



J. Plankton Res. (2019) 41(5): 791–797. First published online November 5, 2019 doi:10.1093/plankt/fbz051

BRIEF COMMUNICATION

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

ATSUSHI YAMAGUCHI^{1,2,3,*}, CARIN J. ASHJIAN¹, ROBERT G. CAMPBELL⁴ AND YOSHIYUKI ABE⁵

¹BIOLOGY DEPARTMENT, WOODS HOLE OCEANOGRAPHIC INSTITUTION, 266 WOODS HOLE RD., WOODS HOLE, MA 02543, USA ²GRADUATE SCHOOL OF FISHERIES SCIENCES, HOKKAIDO UNIVERSITY, 3-1-1 MINATO-CHO, HAKODATE 041-8611, JAPAN ³ARCTIC RESEARCH CENTER, HOKKAIDO UNIVERSITY, KITA-21 NISHI-11 KITA-KU, SAPPORO 001-0021, JAPAN ⁴GRADUATE SCHOOL OF OCEANOGRAPHY, UNIVERSITY OF RHODE ISLAND, NARRAGANSETT, RI 02882, USA ⁵ATMOSPHERE AND OCEAN RESEARCH INSTITUTE, THE UNIVERSITY OF TOKYO, 5-1-5, KASHIWANOHA, KASHIWA-SHI, CHIBA 277-8564, JAPAN

*CORRESPONDING AUTHOR: a-yama@fish.hokudai.ac.jp

Received April 24, 2019; editorial decision July 16, 2019; accepted August 5, 2019

Corresponding editor: Marja Koski

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

KEYWORDS: copepods; vertical distribution; mesopelagic; *Paraeuchaeta*; molt increment; Arctic

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, *Paraeuchaeta 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 (molt increment, MI) as the wet (WM), dry (DM) and ash-free dry masses (AFDM) of each species.

METHOD

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 m² mouth area opening–closing net equipped with a 53 or 150 µm mesh were made from just above the sea floor and at shallower levels (e.g. 0–50, 50–100, 100–200, 200–1500 and 1500–2800 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 Mendeleev 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 2000 m (0 – the bottom of thermocline (Th), Th – 250 m, 250–500, 500–1000 and 1000–2000 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 DM values. To obtain the 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. MI (%) between the stages in the WM, DM and AFDM were calculated using the following equation (Mauchline, 1998):

$$\text{MI} = \frac{100 \times (\text{post-molt mass} - \text{pre-molt mass})}{\text{pre-molt mass}}$$

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

RESULTS

For *P. glacialis* in the Arctic Ocean, the vertical centres of distribution ($D_{50\%}$) ranged between 74 (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). OVM 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 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 (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). OVM 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 (WM, DM and AFDM) were correlated with the annual mean $D_{50\%}$ of the post-molt 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:

$$\text{MI} = 313\,329 D_{50\%}^{-1.414} \quad (r^2 = 0.648, P < 0.0001).$$

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) because it occurs over a 24-h 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

