



BODY LENGTH, DRY AND ASH-FREE DRY WEIGHTS, AND  
DEVELOPMENTAL CHANGES AT EACH COPEPODID STAGE IN FIVE  
SYMPATRIC MESOPELAGIC AETIDEID COPEPODS IN THE WESTERN  
ARCTIC OCEAN

BY

YUNOSUKE KOGUCHI<sup>1,6</sup>), KOKI TOKUHIRO<sup>1,2</sup>), CARIN J. ASHJIAN<sup>3</sup>),  
ROBERT G. CAMPBELL<sup>4</sup>) and ATSUSHI YAMAGUCHI<sup>1,5,7</sup>)

<sup>1</sup>) Faculty / Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho,  
Hako-date, Hokkaido 041-8611, Japan

<sup>2</sup>) Present address: Environmental Management Research Institute, National Institute of Advanced  
Industrial Science and Technology, 16-1 Onogawa, Tsukuba, Ibaraki 305-0053, Japan

<sup>3</sup>) Biology Department, Woods Hole Oceanographic Institution, 266 Woods Hole Road., Woods  
Hole, MA 02543, U.S.A.

<sup>4</sup>) Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, U.S.A.

<sup>5</sup>) Arctic Research Center, Hokkaido University, Kita-21 Nishi-11 Kita-ku, Sapporo, Hokkaido  
001-0021, Japan

ORCID iD: Koguchi: 0000-0002-1647-4804

ABSTRACT

Aetideid copepods dominate the mesopelagic layer of the Arctic Ocean and play an important role in the vertical material flux and biodiversity. However, little information about the lengths and weights of their copepodids is available. In this study, we collected five sympatric aetideid copepods, *Chiridius obtusifrons* Sars G.O., 1902, *Gaetanus tenuispinus* (Sars G.O., 1900), *Gaetanus brevispinus* (Sars G.O., 1900), *Aetideopsis multiserrata* (Wolfenden, 1904), and *Aetideopsis rostrata* Sars G.O., 1903, from the Arctic Ocean and examined their body lengths, dry and ash-free dry weights, and developmental growths at each copepodid stage. Highly significant length-weight relationships were obtained among copepodids for all species. Within genera, individuals of the same length were heavier at shallower depths. This may result from the greater nutritional availability to species within genera inhabiting shallower depths. Common to all species, the organic content (ash-free dry weight per dry weight) was high for the early copepodid stages. This may be due to the residual organic content of lipid-rich eggs retained in the non-feeding nauplii. The largest growth in females occurred at C5/C6, whereas the largest growth in males occurred at C4/C5, as determined by moult increment and proportion of growth in weight. These sex differences in weight growth could be due to the degeneration of the feeding appendage and cessation of feeding in C6 males of aetideid copepods.

<sup>6</sup>) Co-corresponding author; e-mail: makaroni1009@eis.hokudai.ac.jp

<sup>7</sup>) Co-corresponding author; e-mail: a-yama@fish.hokudai.ac.jp

Key words. — Aetideidae, mesopelagic copepods, moult increment, organic contents, prosome length

## RÉSUMÉ

Les copépodes Aetideidae dominent la zone mésopélagique de l'Océan Arctique et jouent un rôle important dans le flux vertical de matière et dans la biodiversité. Cependant, peu d'informations sur les longueurs et les poids de leurs copépodites sont disponibles. Dans cette étude, nous avons collecté cinq espèces sympatriques d'Aetideidae, *Chiridius obtusifrons* Sars G.O., 1902, *Gaetanus tenuispinus* (Sars G.O., 1900), *Gaetanus brevispinus* (Sars G.O., 1900), *Aetideopsis multiserrata* (Wolfenden, 1904), et *Aetideopsis rostrata* Sars G.O., 1903, dans l'Océan Arctique et nous avons examiné leur longueurs du corps, leur poids sec et leur poids sec sans cendres ainsi que leur croissance au cours du développement à chaque stade copépoditique. Des relations longueur-poids hautement significatives ont été obtenues chez les copépodites pour toutes les espèces. Au sein des genres, les individus de même longueur étaient plus lourds lorsque la profondeur était moindre. Ceci peut résulter de la plus grande disponibilité nutritionnelle pour les espèces des genres vivant à de plus faibles profondeurs. Pour toutes les espèces, le contenu organique (poids sec sans cendres par poids sec) était élevé chez les premiers stades copépoditiques. Ceci peut être dû au contenu organique résiduel des œufs riches en lipides conservé par les nauplies qui ne s'alimentent pas. La plus forte croissance chez les femelles a été observée aux stades C5/C6, tandis que la plus forte croissance chez les mâles se situe aux stades C4/C5, tel que déterminé par l'accroissement de la mue et le pourcentage de la croissance en poids. Ces différences de la croissance en poids entre sexes pourraient être dues à la atrophie des appendices buccaux et l'arrêt de la nutrition chez les mâles C6 des copépodes Aetideidae.

