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2 Ontogenetic vertical migration of the mesopelagic carnivorous copepod *Paraeuchaeta* spp. is  
3 related to their increase in body mass

4  
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18 Abstract

19 Two dominant mesopelagic carnivorous *Paraeuchaeta* copepods, *P. glacialis* in the western  
20 Arctic Ocean and *P. elongata* in the western subarctic Pacific, exhibited specialized ontogenetic  
21 vertical migration patterns with deeper occurrences of early copepodids (C1) and adults (C6F/M)  
22 and shallower occurrences of older copepodids C3-C5. Moulting increments in body masses (wet,  
23 dry and ash-free dry masses) exhibited highly significant negative correlations with habitat depth.  
24 These facts suggest that both *Paraeuchaeta* species spend their reproductive (C6F/M) and early  
25 developmental (C1) stages in deeper layers to avoid predation and migrate upwards to where prey  
26 is abundant during the middle-late copepodid stages (C3-C5) to achieve greater mass growth.

27

## Introduction

Ontogenetic vertical migration (OVM) of calanoid copepods, such as *Calanus finmarchicus*, *Calanus hyperboreus*, *Neocalanus cristatus*, and *Neocalanus plumchrus*, at high latitudes is well known and is commonly characterized by a descent in preferred depth in the late diapausing stages (C4-C6) (Miller et al., 1984; Conover, 1988). In the early copepod stages, these suspension feeders feed in the surface layers during the productive season, when phytoplankton and microzooplankton are abundant. In later life stages, these organisms descend to deeper layers after accumulating lipids to diapause during fall and winter (Conover, 1988; Atkinson, 1991), when food near the surface is scarce. This diapause at depth reduces predation mortality during the winter (Miller et al., 1984; Mauchline, 1998).

Some mesopelagic and bathypelagic copepods are known to exhibit a specialized OVM pattern, being found at shallower depths as their developmental stages progress (i.e., developmental ascent) (Yamaguchi et al., 2004 and references therein). The approximate ranges of this specialized OVM are reported to be 300-600 m (Yamaguchi et al., 2004), which is comparable but opposite to the normal OVM patterns of the Calanidae copepods. Specialized OVMs have been observed for a number of species (Morioka, 1975; Weikert and Koppelman, 1993; Richter, 1994; Falkenhaus et al., 1997; Yamaguchi et al., 2004). These species include both suspension feeders (e.g., *Chiridius armatus*, *Chiridius obtusifrons*, *Gaetanus variabilis*, *Lucicutia longicauda*, *Metridia asymmetrica*, and *Metridia curticauda*) and predatory feeders (e.g., *Paraeuchaeta elongata*, *Paraeuchaeta birostrata*, and *Paraeuchaeta rubra*) (Ohtsuka and Nishida, 1997). The driver for this specialized OVM pattern in meso- and bathypelagic copepods is poorly understood, especially since limited information on these species is available. Whether the specialized OVMs of meso- and bathypelagic copepods are related to season is unknown.

In the present study, we found that two dominant, carnivorous *Paraeuchaeta* copepods, *P. glacialis* in the western Arctic Ocean and *P. elongata* in the western subarctic Pacific, exhibited specialized OVM patterns. These OVM patterns are discussed relative to growth (moult increment) as the wet, dry, and ash-free dry masses of each species.

## Methods

The data or samples from two previous expeditions were available for detailed examination. In the western Arctic Ocean, the samples had been collected during the year-long Surface Heat Budget of the Arctic Ocean (SHEBA) expedition (e.g., Ashjian et al., 2003). Stratified vertical hauls from a 1 m<sup>2</sup> mouth area opening-closing net equipped with a 53 µm or 150 µm mesh were made from just above the sea floor and at shallower levels (e.g., 0–50 m, 50–100 m, 100–200 m, 200–1,500 m, and 1,500–2,800 m) for daytime hours at 10-14 day intervals (a total of 30 sampling dates) as the SHEBA ice station drifted through the Canada Basin to the Mendeleyev Basin (74°41'N-80°15'N, 143°55'W-168°00'W) from 27 October 1997 to 29 September 1998 (Ashjian et al., 2003). Although these samples previously had been examined to enumerate the dominant zooplankton types, less abundant species were under-quantified during the original analysis. In the present analysis, whole samples (rather than splits) were re-examined for the abundances of rarer species. In the western subarctic Pacific, samples were collected during a study in the Oyashio region (41°30'N-42°30'N, 145°00'E-146°00'E; Yamaguchi and Ikeda, 2002). Stratified vertical hauls with a 60-cm diameter opening-closing net equipped with a 100 µm mesh were made down to 2,000 m (0–the bottom of thermocline (Th), Th–250 m, 250–500 m, 500–1,000 m, 1,000–2,000 m) at monthly intervals (a total of 15 dates) from 4 September 1996 to 5 October 1997. For both studies, the samples were preserved with 4-5% buffered formalin-seawater. The annual mean vertical profiles of temperature at each region were calculated from CTD casts.