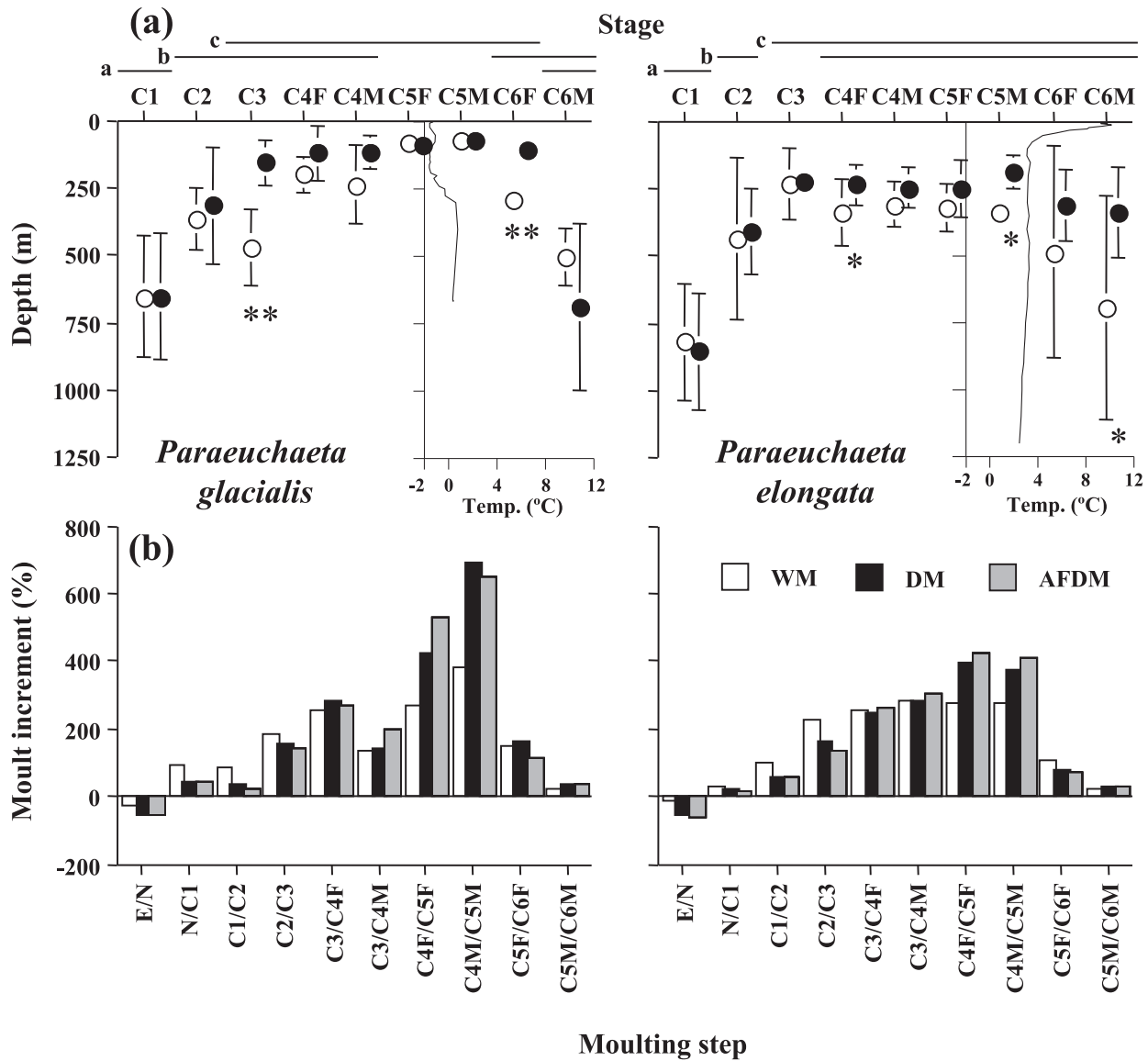


Fig. 1. *P. glacialis* (left) and *P. elongata* (right). **(a)** Ontogenetic changes in annual mean vertical distribution centre ($D_{50\%}$, symbols) and standard deviation (bars). Open and solid symbols denote day (midnight sun) and night (polar night) data, respectively. Asterisks indicate significant 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 MI in WM, DM and AFDM. E: egg, N: nauplius, C: copepodid stage, F: female and M: male.