Mots clés. — Aetideidae, copépodes mésopélagiques, accroissement de la mue, contenus organiques, longueur du prosome

## INTRODUCTION

In Arctic marine ecosystems, zooplankters are important secondary producers and play important roles in energy transfer for higher trophic-level organisms and vertical material transport (Lowry et al., 2004; Wassmann et al., 2006). Copepods are the most dominant zooplankton taxa in the Arctic Ocean (Thibault et al., 1999; Ashjian et al., 2003). Ecological information on Arctic planktonic copepods is generally available for the dominant surface-dwelling copepod species (e.g., *Pseudocalanus* spp.) and the interzonal, biomass-dominant copepods that have a diapause phase at deeper depths (e.g., *Calanus* spp.). However, the species diversity of copepods is known to be high in the deep sea, especially in mesopelagic zones (Auel & Hagen, 2002; Kosobokova et al., 2011; Smoot & Hopcroft, 2017), and these species have received much less attention.

In the mesopelagic zone of the Arctic Ocean, copepods belonging to Aetideidae are dominant and characterized by high species diversity (Richter, 1995; Markhaseva, 1996; Auel, 1999). Aetideid copepods are omnivores or detritivores, opportunistic feeders, and carnivores (Richter, 1995; Auel, 1999; Sano et al., 2013, 2015). The occurrence of species-specific food preferences (Laakmann et al.,

2009a, b; Sano et al., 2013, 2015) and species-specific vertical segregations within the family (Kosobokova & Hirche, 2000; Auel & Hagen, 2002; Laakmann et al., 2009a; Smoot & Hopcroft, 2017) are well documented. Although the environmental conditions of the deep Arctic Ocean are homogeneous (cold and dark), the coexistence of many aetideid species is thought to have been achieved by vertical displacement of species and food segregation (Laakmann et al., 2009a, b; Laakmann & Auel, 2010). Mesopelagic copepods have been reported to substantially affect vertical material flux to the deep sea by feeding on sinking particles and egesting faecal pellets (Dilling et al., 1998; Wilson et al., 2010). Aetideid copepods in the Greenland Sea consume 40% of the particulate organic carbon flux that reaches their habitat depth (Auel, 1999). These facts suggest that Aetideidae is an important copepod family in the Arctic Ocean because of their high species diversity and ability to affect the vertical distribution of organic carbon.

For mesopelagic copepods, the body length and weight of each copepodid stage and their moult increments reflect their growth rate and time spent at each stage (Yamaguchi & Ikeda, 2000; Yamaguchi et al., 2019, 2020). However, owing to difficulties in species identification, especially in the early copepodid stages, information on the length and weight of each copepodid stage of Aetideidae in the Arctic Ocean is scarce. In addition, developmental changes in length and weight remain unknown.

In this study, we examined a year-round time series of zooplankton samples collected from the drifting ice station at the Surface Heat Budget of the Arctic Ocean (SHEBA) project in the western Arctic Ocean. Using these samples, we recently presented species identification keys on five sympatric aetideid copepods (Koguchi et al., 2022). In this study, we determined the length and weight of five sympatric aetideid species, including all copepodid stages except the C1 and C2 stages of one species (*Aetideopsis rostrata* Sars G.O., 1903). Organic contents (ash-free dry weight fraction within the dry weight) were also determined, and the moult increments and proportions of growth among the stages were calculated and compared. Through inter-species comparisons of the five sympatric aetideid species, we discuss the mechanisms underlying the coexistence of the five species in the mesopelagic layer of the Arctic Ocean.

## MATERIAL AND METHODS

### Field sampling

Zooplankton sampling was conducted at Ice Station SHEBA at 10-14-day intervals from 27 October 1997 to 29 September 1998. Vertically stratified samples were collected using a closing net with a 1-m<sup>2</sup> mouth area equipped with a 150- $\mu$ m or 53- $\mu$ m mesh from two to seven depth layers over a depth range of 0-3500 m. Ice

Station SHEBA drifted from the Canadian Basin to the Mendeleev Basin during the one-year sampling period (Ashjian et al., 2003). Because of this drift, the water depth varied from 352 m to 3800 m during the sampling period. Consequently, collection depths and numbers of layers sampled ranged from 0 to 100 m to 0–3500 m and from two to seven layers, respectively. All zooplankton samples were preserved in seawater with 4% buffered formaldehyde.

