N. cristatus*, *N. flemingeri* and *N. plumchrus*) species. All six copepodite stages (C1-C6) of each species were enumerated under a dissecting microscope. Copepods were separated by sex for stages C4 to C5 of *Eucalanus* and *Metridia,* and for stage C6 for all species. The abundance of C1 and C2 stages of *Calanus* and *Metridia* species may be underestimated due to their smaller body size compared to the net mesh opening.

2.2 Biomass estimation

Carbon-based biomass (B: mg C m^{-2}) was computed as the sum of animal dry weight (DW: mg DW $individual^{-1}$) for all copepodite stages (C1 to C6) multiplied by their abundance (N: individuals m^{-2}). We thawed frozen samples and briefly rinsed each species and stage with Milli-Q water. Dry weight was determined with a microbalance (Sartorius SE2: accuracy ±0.1 µg) after freeze drying copepods for 3 hours and drying at 60˚C for 6 hours. The DWs of some missing species and stages were used from previous analyses (Kobari et al., 2003, 2004; Padmavati, 2003) and unpublished data (Table 1). Since there is some loss of dry weight from the frozen samples (Williams and Robins, 1982), we assumed a loss factor of 0.28 during the freezing/thawing process (Kobari and Ueda, unpublished data). Carbon content was assumed to be 40% of dry weight (Peters and Downing, 1984). From these parameters, copepod biomass is given by the equation:

$$B = \sum^{n} 0.4 \times DW_i \times N_i \qquad (1)$$

where i is copepodite stage and n is the total number of developmental stages identified.

2.3. Gut pigment and grazing estimation

Gut pigment contents were analyzed for the dominant species and stages. The frozen samples were thawed with filtered seawater. The dominant copepodite stages of *C. pacifica* (C5), *E. bungii*

140 (C6 females), *M. pacifica* (C6 females), *N. cristatus* (C5) and *N. plumchrus* (C5) were sorted under
141 a dissecting microscope under dim light, rinsed in Milli-Q water, then dipped in *N*,
142 *N*-dimethylformamide for pigment extraction. One to ten animals were combined for each
143 measurement. Chlorophyll *a* (CHL) and its degradation products were measured with a Turner
144 Designs fluorometer (TD-700). Gut pigment was calculated as the sum of chlorophyll *a* and
145 phaeopigments, and expressed as the chlorophyll *a* equivalent weight. Estimated gut pigments
146 were converted to grazing rates on phytoplankton sources (V) assuming gut evacuation rates of 2.16,
147 2.52, 2.88, 2.70 and 2.52 hour^{-1} for *C. pacifica*, *E. bungii*, *M. pacifica*, *N. cristatus* and *N.*
148 *plumchrus*, respectively (Tsuda et al., 2005; Landry et al., 1994).

149 The grazing rates of younger stages were estimated using the allometric functions (Peters and
150 Downing, 1984):

151 $$\log (V_1 / V_2) = 0.534 * \log (DW_1 / DW_2) \quad (2)$$

152 where V_1 and V_2 are the grazing rates of copepods with animal dry weight of DW_1 and DW_2,
153 respectively. Then, the community grazing rates on phytoplankton were estimated by summing
154 the products for each developmental stage of abundance estimates and individual grazing rate,
155 assuming a C:CHL ratio of 45 (minimum value at K2). Oxygen consumption rates of copepods
156 were calculated from the formula reported by Ikeda et al. (2001):

157 $$\ln R = 0.124 + 0.780 * \ln CW + 0.073T \quad (3)$$

158 where R is the oxygen consumption rate (μL O_2 individual^{-1} hour^{-1}), CW is the copepod carbon
159 weight (mg C individual^{-1}) and T is ambient temperature (˚C) which is the mean temperature of
160 each sampling stratum. R was converted to carbon units assuming a respiratory quotient of 0.97
161 (protein metabolism: Gnaiger, 1983). Carbon budgets of copepods may be expressed as:

162 $$I = R + G + M + E \quad (4)$$

163 where I is ingestion on both phytoplankton and other particles, R is respiration, G is growth, M is
164 molts and E is egestion. Assuming 0.6 for assimilation efficiency (AE: E=0.4*I), and assuming
165 0.3 for gross growth efficiency (K_1: 0.3*I=G+M) (Ikeda and Motoda, 1978), copepod ingestion rate

166 is converted to the following equation:

167 $$I = R / 0.3 \quad (5)$$

168 We performed a sensitivity analysis for the calculation of copepod ingestion rate, using a lower
169 (AE: 0.7, K_1: 0.25) and upper (AE: 0.5, K_1: 0.35) estimate of combined parameters. The analysis
170 was not considered for R, as they are based on an algorithm derived from hundreds of copepod
171 respiration measurements of copepods including many vertically migrating species (Ikeda et al.,
172 2001). Since ingested carbon could be comprised of phytoplankton plus other materials, copepod
173 ingestion rate was estimated as follows:

174 $$I_{phyto} = V \quad (6)$$

175 $$I_{other} = I - V \quad (7)$$

176 I and E of each copepodite specimen (µg C individual^{-1} hour^{-1}) were computed, expressed on a
177 daily basis (24 hours), and summed for all species and copepodite stages in each depth range (mg C
178 m^{-2} day^{-1}).

179 The carbon budget of feeding and fecal pellets of the copepod community and sinking POC
180 flux at each 50 m layer between 0-150 m was estimated using a box model with the following
181 assumptions:

182 1. Sinking fecal pellet POC (F_Z) at 50 and 100 m (z) is estimated from the power function
183 (Martin et al. 1987) to fit the feces flux at the 150 m reference depth (F_{150}) using the rate of
184 flux attenuation "b" for each deployment from Buesseler et al. (2007) and Lamborg et al.
185 (this issue).

186 $$F_Z / F_{150} = (z / 150)^{-b} \quad (8)$$

187 2. Copepod assimilation and gross growth efficiencies are unchanged in the layers above 150
188 m.

189 3. Decomposition and fragmentation of sinking fecal pellets are not selective.

190

191 *2.4. Active carbon flux*

192 Downward carbon flux by diel migration of *M. pacifica* was calculated as in Al-Mutairi and
193 Landry (2001), assuming the migrants reside above 150 m during 9.5 hours at night and in the
194 underlying layers during 14.5 hours at daytime. Respiration and egestion was computed from
195 equations 3 and 5, applying the ambient temperature for the migrants at the weighted mean depth of
196 their daytime distribution calculated as in Prepas (1984). We assumed a mortality rate (M) of 0.01
197 day^{-1} (Batchelder and Miller, 1989), assimilation efficiency (AE) of 0.6, and gross growth efficiency
198 (K_1) of 0.3.

199 Annual carbon export by ontogenetic migration of *N. flemingeri* was also computed.
200 Respiratory carbon loss for the deep-residing population was estimated from the decrease in dry
201 mass for dormant C5 of *N. plumchrus* (0.0002 day^{-1}: Evanson et al., 2000). We compared the
202 moderate mortality rate (0.0065 day^{-1}: Mackas and Tsuda, 1999) to lower and upper rates reported
203 among previous studies (0.0010 and 0.0095 day^{-1}: Tsuda et al., 2004). Based on the reported life
204 histories (Miller and Clemons, 1988, Kobari and Ikeda, 2001a), the dormant C4 and C6 female
205 populations overwintered until the end of December of the current year and February of following
206 year, respectively. Contribution of the deep-residing animals to carbon flux was assumed to be
207 100% of their body carbon for C6 males, because they died after mating, and 32% for C6 females,
208 by subtracting animal egg production (0.496 mg C: Saito et al. 2000) from animal body carbon
209 (0.726 mg C: estimated from prosome length of 4.3 mm).

210

211 **3. Results**

212 *3.1. Hydrography*

213 Water temperature decreased with increasing depth, reached a sub-minimum of 1.5˚C just
214 below 100-m depth, and then increased slightly (Fig. 1). Sea surface temperature increased from
215 9.6˚C at the beginning of the study period to 11.1 ˚C in mid-August. The seasonal thermocline
216 deepened slightly from 20 to 40 m, extending the depth of the surface mixed layer.

Salinity increased 32.9 at sea surface to 34.4 at 1000-m depth. The permanent halocline, which is a common feature over the subarctic Pacific Ocean (Dodimead et al., 1963; Favorite 1976), appeared from 150 to 200 m, and the depth of halocline was stable over the study period.

Chlorophyll *a* concentration increased with depth and a subsurface maximum occurred at 40 to 60 m at the bottom of thermocline. This subsurface maximum reached 1.0 µg L^{-1} on 6 August and then decreased.