The dominant *Paraeuchaeta* species in each region (*P. glacialis* in the Arctic and *P. elongata* in the Pacific) were sorted and counted according to life stages. Egg sacs and nauplii were sorted from the samples where they were most abundant. For each stage, the distribution centres ( $D_{50\%}$ ) were calculated for both day and night from the abundance data (Pennak, 1943):

$$D_{50\%} = d_1 + d_2 \times \frac{50 - p_1}{p_2}$$

where  $d_1$  is the depth (m) of the upper end of stratification sampling of the 50% individual occurrence layer,  $d_2$  is the towed depth (m) of the 50% individual occurrence layer,  $p_1$  is the

cumulative individual percentage (%) that occurred at depths shallower than the 50% individual occurrence layer, and  $p_2$  is the individual percentage (%) at the 50% individual occurrence layer.

The means and standard deviations of the vertical distribution centres of abundance ( $D_{50\%}$ ) were calculated for both day (n=5) and night (n=13) for the Oyashio region, or for polar night (mid-November to early February, n=5) and for midnight sun (late April to August, n=3) for the Arctic Ocean. Differences in  $D_{50\%}$  between day and night (or between polar night and midnight sun) within the stage were tested by the Mann-Whitney  $U$ -test. Based on the  $D_{50\%}$  of each stage, the OVM occurrences were evaluated using one-way ANOVA and the Tukey-Kramer post hoc test.

Wet masses (WM) were determined for batches of pooled specimens (2-21 individuals from each stage) after briefly rinsing the animals in distilled water, blotting them on filter paper, and then placing them into a pre-weighed combusted aluminium pan. Specimens then were dried in a drying oven at 60°C for 5 h to obtain dry mass (DM) values. To obtain the ash-free dry mass (AFDM), the ash content was determined by weighing the specimens before and after combustion at 480°C for 5 h. A microbalance (CAHN, C-33 or Mettler Toledo, MT5) was used for weighing with a precision of 1 µg. Moulting increments (MI, %) between the stages in the WM, DM, and AFDM were calculated using the following equation (Mauchline, 1998):

$$MI = 100 \times (\text{post-moult mass} - \text{pre-moult mass}) / \text{pre-moult mass}.$$

The relationships between the MI (Y, %) and the annual mean  $D_{50\%}$  of a post-moult stage (X, m) were expressed with the power equation:  $Y = a X^b$ .

## Results

For *P. glacialis* in the Arctic Ocean, the vertical centres of distribution ( $D_{50\%}$ ) ranged between 74 m (seen for C5M during the polar night) and 690 m (seen for C6M during the polar night) (Fig. 1a). Day-night differences in  $D_{50\%}$ , characterized by shallower depths during the polar night, were detected for C3 and C6F ( $p < 0.01$ ,  $U$ -test). Ontogenetic vertical migration was highly significant ( $p < 0.0001$ , one-way ANOVA), with the deepest occurrences for C1 and C6M and the shallowest occurrences for C5F/M. Three groups (a-c) of life stages (a: C1; C6M, b: C2; C3;

C4F/M; C6F/M, and c: C3, C4F/M, C5F/M, C6F) were identified on the basis of the Tukey-Kramer post hoc tests (Fig. 1a). Based on the  $D_{50\%}$  data for both the polar night and midnight sun seasons (year-round data), the magnitude of the OVM was calculated as 577 m. The annual mean temperatures ranged between -1.8 and 1.5°C. The moult increments (MI) for *P. glacialis* were negative for the eggs/nauplii (E/N) and were positive for the remaining stages, and ranged between -49.5% (E/N, AFDM) and 683.2% (C4M/C5M, DM) (Fig. 1b). The greatest MI was seen for C4M/C5M followed by C4F/C5F for all mass units (WM, DM, and AFDM).