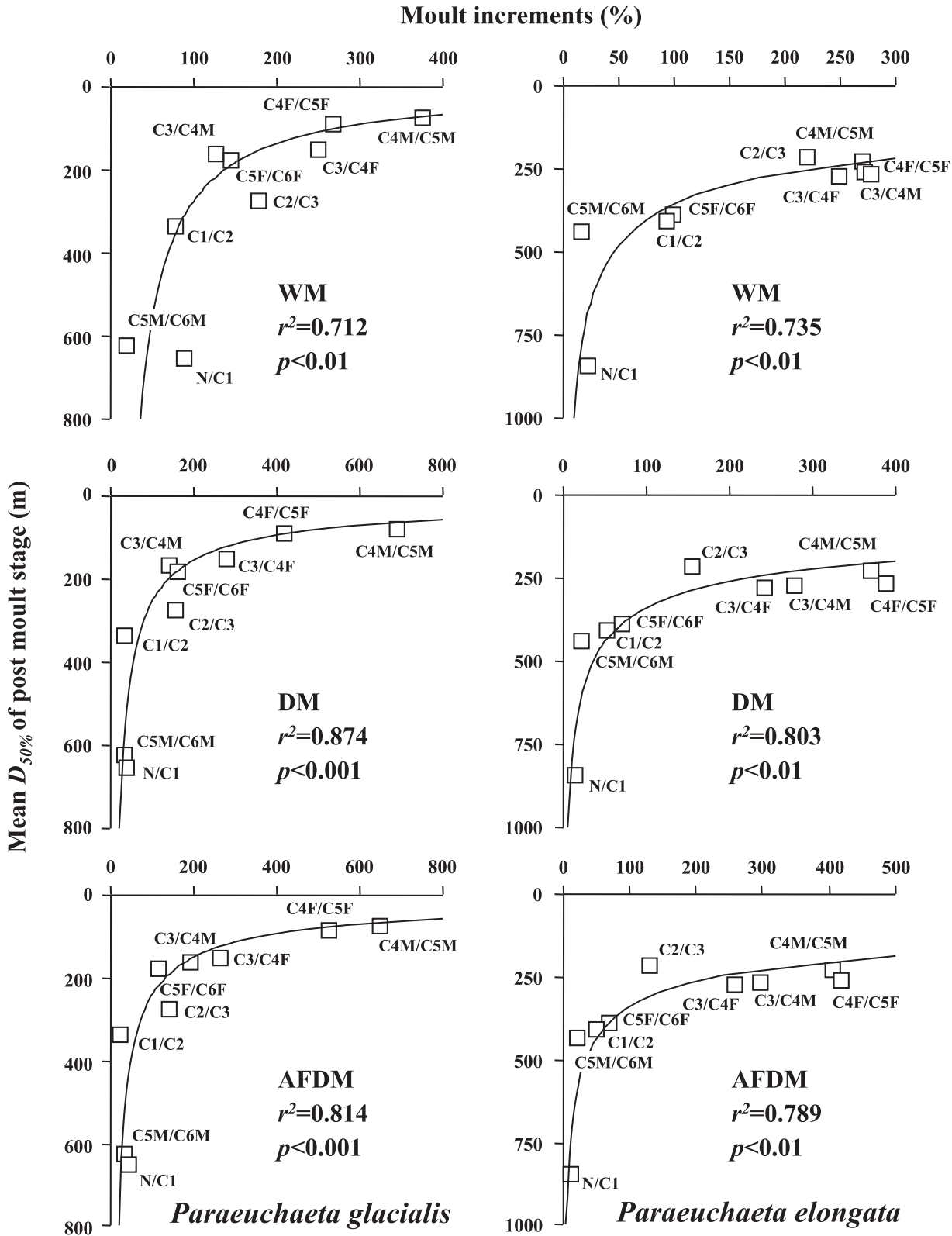
the surface layer during both the midnight sun and polar night seasons (Fig. 1a).

Ontogenetic vertical migration

The 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



Downloaded from https://academic.oup.com/plankt/article-abstract/41/5/791/5613086 by Hokkaido University Library user on 27 November 2019

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

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*.

Molt increments

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-molt 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 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.