3.2. Depth distribution of the copepod community

The ontogenetically migrating copepods were numerically abundant near surface throughout the day, with a secondary peak in the 200-300 m layer (Fig. 2a). *N. plumchrus* was abundant above 50 m (Fig. 2b). *N. cristatus* was the predominant component of the copepod community in the subsurface layer from 50 to 100 m, and they were abundant in 0-50 m as well as 50-100 m (see below). Both species also contributed substantially to abundance in deep waters below 500-m depth. *E. bungii* predominated in the layers from 50 to 400 m (Fig. 2b) and contributed to a mesopelagic peak in the copepod community (Fig. 2a). *M. pacifica* accounted for half of the copepod abundance between 100 and 200 m in the day time and was found near surface at nighttime. *N. flemingeri* resided from 200 to 500 m throughout the day. *Calanus jashinovi* and *C. pacificus* comprised a small proportion, by number, of the ontogentically migrating copepod community in the water column (Fig. 2b).

The depth-distribution patterns of copepod biomass were similar to those of abundance with the notable exception of *N. cristatus* (Fig. 2c, d). This species had the largest body weight of all the ontogenetic migrating copepods (Table 1) and contributed significantly to the copepod biomass throughout the water column, especially in the 50-100 m layer and below 500 m. *E. bungii* was a predominant component of the copepod biomass between 100 and 300 m depth, and *N. flemingeri* contributed significantly to the copepod biomass from 300 to 500 m.

3.3. Vertical distributions of dominant species copepodite stages

C. pacificus concentrated C6 males and females above 50-m depth, while animals residing in the other layers were almost entirely C5 (Fig. 3). *E. bungii* exhibited two abundance peaks between 0-50 m and 200-300 m. Although all copepodite stages of *E. bungii* were found, the most predominant stage throughout the water column was C3. *M. pacifica* was a strong diel vertical migrator, and was distributed between 50 and 400 m during day time and between 0-50 m layer during nighttime. Although *M. pacifica* C5 appeared throughout the water column, younger copepodites dominated in the layers from 50 to 150 m and adults (especially C6 males) were most abundant in deep waters.

N. cristatus were more abundant subsurface in day time (particularly 50 to 100 m), and their abundance in the surface 0-50 m was variable at night (Fig. 4). Although all copepodite stages were present, C5 dominated between 0-50 m and younger copepodites from C1 to C4 occurred above 200 m. *N. flemingeri* resided mainly between 200 and 500 m throughout the day and night. The low numbers of *N. flemingeri* above 200 m depth were dominated by C4, and below 200 m were almost exclusively C6 females. *N. plumchrus* was most abundant in the surface 0-50 m with a secondary peak between 300 and 400 m. The most predominant stage throughout the water column for *N. plumchrus* was C5, with younger copepodites occurring above 150-m depth.

Temporal changes (between day-night and over the 18-day sampling period) in vertical distribution differed among the species (Figs. 5 and 6). Depth distribution of *M. pacifica* was statistically different between daytime and nighttime (Kolomogorov-Sminov test, $p<0.05$) indicating a diel vertical migration across the halocline. No consistent change over the sampling period was observed for *C. pacificus, N. flemingeri,* or *N. plumchrus*. Although no continuous upward or downward pattern was observed, *E. bungii* developed into overwintering stages (C3 to C5 and C6 female) and spread their depth distribution downward. *N. cristatus* decreased in abundance near surface over the course of the summer.

3.4. Ingestion and egestion

In the euphotic zone (~50 m depth: Buesseler et al. 2007), picophytoplankton contributed the most to primary production and microphytoplankton primary production decreased as summer progressed (Table 2). The ontogenetic copepod community ingestion rate in the surface 0-150 m varied from 213 to 375 mg C m^{-2} day^{-1} and accounted for 26 to 37% of primary production. The copepod ingestion rate decreased during the beginning of the study period, corresponding to the decline of the copepod community biomass. Over the study period, phytoplankton accounted for 37 to 59% of the ingested carbon, thus half of the copepod respiratory requirement was supported by other food sources. Egestion rate in the upper 150 m was estimated to be 85 to 150 mg C m^{-2} day^{-1}, 2 to 4-fold higher than sedimentary POC flux measured at 150 m.

Carbon budgets of ingestion and egestion of the copepod community in the strata from sea surface to 150 m are summarized in Figure 7. Since the ontogenetically migrating copepods concentrated near surface, their ingestion and egestion rates in 0-50 m layer accounted for 86 to 95% of total ingestion and egestion in 0-150 m layer. Although the copepod fecal pellets decreased exponentially with depth, estimated fecal carbon flux was equivalent to 141 to 222% of total sedimentary POC flux at 150-m depth. The difference between the feces and sedimentary POC flux was higher on 12 August when primary productivity was low and picophytoplankton was predominant, compared with that on 1 August. Fecal pellet flux by the copepod community was more than adequate to meet copepod ingestion requirements in the layers of 50-100 m and 100-150 m.

3.5. Carbon flux by diel and ontogenetic migrants

The abundance and biomass of diel migrating *M. pacifica* increased toward the end of the study period (Table 3). Carbon export below 150 m via diel migration combined respiration, egestion, and mortality at depth was estimated to be 3.9 to 16.6 mg C m^{-2} day^{-1}. Respiration and egestion below 150 m was 52% and 38% of the active carbon flux, respectively, whereas mortality

295 was of minor contribution (<12%).

296 The *N. flemingeri* community residing between 150-1000 m was comprised of C4, C5 and C6.
297 Their 150-1000 m integrated biomass was 324.8 mg C m^{-2} (Table 4), of which 89% was C6 females.
298 The biomass gradually decreased over the study period (18 days), from which we estimate a
299 mortality rate of 0.018 day^{-1} (Fig. 8). Using the moderate mortality and the dormancy respiration
300 rates from previous studies (see Discussion), overwintering biomass of C4 decreased to 0.4 mg C
301 m^{-2} and C6 females produced 78.8 mg C m^{-2} in eggs, thus active carbon flux by the *N. flemingeri*
302 ontogenetic migrants is estimated to be 245.6 mg C m^{-2} $year^{-1}$ (Table 4).

303

304 **4. Discussion**

305 *4.1. Community structure of the ontogenetic migrants*

306 Ontogenetic migrating copepod species are a major component of the summer zooplankton
307 community at station K2 in the western subarctic Pacific Ocean, as has been reported previously for
308 the subarctic Pacific and its marginal waters (e.g., Mackas and Tsuda 1999). At K2 ontogenetic
309 copepods accounted for 58%, 31%, and 44% of the mean total mesozooplankton abundance
310 integrated between 0-150 m, 150-1000 m, and 0-1000 m, respectively, and accounted for a
311 considerably higher proportion of the mean mesozooplankton biomass (on the order of 90%
312 between 0-1000 m, although likely an overestimate due to some values of more than 100% in the
313 epipelagic zone) (Steinberg et al. this volume). In the eastern subarctic Pacific Ocean, *Neocalanus*
314 and *Eucalanus* copepods comprised 80% of the summertime zooplankton biomass in the upper 100
315 m (Miller et al., 1984). Ontogenetically migrating copepods comprised up to 70% of summer
316 zooplankton biomass in the coastal and offshore Kurile-Kamchatka region (Vinogradov 1997;
317 Yamaguchi et al., 2002a) and about 60% of the late spring biomass in the coastal Gulf of Alaska
318 (Coyle and Pinchuk, 2003). Our findings compared with previous studies also indicate some
319 geographical differences in community structure of the ontogenetic migrants between the western
320 and eastern subarctic Pacific. Although the most predominant species was *N. plumchrus* at K2

(present study) and in the central Gulf of Alaska (Miller et al., 1984), the second most predominant was *N. cristatus* at station K2 (26%: Fig. 2) and *E. bungii* in the Gulf of Alaska (~15%: Miller et al., 1984). Based on geographical comparison of oceanographic conditions reported by Harrison et al. (1999), summertime chlorophyll *a* concentrations are higher, and temperatures are lower, in the Western Subarctic Gyre than the eastern (indicated in their Table 2), while no phytoplankton bloom was present in either region throughout the year. The combination of the higher food availability and lower temperature in the Western Subarctic Gyre may favor the higher predominance of *N. cristatus* there compared to the Eastern Subarctic Gyre. Indeed, in the Oyashio region where a massive phytoplankton bloom appeared, annual mean biomass of *N. cristatus* (2.3 g C m^{-2}: Kobari et al., 2003) was higher than that of *N. plumchrus* (1.1 g C m^{-2}: Kobari et al., 2003) and *E. bungii* (0.9 g C m^{-2}: Shoden 2000). In the present study, however, we cannot explain by what mechanism higher food availability and lower temperatures favor *N. cristatus*, over *E. Bungii*, for example, in the copepod community at K2.