For *P. elongata* in the Oyashio region,  $D_{50\%}$  ranged between 189 m (for C5M during night) and 852 m (for C1 during night) (Fig. 1a). The diel changes in  $D_{50\%}$  with nocturnal ascent were observed for C4F, C5M, and C6M ( $p < 0.05$ , *U*-test). Ontogenetic vertical migration was clearly detected ( $p < 0.0001$ , one-way ANOVA), as seen in the deep occurrences of C1 and the much shallower occurrences of C3-C5 ( $D_{50\%}$  at 189-250 m). The magnitude of OVM was 614 m. The annual mean temperatures ranged between 2.6 and 10.0°C. The MI of *P. elongata* was negative at E/N and positive for the other stages, as for *P. glacialis*, and ranged between -51.7% (E/N, AFDM) and 418.6% (C4F/C5F, AFDM) (Fig. 1b). The MI of *P. elongata* was highest for stages C4/C5, but the values were lower than those of *P. glacialis*. The MIs of stages C3/C4 and C4/C5 had similar values.

For both *P. glacialis* and *P. elongata*, the MIs of all life stages based on all three measures (wet mass, dry mass, and ash free dry mass) were correlated with the annual mean  $D_{50\%}$  of the post-moult stages ( $r^2 = 0.686-0.847$ ,  $p < 0.01$ ) (Fig. 2). The regressions between MI and  $D_{50\%}$  in the form of power functions showed no differences between species (ANCOVA;  $F_{1,42} = 0.004$ ,  $p = 0.95$ ) and units (ANCOVA;  $F_{2,42} = 0.859$ ,  $p = 0.43$ ) and showed no interaction between species and units (ANCOVA;  $F_{2,42} = 0.238$ ,  $p = 0.79$ ); thus, based on all data for MI (%) and  $D_{50\%}$  (m), the overall regression was computed as:

$$MI = 313329 D_{50\%}^{-1.414} (r^2 = 0.648, p < 0.0001).$$

## Discussion

### Day-night differences in depth distributions

Day-night differences in the depth distributions of *P. glacialis* and *P. elongata* were interpreted as nocturnal ascent (Fig. 1a). For *P. elongata*, this nocturnal ascent is a diel vertical migration (DVM), since it occurs over a 24-hour period, while for *P. glacialis*, the interval between day and night was on the order of months, so this redistribution is analogous to DVM but takes place over a much longer period. Nocturnal ascent has been reported previously for the C4-C6 stages of *P. elongata* (Yamaguchi and Ikeda, 2002; Abe et al., 2012). In the present study, *P. elongata* did not enter the warm upper 100 m level, consistent with avoidance of high temperatures and with the warm surface water acting as a barrier to upward migration (Morioka, 1975). In the Arctic, adult (C6F/M) *P. norvegica* have previously been reported to remain at 400-500 m throughout the day during the summer (midnight sun) (Fleddum et al., 2001), in contrast with observations in the SHEBA data, in which C6F were found at ~100 m during the polar night (Fig. 1a). Since the SHEBA samples were collected under substantial, but not complete, ice cover, light penetration may have been reduced at those depths (Lindsay, 2003). The upper water column temperatures were also very cold, at approximately -1.8°C. Without a high thermal barrier and under low light penetration, *P. glacialis* might have been able to stay near the surface layer during both the midnight sun and polar night seasons (Fig. 1a).

#### Ontogenetic vertical migration (OVM)

The ontogenetic vertical migration (OVM) of both *P. glacialis* and *P. elongata* was characterized by C1 and C6M being found at the deepest depths, C3-C5 at shallow depths, and C2 and C6F at intermediate depths (Fig. 1a). For *P. elongata*, similar OVM patterns with the C1 stage at the deepest depths were reported in the Japan Sea (Morioka, 1975), Oyashio region (Yamaguchi and Ikeda, 2002; Abe et al., 2012), and British Columbia (Campbell, 1934; Tommasi et al., 2014). The magnitudes of these OVMs was reported to be 415-675 m (Abe et al., 2012), consistent with this study (614 m). For *P. glacialis*, this is the first report of OVM.

The OVM of *Paraeuchaeta* spp. differs from that of the suspension feeding Calanidae copepods (Miller et al., 1984; Conover, 1988), which undergo diapause at depth during the food-scarce season. For Calanidae, spending diapause in a deep layer is thought to be a strategy to