### Prosoma length

Using a stereomicroscope, the five dominant aetideid copepods — *Chiridius obtusifrons* Sars G.O., 1902, *Gaetanus tenuispinus* (Sars G.O., 1900), *Gaetanus brevispinus* (Sars G.O., 1900), *Aetideopsis multiserrata* (Wolfenden, 1904), and *A. rostrata* — were sorted, identified, and each copepodid stage was enumerated. While other aetideid species occurred in the samples, we concentrated on the above-mentioned species because of the dominant numbers of individuals. We have published elsewhere details of species identification methods of them down to the C1 stage (Koguchi et al., 2022). Note that no C1 and C2 stages of *A. rostrata* occurred in the samples, because of the deepest occurrence of this species (cf. Koguchi et al., 2022). Based on the presence or absence of leg 5, we identified males and females of C4 and C5. The specimens of each species/stage when they were most abundant in the samples were used for the subsequent length and weight measurements. For details on the abundance of each species/stage in each sample, see Koguchi et al. (2022). The prosoma length (PL) was measured for 5–10 individuals at each copepodid stage under a stereomicroscope using an eyepiece micrometre with a precision of 10  $\mu\text{m}$ .

### Dry and ash-free dry weight

The dry weight (DW) and ash-free dry weight (AFDW) of the five aetideid species were measured at each copepodid stage using formaldehyde-preserved samples. Each copepodid stage of each species was pooled into five duplicate batches, including 2–15 individuals of each stage, selected depending on body weight, rinsed briefly in distilled water, blotted dry using filter paper, and placed in a pre-weighed, pre-combusted aluminium pan. The specimens were dried in an oven at 60°C for 5 h, and the DW was determined using an electronic balance (XP6 Micro Balance; Mettler Toledo, Greifensee, Switzerland) with a precision of 1  $\mu\text{g}$ . The ash weight was determined by reweighing the same samples after combusting them at 480°C for 5 h. The AFDW was then determined based on the difference between DW and ash weight (AFDW = DW – Ash weight). The organic content, expressed as a percentage of AFDW in DW (% DW), was also calculated. Based on the PL, DW, and AFDW data for each copepodid stage, a

length-weight relationship for each species was expressed by the power equation  $W = a \times L^b$ , where  $W$  is the DW or AFDW ( $\mu\text{g}$ ),  $L$  is the PL (mm), and  $a$  and  $b$  are fitted constants. For organic content, differences among copepodid stages of a species, and among the same copepodid stage of different species, were tested using one-way ANOVA. For ANOVA, we confirmed that the normal distribution of each stage ( $n = 5$ ) and the variances of the residuals were at the same levels. We performed ANOVA by using the software StatView.

Based on the PL, DW, and AFDW data, the moult increment (MI; %) was calculated using the following formula (Mauchline, 1998) for all three attributes:

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

To evaluate the proportion of growth at each stage, the proportions of growth (PG; %) at  $C_{n-1}/C_n$  for PL, DW, and AFDW were determined for females and males, and the values of the adults were set as 100% (Yamaguchi et al., 2020).

$$\text{PG}(\%) \text{ at } C_{n-1}/C_n = \sum_{n=1}^6 \frac{(\text{Value of } C_n - \text{Value of } C_{n-1})}{\text{Value of adult (C6)}} \times 100$$

## RESULTS

### Length and weights

The length and weight data at each stage and length-weight relationships based on the power equation for the five sympatric aetideid copepods in the Arctic Ocean are summarized in tables I-X. Within the same genus, the PL varied with the species. For the genus *Gaetanus*, the PLs of *G. brevispinus* were larger than those of *G. tenuispinus* for all copepodid stages. For the genus *Aetideopsis*, *A. rostrata* was larger than *A. multiserrata* for all stages. For all species, the length-weight equations (DW-PL and AFDW-PL) were highly significant ( $r^2 = 0.982 - 0.992$ ,  $p < 0.0001$ ). Inter-species comparison in terms of the weights at the same PL revealed that *Chiridius obtusifrons* was the heaviest, followed by *A. multiserrata*, *A. rostrata*, *G. tenuispinus*, and *G. brevispinus* (fig. 1).

### Organic contents

The mean organic contents of the five aetideid copepods at each copepodid stage are shown in fig. 2. Overall, the organic content ranged between 77.9% and 96.3% of the DW. Within species, the organic content was higher in the early copepodid stages than in the late copepodid stages ( $p < 0.05$ , one-way ANOVA). This ontogenetic pattern for organic content was found among all studied aetideid copepod species studied here. Inter-species differences were detected in seven of the nine stages examined ( $p < 0.05$ , one-way ANOVA).