4.2. Life cycle timing

At Station Papa in the eastern subarctic Pacific, the three *Neocalanus* copepods and *Eucalanus bungii* are reported to actively feed at the surface during April to July, migrate to mesopelagic layers during August to September, and remain dormant at depth thereafter (Miller et al., 1984; Miller and Clemons, 1988). *M. pacifica,* however, appears at the surface throughout the year (Batchelder, 1986) and seasonal migration for dormancy is obscure compared with those in the Oyashio region (Padomavati et al., 2004). In the Western Subarctic Gyre, younger copepodites of the copepod community appear in the surface layers from June to July, and their abundance and stage composition show the same timing as those in the eastern subarctic Pacific (Tsuda and Sugisaki, 1994; Tsuda et al., 2005). Results from these previous studies would predict that our sampling period (July to August) was in the surface development season for *M. pacifica* and toward the beginning of dormancy for the three *Neocalanus* copepods and *E. bungii*. Copepod depth

distribution indicated a distinct diel migration for *M. pacifica* and surface concentration of adult males and females for *C. pacificus* (Figs. 3 and 5). There were no obvious dormant populations at mesopelagic depths of either *C. pacificus* or *M. pacifica*, thus we consider they were likely still active. The majority of the population of *N. cristatus* and *N. plumchrus* resided at the surface over the study period, but C5 was the most predominant stage of the surface population for *N. cristatus* (48%) and *N. plumchrus* (85%) in the 0-150 m layer (Fig. 4), thus they were also active, but nearing the end of their surface development. The temporal changes in depth distribution of *E. bungii* indicate they molted into dormant stages with some fraction migrating to the mesopelagic layers as the summer progressed (Fig. 5). These results suggest that *E. bungii* had already begun its downward ontogenetic migration for dormancy and *N. cristatus* and *N. plumchrus* were producing imminent migrant populations. For *N. flemingeri,* stages C4 and C6 females predominated and resided between 200-500 m during the study period (Fig. 4). Our findings are consistent with previous results in the eastern and western subarctic Pacific, where C4 and/or adult female *N. flemingeri* resided at 200 to 1000 m during late summer to winter (Miller and Clemons, 1988; Kobari and Ikeda, 2001a), and thus we consider the majority of their population to be dormant.

4.3. Impacts on particulate carbon flux

We used moderate values of assimilation efficiency (0.6) and gross growth efficiency (0.3). As these parameters are crucial for our estimation of ingestion and egestion rates, we compare the community growth rate estimated from ingestion rate in the present study (Table 2) with the growth rate previously reported for these copepod populations (Vidal and Smith, 1989). As C5 of both *N. plumchrus* and *N. cristatus* composed more than 83% of the biomass of the copepod community residing in the upper 150 m (Fig. 2), growth rate of the copepod community should be close to that of these two species. Vidal and Smith (1989) estimated growth rate to be 0.04 day^{-1} for *N. plumchrus* and 0.05 day^{-1} for *N. cristatus* in the southeastern Bering Sea. The community growth rates estimated from our moderate values (0.03-0.04 day^{-1}) were comparable, whereas they were

lower or higher for the other pairs of the two parameters used in our sensitivity analysis (0.02 - 0.09 day^{-1}, Table 2). These results suggest that the moderate assimilation efficiency and gross growth efficiency values we used are reasonable for the estimation of ingestion and egestion rates.

In the present study, we assumed a low-end C:CHL ratio for this site (measured during a diatom bloom around Station K2, Tsuda et al. 2005) to estimate the contribution of phytoplankton to ingested carbon. As phytoplankton composed approximately half of the ingested carbon (37-59%: Table 2) our estimates indicate that non-phytoplankton food resources were also important in fueling the metabolic requirements of these copepods (Table 2). Cyanobacteria were present in copepod guts that we examined on-board ship using epifluorescence microscopy. Since these ontogenetically migrating copepods cannot effectively feed on picoplankton (Frost et al., 1983), the cyanobacteria were likely consumed as part of a larger marine snow particle or in the guts of microzooplankton prey. Over the last two decades evidence has been increasing that in addition to phytoplankton, ontogenetically migrating copepods feed on various other particulate resources such as sinking POC and ciliates (Hattori, 1989; Dagg, 1993b; Gifford, 1993; Kobari et al., 2003) and that the majority of their ingested carbon is supplied from non-phytoplankton materials (Dagg, 1993a; Tsuda et al., 2005). Studies of diel vertical migrators in the subtropical Atlantic also showed that migrants fed on a wide variety of plant, animal, and detrital material (Schnetzer and Steinberg 2002a) and that the majority the migrant diet originated from non-plant material (Schnetzer and Steinberg 2002b). It has long been considered that ingestion and egestion of phytoplankton by zooplankton is a major pathway to production of sinking particles (Fowler and Knauer, 1986). However, our findings suggest that transformation of microbial assemblages and non-phytoplankton materials to fecal pellets by ontogenetically migrating copepods is an important carbon pathway during seasons of pico-phytoplankton dominated waters in the western subarctic Pacific Ocean.

In our estimates, fecal pellet flux by ontogenetically migrating copepods is considerably higher than the sedimentary POC flux at 150-m depth (141-223 %), even though fecal pellet flux is

399 also reduced by coprophagy by the copepod community in each layer (Fig. 7). These estimates are
400 also much higher than direct observation and enumeration of cylindrical pellets egested by these
401 copepods and some euphausiids in the sedimentary POC in traps at 150-m depth (10-23%: Wilson
402 et al., this issue), suggesting most of the fecal pellets produced by the ontogenetic migrants may be
403 fragmented or consumed by zooplankton and bacteria in surface layers (and thus not recognizable
404 as pellets in traps, see also Wilson et al. this volume). According to results from the subtropical
405 Atlantic Ocean (Huskin et al., 2004), copepod fecal pellets were equal to 31 to 65% of the
406 sedimentary POC flux at 200 m but their contribution decreased at stations where omnivorous,
407 detritivorous copepods (*Oithona* and *Oncaea*) were abundant. Although the majority of these
408 small copepods could not be collected because of the coarse mesh size in the present study (see
409 Steinberg et al. this issue), Yamaguchi et al. (2002a) reported that cyclopoids were the most
410 predominant group during August at Station KNOT (44˚N, 155˚E) in zooplankton samples
411 collected by a fine mesh. These small omnivorous copepods are thought to be responsible for
412 decomposition and fragmentation of fecal pellets (Gonzalez and Smetacek 1994). Moreover,
413 euphausiids and ostracods were abundant in the upper layers (see Steinberg et al. this issue).
414 Euphausiids are known to feed on phytoplankton, microzooplankton, and detritus (Mauchline 1980),
415 and ostracods are considered to be opportunistic feeders on any large pieces of food they encounter
416 (Angel 1983; Vannier et al. 1998). Thus these taxa are also possible contributors to fragmentation
417 of fecal pellets produced by the ontogenetically migrating copepods in surface layers (see also
418 Wilson et al., this issue).
419
420 *4.4. Active carbon flux by diel and ontogenetic migration*
421 Active transport of carbon by feeding in surface waters and metabolism (i.e., respiration,
422 excretion, egestion) and mortality at depth during migrations is an important pathway of carbon
423 transport into the ocean's interior. Respiratory carbon flux across 150 m by diel migration in the
424 world oceans is estimated to be on average 1 to 20 mg C m^{-2} day^{-1} (Al-Mutairi and Landry, 2001;

Dam et al., 1995; Longhurst et al., 1990; Le Borgne and Rodier, 1997; Steinberg et al., 2000; Zhang and Dam, 1997), and can be significant compared to passive carbon flux as measured by sediment traps, especially at K2 (Table 4; Steinberg et al., in press). As *M. pacifica* was abundant and exhibited a consistent diel migration in the present study (Figs. 3 and 5), this species contributed significantly to respiratory carbon flux. Although mortality rate at depth is a crucial parameter for the estimation of active carbon flux by diel migrations, there is limited knowledge on the field mortality rate for *M. pacifica* (0.01 to 0.06 day^{-1}: Batchelder and Miller, 1989). Previous studies showed lower mortality rates for *Neocalanus* and *Eucalanus* species at mesopelagic depths (0.001 to 0.0095 day^{-1}) than those in upper layers (0.02 to 0.075 day^{-1}) (Mackas and Tsuda, 1999;Tsuda et al., 2004). Because we assumed a surface mortality rate in our calculations, mortality flux could be overestimated, and thus would be a minor component of the diel migratory flux. Respiratory carbon flux by this single copepod species at K2 was comparable to previously reported active C flux by the entire meso- and macrozooplankton community in other regions (Table 4). At K2, however, the respiratory carbon flux by *M. pacifica* accounted for a small fraction (15%) of the active carbon transport by the entire diel migrating community (Table 4), with other large components (other copepod species, ostracods, chaetognaths) contributing to the respiratory flux in the western subarctic Pacific Ocean (Steinberg et al., in press, this issue).