ACKNOWLEDGEMENTS

We thank the crew members of the CCGS *Des Groseilliers* and the SHEBA project members, especially Harold ‘Buster’ Welch, for assistance in collecting the SHEBA samples and CTD data. We thank the crew members of TS *Oshoro-Maru*, TS *Hokusei-Maru*, RV *Tansei-Maru*, RV *Hokko-Maru* and RV *Hokushin-Maru* for help during field sampling in the Oyashio region. Collection of the SHEBA samples was supported in part by grants #OCE9707184 to C.J.A. and #OCE9707182 to R.G.C. from the US National Science Foundation. Part of this study was supported by a Grant-in-Aid for Scientific Research 17H01483 (A), 15KK0268 (Joint International Research), 19H03037 from the Japan Society for the Promotion of Science (JSPS). This work was partially conducted for the Japanese ‘Arctic Challenge for Sustainability’ (ArCS) project.

REFERENCES

- Abe, Y., Ishii, K., Yamaguchi, A. and Imai, I. (2012) Short-term changes in population structure and vertical distribution of mesopelagic copepods during the spring phytoplankton bloom in the Oyashio region. *Deep-Sea Res. I*, **65**, 100–112.

- Ashjian, C. J., Campbell, R. G., Welch, H. E., Butler, M. and Van Keuren, D. (2003) Annual cycle in abundance, distribution, and size in relation to hydrography of important copepod species in the western Arctic Ocean. *Deep-Sea Res. I*, **50**, 1235–1261.
- Atkinson, A. (1991) Life cycles of *Calanoides acutus*, *Calanus simillimus* and *Rhincalanus gigas* (Copepoda: Calanoida) within the Scotia Sea. *Mar. Biol.*, **109**, 79–91.
- Auel, H. (1999) The ecology of Arctic deep-sea copepods (Euchaetidae and Aetideidae). Aspects of their distribution, trophodynamics and effect on the carbon flux. *Ber. Polarforsch.*, **319**, 1–97.
- Auel, H. (2004) Egg size and reproductive adaptations among Arctic deep-sea copepods (Calanoida, *Paraeuchaeta*). *Helgol. Mar. Res.*, **58**, 147–153.
- Auel, H. and Hagen, W. (2002) Mesozooplankton community structure, abundance and biomass in the Central Arctic Ocean. *Mar. Biol.*, **140**, 1013–1021.
- Auel, H. and Hagen, W. (2005) Body mass and lipid dynamics of Arctic and Antarctic deep-sea copepods (Calanoida, *Paraeuchaeta*): ontogenetic and seasonal trends. *Deep-Sea Res. I*, **52**, 1272–1283.
- Bollens, S. M. and Frost, B. W. (1991) Ovigerity, selective predation, and variable diel vertical migration in *Euchaeta elongata* (Copepoda: Calanoida). *Oecologia*, **87**, 155–161.
- Campbell, M. H. (1934) The life history and post embryonic development of the copepods, *Calanus tonsus* Brady and *Euchaeta japonica* Marukawa. *J. Biol. Bd. Can.*, **1**, 1–65.
- Conover, R. J. (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia*, **167/168**, 127–142.
- Falkenhaus, T., Tande, K. S. and Semenova, T. (1997) Diel, seasonal and ontogenetic variations in the vertical distributions of four marine copepods. *Mar. Ecol. Prog. Ser.*, **149**, 105–119.
- Fleddum, A., Kaartvedt, S. and Ellertsen, B. (2001) Distribution and feeding of the carnivorous copepod *Paraeuchaeta norvegica* in habitats of shallow prey assemblages and midnight sun. *Mar. Biol.*, **139**, 719–726.
- Ikeda, T. and Hirakawa, K. (1996) Early development and estimated life cycle of the mesopelagic copepod *Paraeuchaeta elongata* in the southern Japan Sea. *Mar. Biol.*, **126**, 261–270.
- Kaartvedt, S. and Titelman, J. (2018) Planktivorous fish in a future Arctic Ocean of changing ice and unchanged photoperiod. *ICES J. Mar. Sci.*, **75**, 2312–2318.