avoid predation pressure in surface layers during the food-scarce season, when little food is available to mitigate the risk of predation (Miller et al., 1984; Conover, 1988). Even for *Paraeuchaeta* spp., the early life stages (eggs, nauplii, and early copepodids) may be vulnerable to predation in the surface layers and thus avoid predation by remaining deeper. In addition, the ovigerous (egg-carrying) *Paraeuchaeta* C6F do not perform DVM and remain in a deeper layer throughout the day, presumably to avoid predation while carrying eggs (Bollens and Frost, 1991; Vestheim et al., 2001). Since the fecundity of *Paraeuchaeta* spp. is low (*K*-selection) (Mauchline, 1998; Auel, 2004), remaining in a deeper layer during the reproductive (C6F/M) and early developmental stages (C1, C2), when vulnerable to predation, may be an adaptive trait to reduce mortality due to predation. In the Arctic Ocean, recent ice melt is expected to increase visual predation pressure from pelagic fish by increasing light penetration in the open ocean (Varpe et al., 2015; Langbehn and Varpe, 2017; Kaartvedt and Titelman, 2018). From this point of view, the predation-induced OVM pattern of the Arctic *P. glacialis* may be altered in the environmental conditions of the near future, but it is of note that the OVM pattern was strong even for the subarctic *P. elongata*.

#### Moult increments (MI)

For both *P. glacialis* and *P. elongata*, the MIs were greatest at the transition from C4 to C5 (Fig. 1b). This observation contrasts with a previous study in the Japan Sea in which the MI of *P. elongata* was reported to peak at an earlier stage transition (C3/C4) and at a higher MI (550% in DM) (Morioka, 1975; Ikeda and Hirakawa, 1996) than seen here. This regional difference in stage specific maximum MI may have occurred because the C3 stage was found at the shallowest depth in the Japan Sea (Morioka, 1975), while stages C3-C5 were found at shallowest depths for both species and regions studied here. The negative mass growth in E/N (Fig. 1b) likely occurred because the naupliar development of *Paraeuchaeta* spp. does not require food (Ikeda and Hirakawa, 1996; Ozaki and Ikeda, 1997). The observed limited mass growth of the older male stages C5M/C6M of both species (Fig. 1b) may result from cessation of feeding accompanied by degeneration of the feeding appendages in C6M of *Paraeuchaeta* spp. (Campbell, 1934) (Fig. 1b).

For several other *Paraeuchaeta* species, the maximum MI from the DM data of the developmental stages has been calculated at 186-481%, with a peak MI at C3/C4 (*P. antarctica*, *P. barbata*) or C4/C5 (*P. glacialis/norvegica*, *P. polaris*) transitions (Auel, 1999; Auel and Hagen, 2005). These MI values and maximum stages correspond well with the results of Ikeda and Hirakawa (1996) and of this study.

#### Relationship between MI and OVM

Both *Paraeuchaeta* spp. had highly significant, non-linear correlations between MI and OVM expressed using a power function including all mass units (Fig. 2). To achieve the observed high MI, massive feeding is required during the post-moult stages. Based on in situ feeding experiments evaluated by gut evacuation, the feeding rates of the C4 and C5 stages of *Paraeuchaeta* spp. are higher than those of the C6F stage (Øresland, 1991; Tönnesson et al., 2006). These observations are consistent with the high MI of C3/C4 and C4/C5 in this study. The primary food for *Paraeuchaeta* spp. is small copepods (Yen, 1983). Both abundance and biomass of small copepods are high near the surface layer and decrease exponentially with increasing depth (Auel and Hagen, 2002; Yamaguchi et al., 2002). Thus, the greater mass growth at shallower depths may be related to higher food availability. From this point of view, the upward migration of C3-C5 during OVM in *Paraeuchaeta* spp. may be a strategy to achieve greater mass growth at these stages.

In conclusion, the specialized OVM of two *Paraeuchaeta* species (*P. glacialis* and *P. elongata*), with C1 and C6M occurring at the deepest depths, C3-C5 at the shallowest depths, and C2 and C6F at intermediate depths, may to avoid predation at the reproductive/egg-bearing (C6F/M) and early developmental stages (eggs, nauplius, and C1). The middle-late copepodid stages (C3-C5), which may be less vulnerable to predation, may migrate into shallower depths, where their food is available in sufficient densities to achieve high mass growth.

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Figure captions

Fig. 1. *Paraeuchaeta glacialis* (left) and *Paraeuchaeta elongata* (right). (a) Ontogenetic changes in annual mean vertical distribution centre ( $D_{50\%}$ , symbols) and standard deviation (bars). Open and solid symbols denote day (midnight sun) and night (polar night) data, respectively. Asterisks indicate significant day-night differences (\*:  $p < 0.05$ , \*\*:  $p < 0.01$ ;  $U$ -test). Vertical distributions of annual mean temperature are shown. Lines (a-c) at the top abscissa denote that significant differences in  $D_{50\%}$  were detected for stages not connected with the same line ( $p < 0.05$ , Tukey-Kramer test). (b) Ontogenetic changes of moult increments in wet mass (WM), dry mass (DM), and ash-free dry mass (AFDM). E: egg, N: nauplius, C: copepodid stage, F: female, M: male.