Ontogenetic migrants can also play an important role in active carbon flux due to respiratory and mortality loss during dormancy (e.g. Longhurst and Williams, 1992). Compared to a relatively minor carbon loss due to mortality and respiration at depth of ontogenetic migrating copepods of 0.28 g C m^{-2} $year^{-1}$ in the subarctic Atlantic Ocean (Longhurst and Williams, 1992), *Neocalanus* copepods produced a substantial carbon flux of 4.3 g C m^{-2} $year^{-1}$ in the western subarctic Pacific Ocean (Kobari et al., 2003;), and from 1.7 to 9.3 g C m^{-2} $year^{-1}$ in the eastern subarctic Pacific and Southern Oceans (Bradford-Grieve et al., 2001). Contrary to copepod species that feed and spawn eggs at the surface, *Neocalanus* species accumulate a large amount of lipids in their body during surface development, consume them at depth for reproduction, and die

there (Kobari and Ikeda 1999, 2001a, b; Tsuda et al., 1999, 2004). Such behavior is an effective component of the biological pump in some high latitude regions studied, but measurements of the magnitude of this flux are based on estimated mortality rates at depth, which vary. Using the moderate mortality rate for dormant populations (0.0065 day^{-1}: Mackas and Tsuda, 1999), ontogenetic migratory flux by *N. flemingeri* was equivalent to 9% of the sedimentary POC flux at 1000-m depth (Table 5, see Honda et al., 2002 for details of sediment trap flux). In the present study our mortality rate was estimated to be 0.018 day^{-1} (Fig. 8), higher than previously reported (0.0065 day^{-1}: Mackas and Tsuda 1999, 0.0034 day^{-1}: Tsuda et al. 2001, 0.0010 to 0.0095 day^{-1}: Tsuda et al. 2004). While ontogenetic migratory flux is estimated to be 308.6 mg C m^{-2} $year^{-1}$ using our mortality rate, the survival (5% of migrant biomass) is much smaller than the previous estimate (14% of migrant biomass: Kobari et al., 2003). Using minimum (0.001 day^{-1}) and maximum mortality rates (0.0095 day^{-1}) for the dormant population (see Material and methods), the ontogenetic migratory flux ranged from 155 to 273 mg C m^{-2} $year^{-1}$ (Table 4). Thus even at the minimum mortality rate, ontogenetic migratory flux is equivalent to 6% of sedimentary POC flux at 1000 m. These results suggest that the active carbon flux by ontogenetic migration has significant roles in biogeochemical cycles in the subarctic Pacific Ocean.

Although *N. cristatus* and *N. plumchrus* still resided at the surface during our study period (Fig. 4), they should ultimately be included as contributors to the ontogenetic migratory flux. As described above (see Life cycle timing), *N. cristatus* and *N. plumchrus* were proceeding to the end of their surface development seasons and thus the C5s residing above 150 m are considered to be an imminently migrant biomass (2605 mg C m^{-2}). Following our assumptions (see Materials and Methods), the potential carbon flux by these two species is estimated to be 1719 mg C m^{-2} $year^{-1}$(Table 4) . Thus, active carbon flux by ontogenetic migration of all three *Neocalanus* copepod species is 1965 mg C m^{-2} $year^{-1}$ in the Western Subarctic Gyre and equivalent to 73% of the sedimentary POC flux at 1000 m (Table 4). Steinberg et al. (in press) showed that carbon demands of bacteria and zooplankton vastly exceeded the delivery of sinking POC in the

mesopelagic layers and suggest that diel vertical migration plus carnivory supports a greater fraction of the mesopelagic biological carbon demand than sinking POC. Indeed, overwintering *Neocalanus* copepods are major food items for myctophid *Stenobrachius nannochir* residing at mesopelagic depths throughout the day (Moku et al. 2000). We suggest that the respiratory and mortality flux during dormancy of the ontogenetic migrants is part of this important carbon pathway to the mesopelagic in systems where they dominate the zooplankton community, and could help fuel mesopelagic carbon demand at depth.

5. Conclusion

We investigated the community structure of ontogenetically migrating copepods and their impact on carbon transport to mesopelagic depths. These copepods produced sinking fecal pellets through feeding on not only phytoplankton but also non-phytoplankton materials during the copepods' surface development season when the microbial food web was predominant. Ontogenetically migrating copepods produced a significant carbon flux by their diel (4 to 17 mg C m^{-2} day^{-1}) and ontogenetic vertical migration (1965 mg C $year^{-1}$) as well as their fecal pellet flux (5 to 6 mg C m^{-2} day^{-1}: Wilson et al., this issue). In particular, the mortality flux during dormancy is more significant in the subarctic Pacific Ocean vs. in other oceans, where in the former ontogenetic migrants with life cycles that end at depth predominate. As diel and ontogenetic vertical migrations are common throughout the world's oceans, inclusion of this active C flux results in a more accurate measure of global carbon sequestration in the deep sea.

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681

681 Figure captions

682 Figure 1.

683 Vertical profiles of water temperature (solid line), salinity (dotted line) and chlorophyll *a*
684 concentration (solid circles) down to 1000 m in each IONESS deployment at Station K2 in
685 the Western Subarctic Gyre during summer of 2005.

686 Figure 2.

687 Depth distribution of abundance (2a), biomass (2c), and species composition (2b and 2d) for
688 ontogenetically migrating copepods in the layers above 1000-m depth at Station K2 in the
689 Western Subarctic Gyre during summer of 2005. Abundance, biomass, and species
690 composition are mean of n=4 day and nighttime IONESS deployments during the study
691 period. Error bars indicate ±1 standard error. CJ: *Calanus jashinovi*, CP: *C. pacificus*, EB:
692 *Eucalanus bungii*, MO: *Metridia okhotensis*, MP: *M. pacifica*, NC: *Neocalanus cristatus*, NF:
693 *N. flemingeri*, NP: *N. plumchrus*.

694 Figure 3.

695 Depth distribution of abundance and stage composition of *Calanus pacificus* (CP: top),
696 *Eucalanus bungii* (EB: middle) and *Metridia pacifica* (MP: bottom) in the layers above
697 1000-m at Station K2 in the Western Subarctic Gyre during summer of 2005. Abundance
698 and stage composition are mean of n=4 day and nighttime IONESS deployments during the
699 study period. Error bars indicate ±1 standard error.

700 Figure 4.

701 Depth distribution of abundance and stage composition of *Neocalanus cristatus* (NC), *N.*
702 *flemingeri* (NF) and *N. plumchrus* (NP) in the layers above 1000 m at Station K2 in the
703 Western Subarctic Gyre during summer of 2005. Abundance and stage composition are
704 mean of n=4 day and nighttime IONESS deployments during the study period. Error bars
705 indicate ±1 standard error.

706 Figure 5.

707 Temporal changes in abundance of *Calanus pacificus* (CP), *Eucalanus bungii* (EB) and
708 *Metridia pacifica* (MP) above 1000-m depth at Station K2 in the Western Subarctic Gyre
709 during summer of 2005. Sampling date is indicated at the bottom along with time of
710 sampling (N=night, D=day). Shaded area indicates overwintering stages.

711 Figure 6.

712 Temporal changes in abundance of *Neocalanus cristatus* (NC), *N. flemingeri* (NF) and *N.*
713 *plumchrus* (NP) above 1000-m depth at Station K2 in the Western Subarctic Gyre during
714 summer of 2005. Sampling date is indicated at the bottom along with time of sampling
715 (N=night, D=day). Shaded area indicates overwintering stages.

716 Figure 7.

717 Schematic diagram showing ingestion (I), egestion (E) and fecal pellet flux (FP Flux) by
718 ontogenetically migrating copepods (OMC) in three depth strata within the upper 150 m at
719 Station K2 in the Western Subarctic Gyre during summer of 2005. Units are mg C m^{-2} day^{-1}.
720 FP flux was estimated from the 50 m egestion rate and equation 8 and the POC flux
721 attenuation coefficient "b" (see Materials and methods). FPD: Decrease in fecal pellet flux
722 from *i* m to *j* m ($FPD = FP_i - FP_i (j / i)^{-0.52}$). *: POC Flux is from Buesseler et al. (2007).

723 Figure 8.

724 Temporal changes in biomass of migrant stages (C4-C6) of *Neocalanus flemingeri* residing
725 between 150-1000m depth at Station K2 in the Western Subarctic Gyre during the end of July
726 to mid-August 2005. Regression line and equation are superimposed.