- Langbehn, T. J. and Varpe, Ø. (2017) Sea-ice loss boosts visual search: fish foraging and changing pelagic interactions in polar oceans. *Glob. Chang. Biol.*, **23**, 5318–5330.
- Lindsay, R. W. (2003) Changes in the modeled ice thickness distribution near the surface heat budget of the Arctic Ocean (SHEBA) drifting ice camp. *J. Geophys. Res.*, **108**, 3194. doi: 10.1029/2001JC000805.
- Mauchline, J. (1998) The biology of calanoid copepods. *Adv. Mar. Biol.*, **33**, 1–710.
- Miller, C. B., Frost, B. W., Batchelder, H. P., Clemons, M. J. and Conway, R. E. (1984) Life histories of large, grazing copepods in a subarctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the Northeast Pacific. *Prog. Oceanogr.*, **13**, 201–243.
- Morioka, Y. (1975) A preliminary report on the distribution and life history of a copepod, *Paraeuchaeta elongata*, in the vicinity of Sado Island, the Japan Sea. *Bull. Jap. Sea Reg. Fish. Res. Lab.*, **26**, 41–56.
- Ohtsuka, S. and Nishida, S. (1997) Reconsideration on feeding habits of marine pelagic copepods (Crustacea). *Oceanogr. Japan*, **6**, 299–320.
- Øresland, V. (1991) Feeding of the carnivorous copepod *Euchaeta antarctica* in Antarctic waters. *Mar. Ecol. Prog. Ser.*, **78**, 41–47.
- Ozaki, K. and Ikeda, T. (1997) The effect of temperature on the development of eggs and nauplii of the mesopelagic copepod *Paraeuchaeta elongata*. *Plankton Biol. Ecol.*, **44**, 91–95.
- Pennak, R. W. (1943) An effective method of diagramming diurnal movements of zooplankton organisms. *Ecology*, **24**, 405–407.
- Richter, C. (1994) Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. *Ber. Polarforsch.*, **154**, 1–87.
- Tommasi, D., Hunt, B. P. V., Allen, S. E., Routledge, R. and Pakhomov, E. A. (2014) Variability in the vertical distribution and advective transport of eight mesozooplankton taxa in spring in Rivers inlet, British Columbia, Canada. *J. Plankton Res.*, **36**, 743–756.
- Tønnesson, K., Nielsen, T. G. and Tiselius, P. (2006) Feeding and production of the carnivorous copepod *Paraeuchaeta norvegica* in the Skagerrak. *Mar. Ecol. Prog. Ser.*, **314**, 213–225.
- Varpe, Ø., Daase, M. and Kristiansen, T. (2015) A fish-eye view on the new Arctic lightscape. *ICES J. Mar. Sci.*, **72**, 2532–2538.
- Vestheim, H., Kaartvedt, S. and Edvardsen, S. (2005) State-dependent vertical distribution of the carnivore copepod *Paraeuchaeta norvegica*. *J. Plankton Res.*, **27**, 19–26.
- Weikert, H. and Koppelman, R. (1993) Vertical structural patterns of deep-living zooplankton in the NE Atlantic, the Levantine Sea and Red Sea: a comparison. *Oceanol. Acta*, **16**, 163–177.
- Yamaguchi, A. and Ikeda, T. (2002) Vertical distribution of three mesopelagic *Paraeuchaeta* species (Copepoda: Calanoida) in the Oyashio region, western subarctic Pacific Ocean. *Bull. Fish. Sci. Hokkaido Univ.*, **53**, 1–10.
- Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S., Ishizaka, J., Ikeda, T. et al. (2002) Community and trophic structures of pelagic copepods down to the greater depths in the western subarctic Pacific (WEST-COSMIC). *Deep-Sea Res. I*, **49**, 1007–1025.
- Yamaguchi, A., Ikeda, T., Watanabe, Y. and Ishizaka, J. (2004) Vertical distribution patterns of pelagic copepods as viewed from the predation pressure hypothesis. *Zool. Stud.*, **43**, 475–485.
- Yen, J. (1983) Effects of prey concentration, prey size, predator life stage, predator starvation, and season on predation rates of the carnivorous copepod *Euchaeta elongata*. *Mar. Biol.*, **75**, 69–77.