Fig. 2. *Paraeuchaeta glacialis* (left) and *Paraeuchaeta elongata* (right). The relationship between vertical distribution depth (annual mean  $D_{50\%}$ , m) and moult increment ( $MI$ , %) in terms of WM, DM, and AFDM for each copepodid stage. Lines represent the fitted regression curves of power functions ( $MI = a D_{50\%}^b$ ).

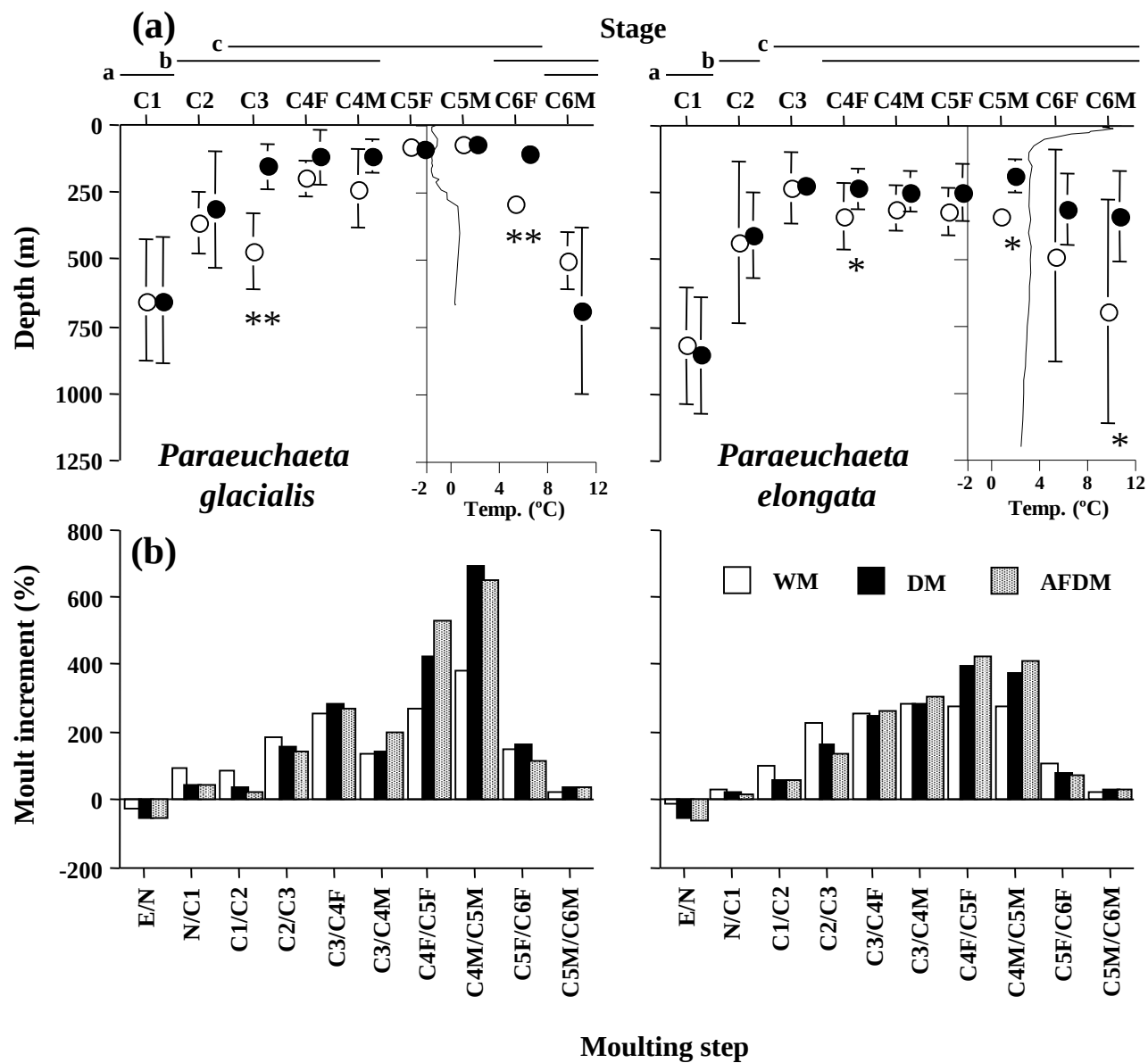


Fig. 1