727

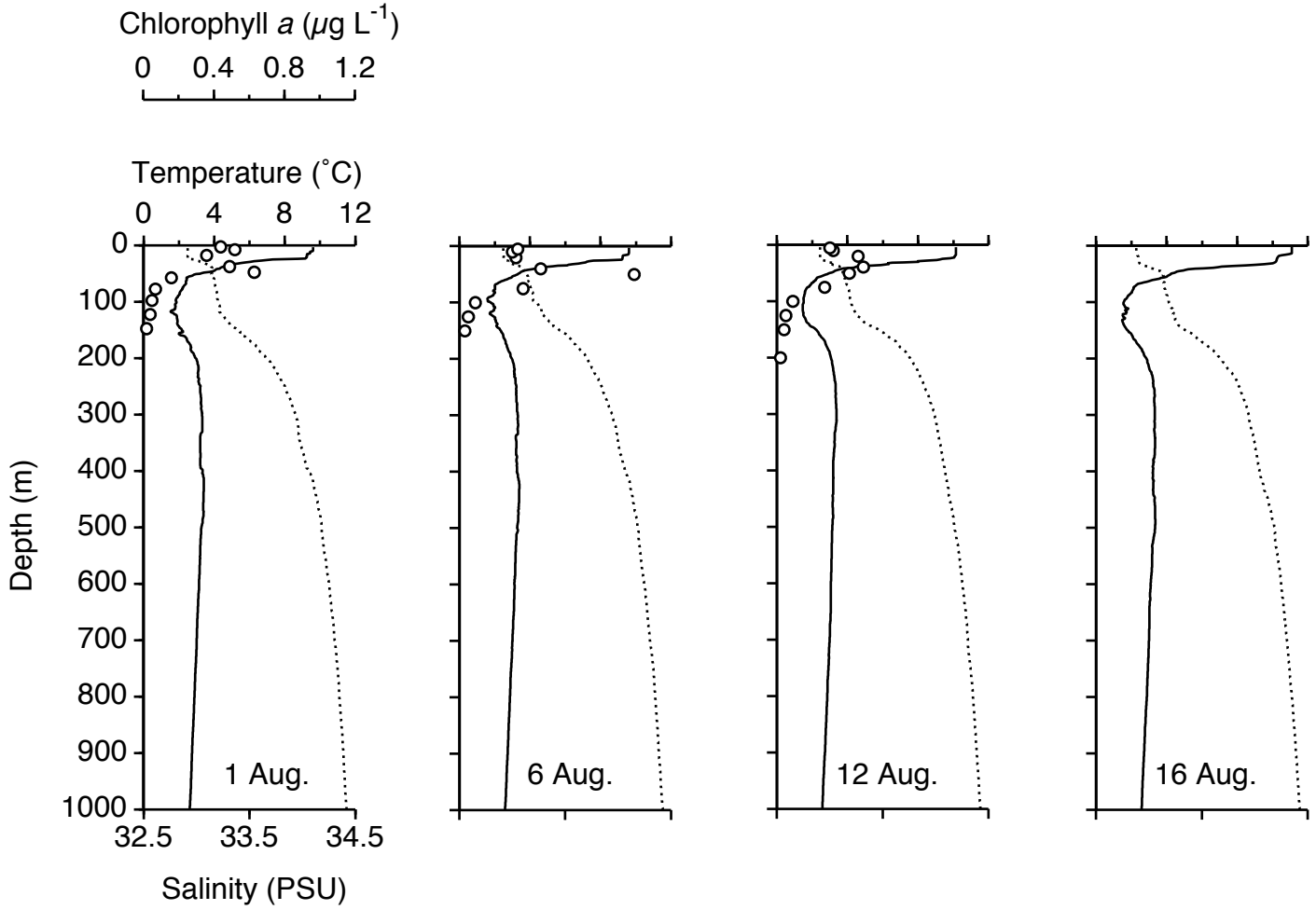

Fig. 1 (Kobari et al.)

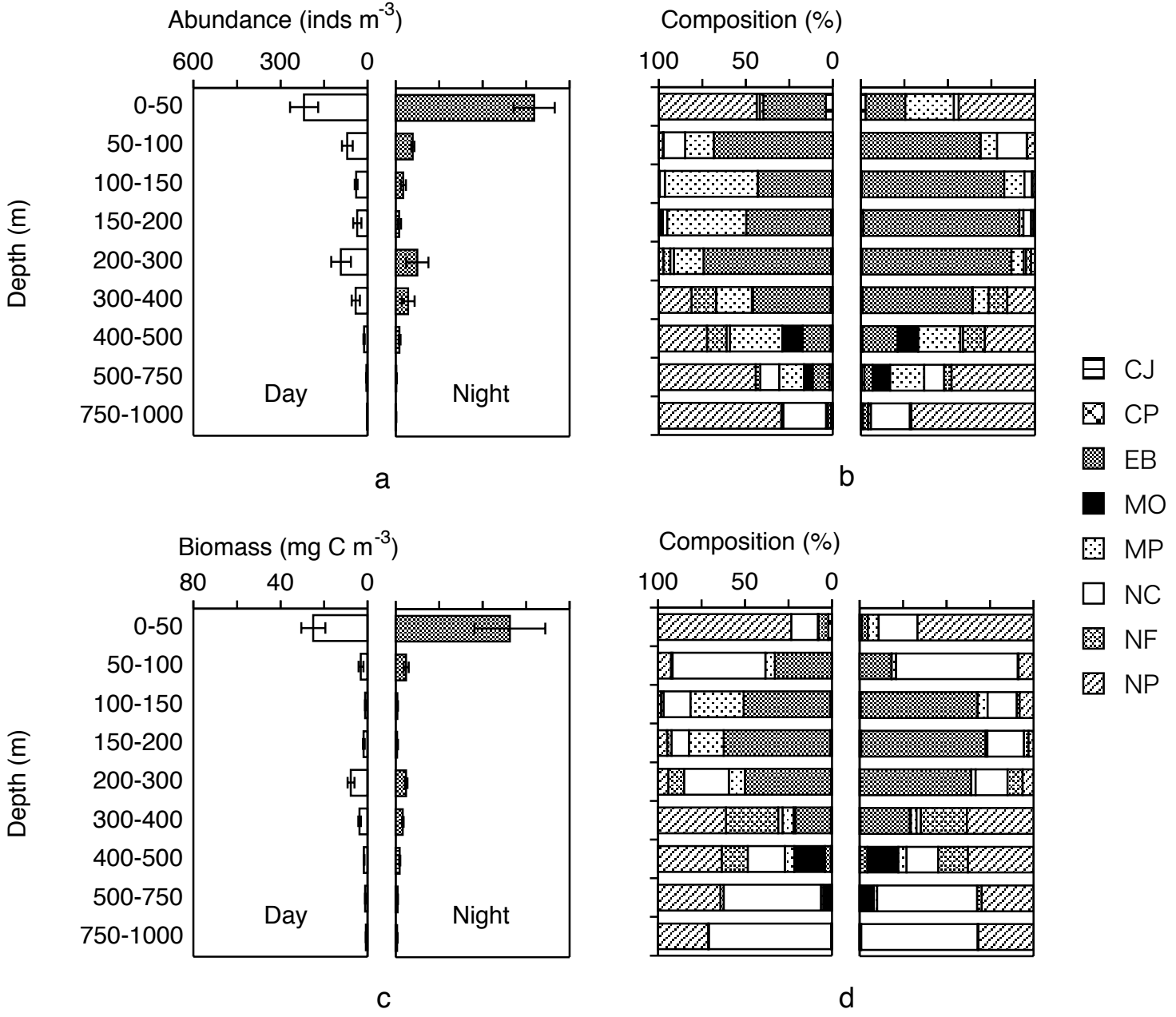

Fig. 2 (Kobari et al.)

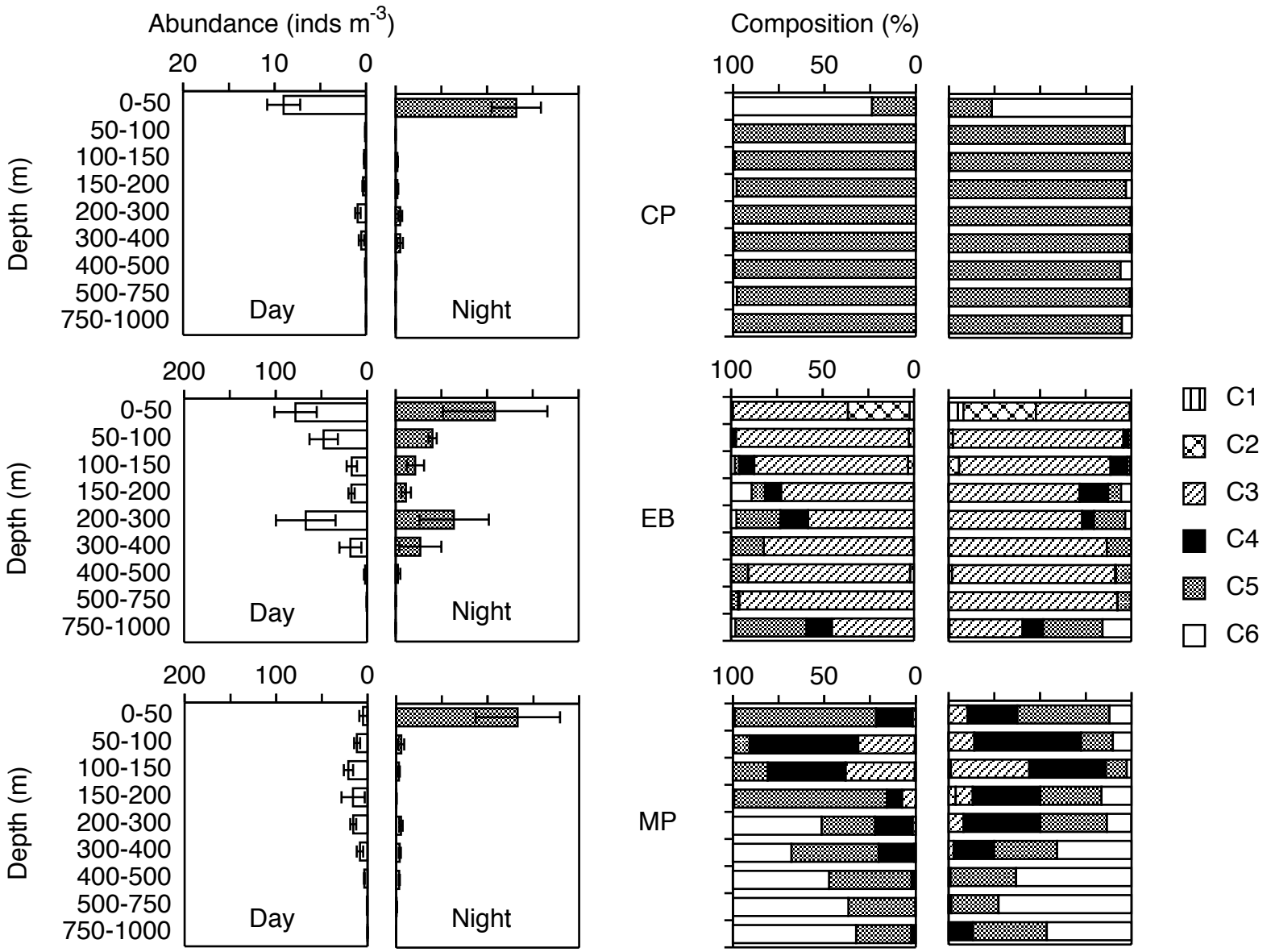

Fig. 3 (Kobari et al.)

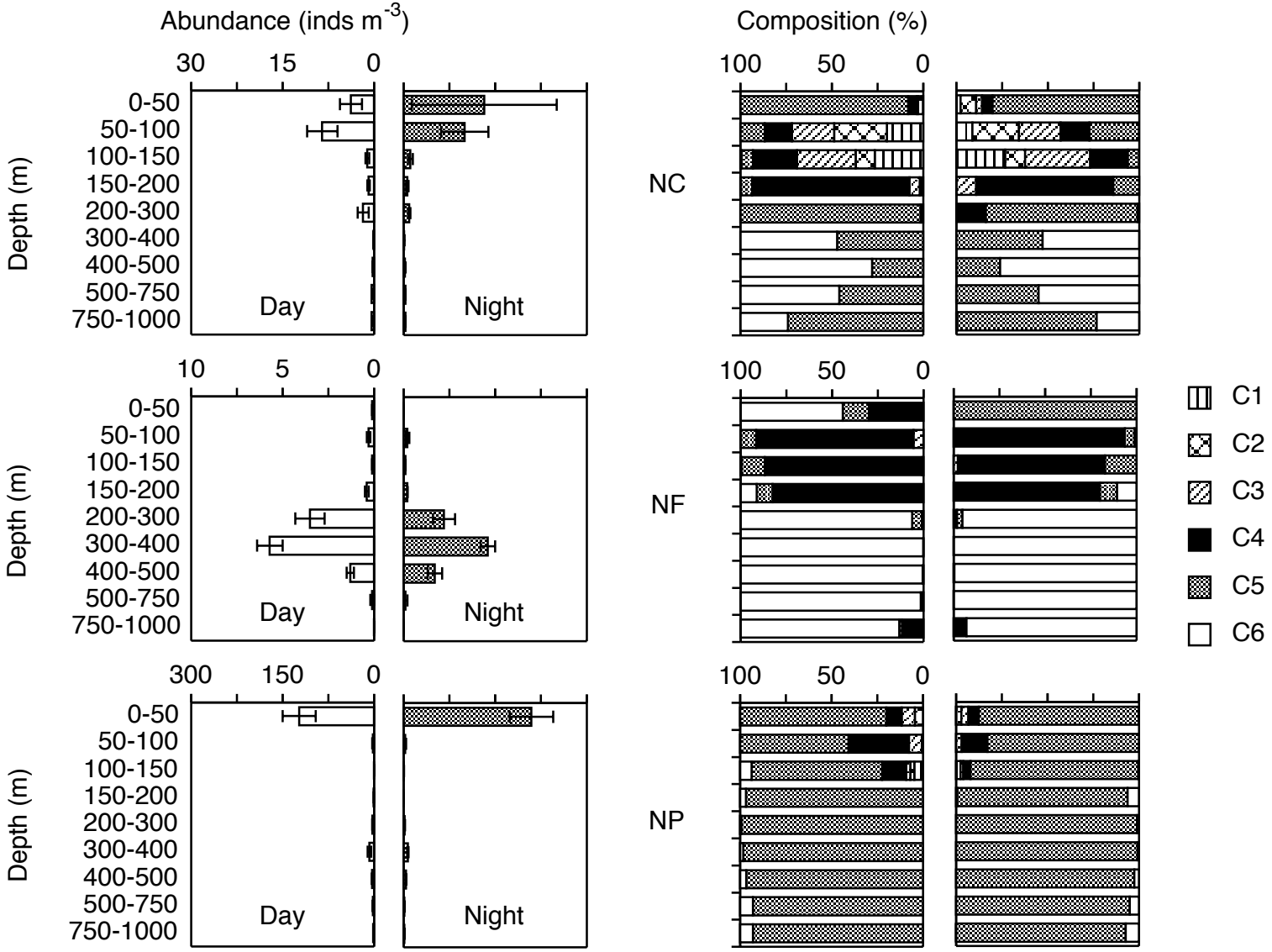

Fig. 4 (Kobari et al.)

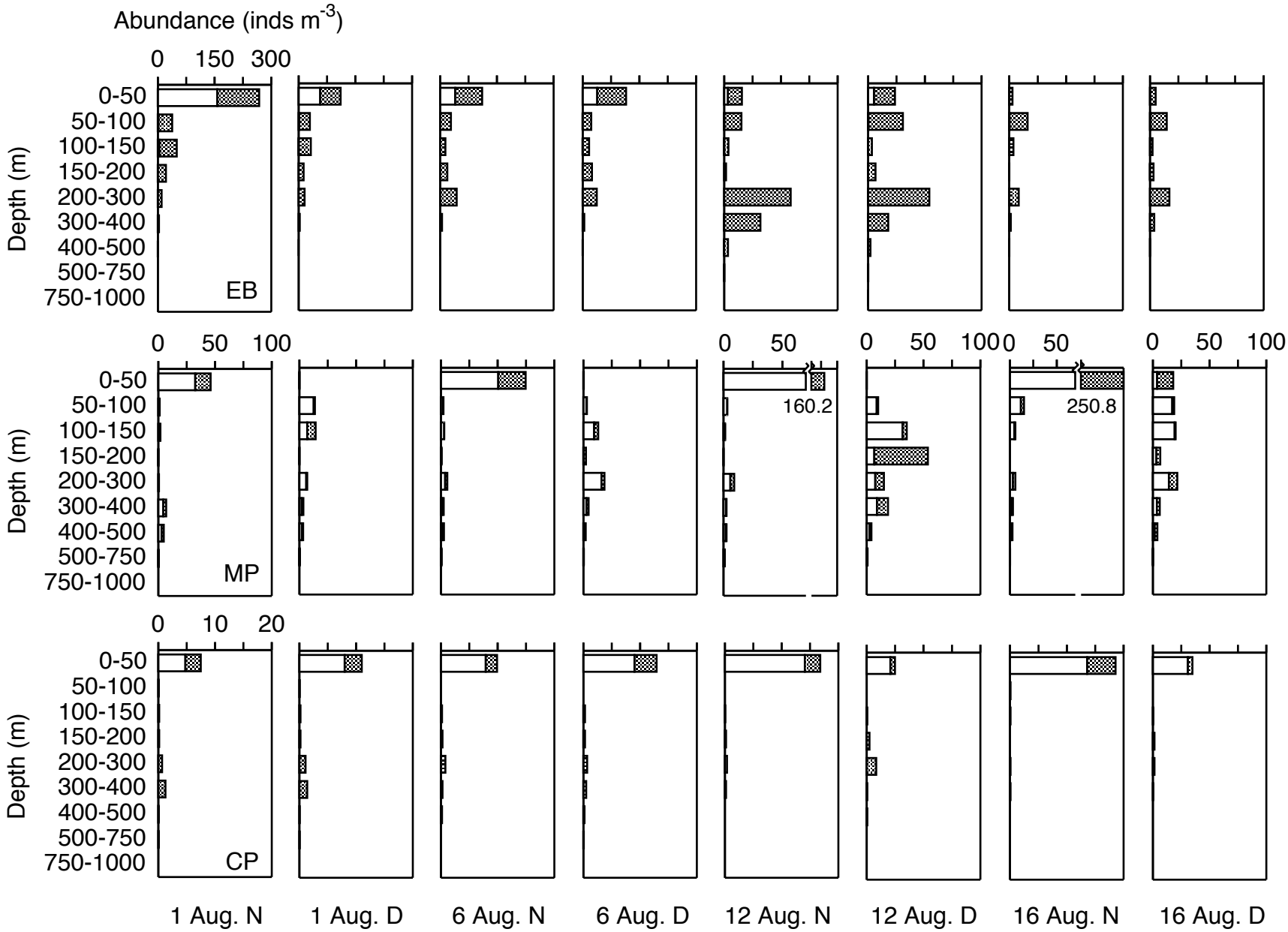

Fig. 5 (Kobari et al.)

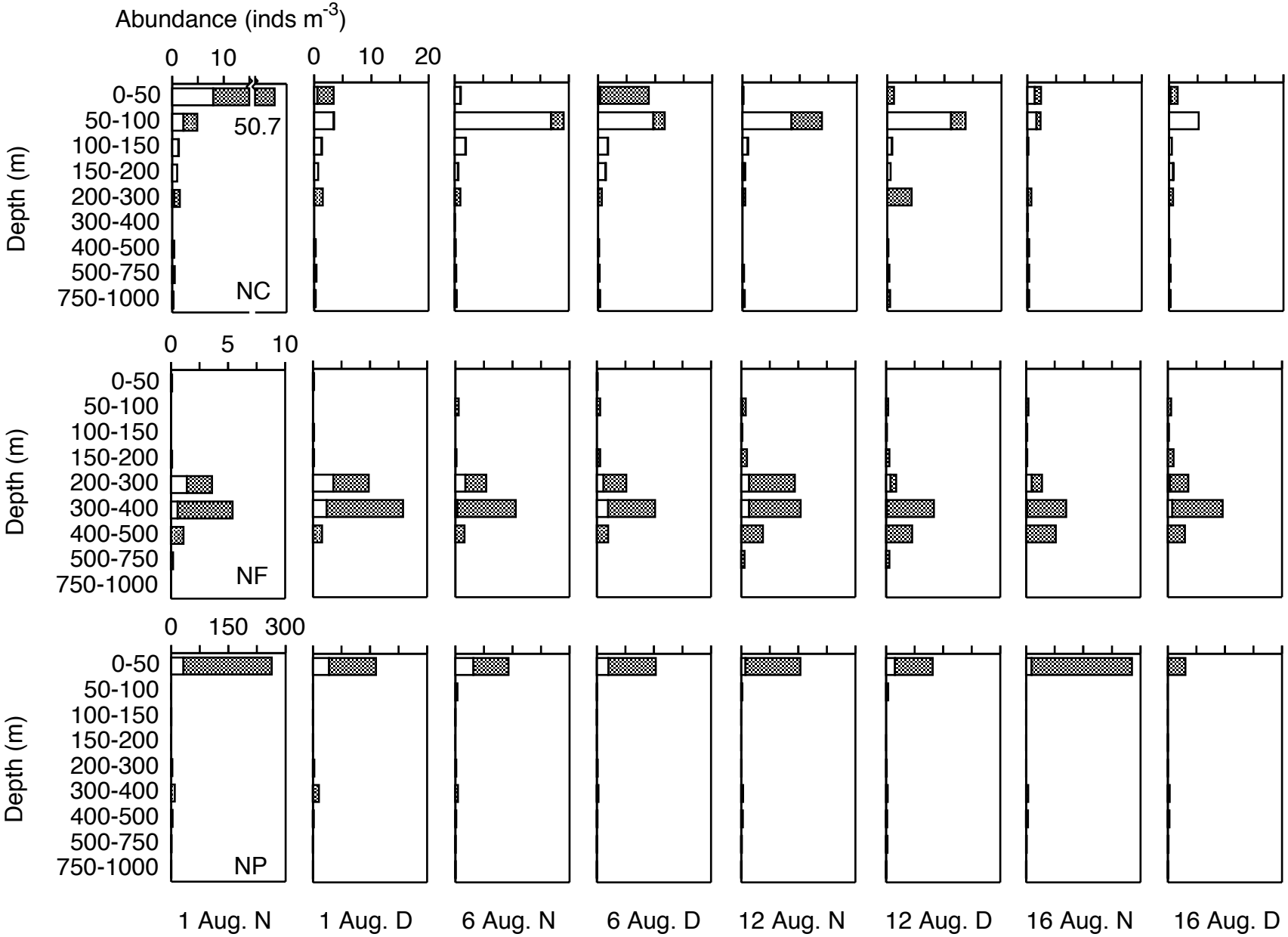

Fig. 6 (Kobari et al.)

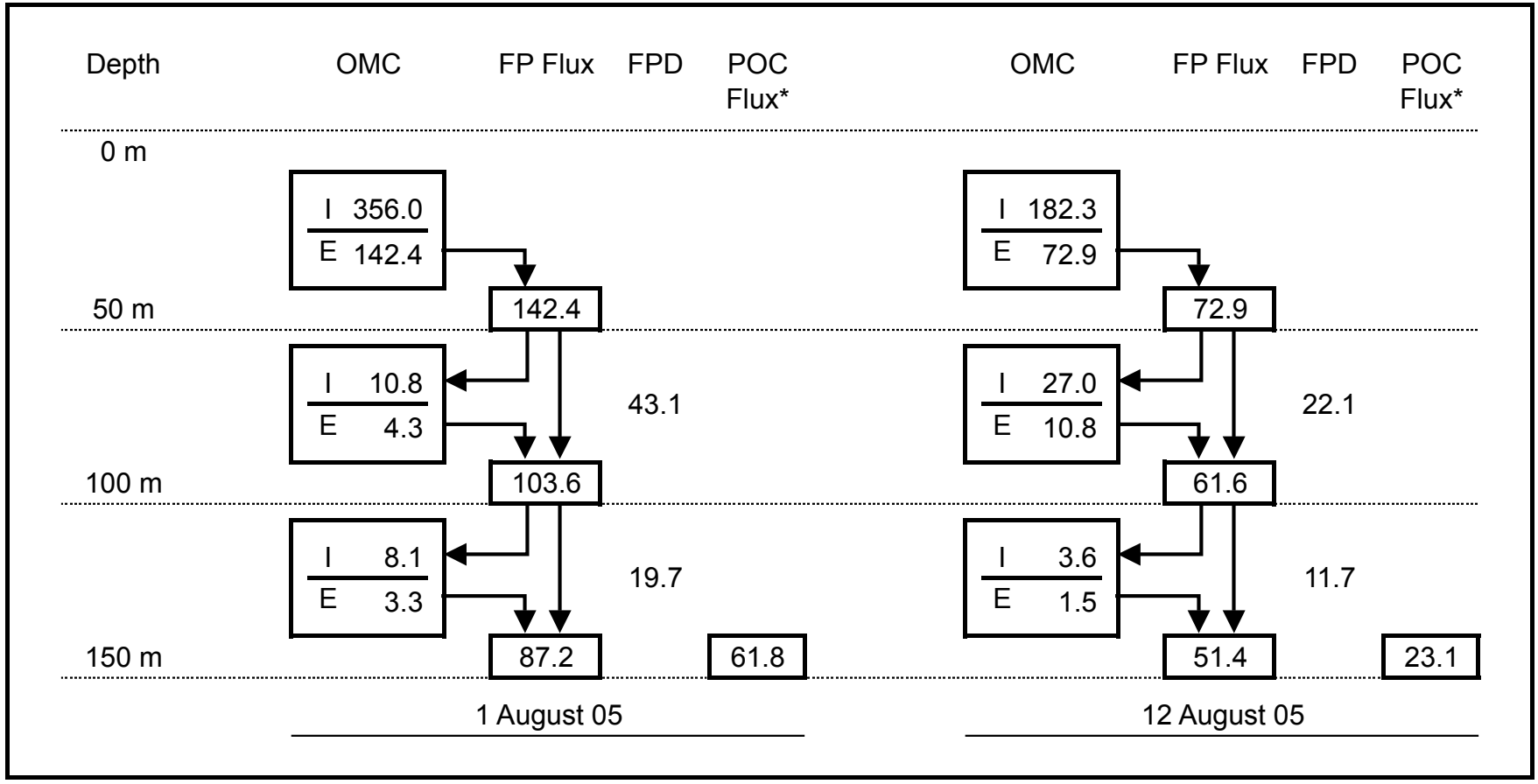

Figure 7 (Kobari et al.)

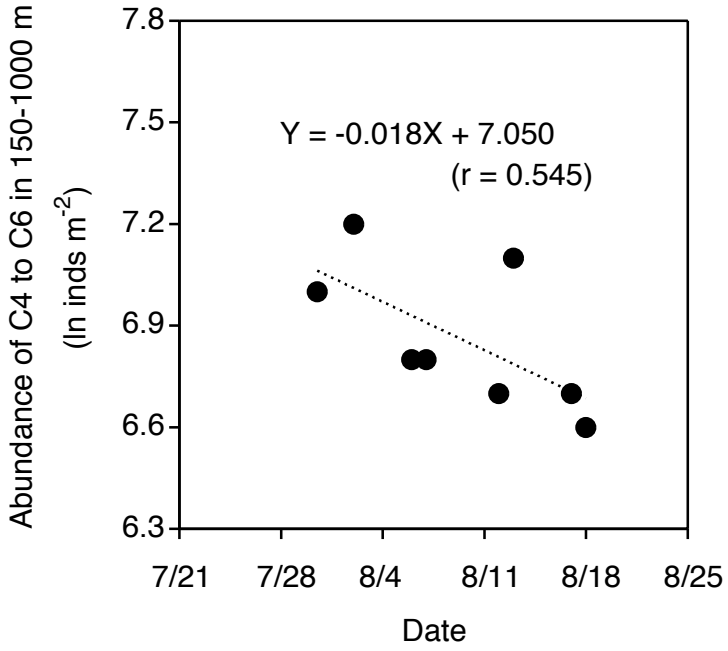

Fig. 8 (Kobari et al.)

Table 1. Dry weight (mg animal^{-1}) of each copepodite stage for ontogenetically migrating copepods at Station K2 in the Western Subarctic Gyre during summer of 2005. -: no occurrence.

Species		C1	C2	C3	C4	C5	C6
					Male / Female	Male / Female	Male / Female
Calanus	*pacificus*	0.006	0.025	0.036	0.061	0.099	0.133 / 0.164
	jashinovi [1]	-	-	-	-	0.257	- / 0.268
Eucalanus	*bungii*	0.025	0.033	0.049	0.099 / 0.094	0.335 / 0.307	- / 0.743
Metridia	*okhotensis* [2]	-	-	-	- / 0.031	0.203 / 0.168	0.087 / 0.403
	pacifica	0.011	0.018	0.026	0.035 / 0.039	0.047 / 0.068	0.049 / 0.183
Neocalanus	*cristatus*	0.025	0.042	0.110	0.347	2.754	4.549 / 5.792
	flemingeri	-	-	0.076	0.197	0.943	0.469 / 1.099
	plumchrus	0.018	0.028	0.076	0.172	0.461	0.836 / 0.267

[1] Kobari unpublished data.

[2] Padmavati (2002).

Table 2. Community ingestion and egestion rates on phytoplankton and other particles for ontogenetically migrating copepods in the surface 0-150 m at Station K2 in the Western Subarcitc Gyre during summer of 2005. Copepod biomass, respiratory requirement, and ingestion and eggestion rates are mean values of day and night. Range in parenthesis is lower and upper end of sensitivity analysis for assimilation efficiency and gross growth efficiency (see Materials and methods).

Parameter	Source	1 Aug.	6 Aug.	12 Aug.	16 Aug,
Primary production (PP: mg C m^{-2} day^{-1}) [1]		590.1	427.5	300.3	355.2
Size composition of PP (%) [1]	Pico	48.2	47.8	56.8	59.9
	Nano	17.7	22.8	21.7	22.5
	Micro	34.1	29.4	21.5	17.6
Biomass (mg C m^{-2})		3370.6	1732.9	1755.0	1823.4
Respiratory requirement (mg C m^{-2} day^{-1})		112.5	64.1	63.9	68.1
Ingestion rate (mg C m^{-2} day^{-1})		374.9	213.7	212.9	227.1
		(250.0-749.9)	(142.5-427.4)	(141.9-425.8)	(151.4-454.1)
Ratio grazed PP (%)		37.4	28.4	26.1	30.6
Ratio grazed (%)	Phytoplankton	58.9	56.7	36.8	47.9
	Others	41.1	43.3	63.2	52.1
Community growth rate (day^{-1})		0.03	0.04	0.04	0.04
		(0.02-0.07)	(0.02-0.04)	(0.02-0.08)	(0.02-0.09)
Egestion rate (mg C m^{-2} day^{-1})		150.0	85.5	85.2	90.8
		(75.0-374.9)	(42.7-128.2)	(42.6-127.7)	(45.4-136.2)
Particulate carbon flux at 150 m (mg C m^{-2} day^{-1})		61.8	-	23.1	-

[1] Boyd et al. (in this volume).

[2] Buesseler et al. (2007).

Table 3 Active carbon flux by diel vertical migration of *Metridia pacifica* via respiration, egestion and mortality at Station K2 in the Western Subarctic Gyre during summer of 2005. Range in parenthesis is lower and upper end of sensitivity analysis for assimilation efficiency and gross growth efficiency (see Materials and methods).

	1 Aug.	6 Aug.	12 Aug.	16 Aug.
Migrant fraction				
Biomass (mg C m^{-2})	78.6	83.2	153.1	262.8
Abundance (10^2 animals m^{-2})	10.5	31.9	82.4	107.3
Weighted mean depth in daytime (m)	179.5	219.5	197.6	158.4
Ambient temperature in daytime (˚C)	3.1	3.2	3.3	3.3
Active carbon flux (mg C m^{-2} day^{-1})				
Respiration	1.5	2.0	4.0	6.4
Egestion	2.0	2.7	5.3	8.6
Mortality	0.5	0.5	0.9	1.6
Total	3.9	5.2	10.2	16.6

Table 3 (Kobari et al.)

Table 4. Comparison of active carbn flux by diel (respiratory only) and ontogengetic migrants (respiratory+mortality) in open-ocean ecosystems. All diel migratory fluxes are means (and do not include active transport by egestion or mortality at depth), and are compared to mean sedimentary C flux from each study. Numbers in parenthesis are range estimated using lower and upper end of mortality rate (see Materials and methods). MESO: meso-zooplankton, MACRO: macrozooplankton, COPE: Copepods, MP: *M. pacifica*, NC: *Neocalanus cristatus*, NF: *N. flemingeri*, NP: *N. plumchrus*, NT: *N. tonsus*. -: no data.

Location	Migrant biomass		Mirgatory	Compared to POC flux		Source
	mg C m^{-2}	Components	Flux	(%)	Depth (m)	
Flux by diel migrants (mg C m^{-2} day^{-1})						
Atlantic Ocean						
NFLUX	29	MESO+MACRO	2	3	150	Longhurst et al. (1989, 1990)
BATS	192	MESO	12	30	150	Dam et al. (1995)
BATS	49	MESO+MACRO	1	5	150	Steinberg et al. (2000)
Pacific Ocean						
Eastern Equator	96	MESO	3	15	150	Zang and Dam (1997)
Eastern Equator	155	MESO	6	20	150	Zang and Dam (1997)
Eastern Equator	53	MESO+MACRO	6	4	150	Le Borgne and Rodier (1997)
Western Equator	47	MESO+MACRO	3	6	150	Le Borgne and Rodier (1997)
ALOHA	158	MESO+MACRO	4	15	150	Al-Mutairi & Landry (2001)
ALOHA	126	MESO+MACRO	3	18	150	Steinberg et al. (in preparation)
K2	1280	MESO+MACRO	20	72	150	Steinberg et al. (in preparation)
K2	116	MP	3	10	150	This study
Flux by ontogenetic migrants (mg C m^{-2} $year^{-1}$)						
Atlantic Ocean						
Ocean Weather Station I	346	COPE	275 [1]	<1	200	Longhurst and Williams (1992)
Southern Ocean						
Subtropical region	-	NT	3400 [1]	262	1000	Bradford-Grieve et al. (2001)
Subtropical Frontal region	-	NT	9300 [1]	-	-	Bradford-Grieve et al. (2001)
Subantarctic region	-	NT	1700 [1]	340	1000	Bradford-Grieve et al. (2001)
Pacific Ocean						
Ocean Weather Station P	-	NC+NF+NP	5000 [1]	185	1000	Bradford-Grieve et al. (2001)
Oyashio	5000	NC+NF+NP	4300 [2]	91	1000	Kobari et al. (2003)
K2	325	NF	246 [2]	9 [3]	1000	This study
			(155-273)	(6-10)		
K2	2605 [4]	NC+NP	1719 [2]	64 [3]	1000	This study

[1] Difference of surface biomass before and after overwintering.

[2] Loss of overwintering biomass by mortality and respiration.

[3] Estimated from a power curve fit (Martin et al. 1987) to sediment trap data using the rate of flux attenuation “b” and annual POC flux of (Honda et al. 2002).

[4] Assumed that C5s residing above 150 m are to be a migrant biomass and develop into C6 male and female equally.