TABLE I

Summary of prosome length (PL), dry weight (DW), and ash-free dry weight (AFDW) data of *Chiridius obtusifrons* Sars G.O., 1902

| Stage | PL (mm)                 | DW ( $\mu\text{g}$ )      | AFDW ( $\mu\text{g}$ )    |
|-------|-------------------------|---------------------------|---------------------------|
| C1    | 0.77 $\pm$ 0.01<br>(10) | 3.38 $\pm$ 0.38<br>(5)    | 3.62 $\pm$ 0.35<br>(5)    |
| C2    | 1.04 $\pm$ 0.02<br>(10) | 10.61 $\pm$ 0.66<br>(5)   | 9.61 $\pm$ 0.71<br>(5)    |
| C3    | 1.30 $\pm$ 0.02<br>(10) | 23.18 $\pm$ 1.81<br>(5)   | 19.93 $\pm$ 1.78<br>(5)   |
| C4F   | 1.75 $\pm$ 0.03<br>(10) | 63.83 $\pm$ 7.99<br>(5)   | 52.97 $\pm$ 7.21<br>(5)   |
| C4M   | 1.71 $\pm$ 0.04<br>(10) | 50.3 $\pm$ 13.12<br>(5)   | 43.23 $\pm$ 11.13<br>(5)  |
| C5F   | 2.36 $\pm$ 0.03<br>(10) | 161.48 $\pm$ 30.23<br>(5) | 142.28 $\pm$ 27.06<br>(5) |
| C5M   | 2.27 $\pm$ 0.05<br>(10) | 216.38 $\pm$ 33.96<br>(5) | 190.08 $\pm$ 31.11<br>(5) |
| C6F   | 3.08 $\pm$ 0.06<br>(10) | 514.48 $\pm$ 60.26<br>(5) | 446.48 $\pm$ 56.13<br>(5) |
| C6M   | 2.30 $\pm$ .005<br>(10) | 177.28 $\pm$ 12.11<br>(5) | 151.48 $\pm$ 11.31<br>(5) |

Values are represented as mean  $\pm$  1 SD. The numbers of replicates are in parentheses. To analyse the body allometry, the power regression model was used  $Y = a \cdot X^b$ , where  $Y$  is DW or AFDW ( $\mu\text{g}$ ) and  $X$  is PL (mm). F, female; M, male.

### Moult increment

The MIs for length and weight of the five aetideid copepods are shown in fig. 3. Throughout the stages and species, the MI ranged from  $-20.3\%$  to  $339.6\%$ . Common for all species, the MI at C5/C6 varied with sex; the MIs of C5/C6 females were much larger than those of males. For C5/C6 males, minus MI (negative growth) was observed for the DW and AFDW of *C. obtusifrons*, and the PL of *G. brevispinus*.

TABLE II

Regression statistics for body allometry of *Chiridius obtusifrons* Sars G.O., 1902

|                  | DW-PL   | AFDW-PL |
|------------------|---------|---------|
| Constant ( $a$ ) | 9.11    | 8.15    |
| Power ( $b$ )    | 3.55    | 3.50    |
| $r^2$            | 0.99    | 0.99    |
| $p$              | <0.0001 | <0.0001 |

TABLE III

Summary of prosome length (PL), dry weight (DW), and ash-free dry weight (AFDW) data of *Gaetanus tenuispinus* (Sars G.O., 1900)

| Stage | PL (mm)                 | DW ( $\mu\text{g}$ )      | AFDW ( $\mu\text{g}$ )    |
|-------|-------------------------|---------------------------|---------------------------|
| C1    | 0.81 $\pm$ 0.02<br>(10) | 4.12 $\pm$ 0.25<br>(5)    | 3.67 $\pm$ 0.33<br>(5)    |
| C2    | 1.11 $\pm$ 0.02<br>(10) | 7.53 $\pm$ 0.50<br>(5)    | 6.80 $\pm$ 0.48<br>(5)    |
| C3    | 1.41 $\pm$ 0.03<br>(10) | 15.50 $\pm$ 1.12<br>(5)   | 14.00 $\pm$ 0.42<br>(5)   |
| C4F   | 1.95 $\pm$ 0.07<br>(10) | 59.73 $\pm$ 11.74<br>(5)  | 54.73 $\pm$ 10.40<br>(5)  |
| C4M   | 1.89 $\pm$ 0.05<br>(10) | 58.40 $\pm$ 3.04<br>(5)   | 52.88 $\pm$ 4.11<br>(5)   |
| C5F   | 2.52 $\pm$ 0.09<br>(10) | 144.30 $\pm$ 31.95<br>(5) | 126.12 $\pm$ 28.43<br>(5) |
| C5M   | 2.53 $\pm$ 0.04<br>(10) | 153.80 $\pm$ 28.10<br>(5) | 135.72 $\pm$ 26.29<br>(5) |
| C6F   | 3.20 $\pm$ 0.09<br>(10) | 376.40 $\pm$ 57.24<br>(5) | 317.52 $\pm$ 51.14<br>(5) |
| C6M   | 2.73 $\pm$ 0.07<br>(10) | 209.45 $\pm$ 34.92<br>(5) | 185.10 $\pm$ 31.58<br>(5) |

Values are represented as mean  $\pm$  1 SD. The numbers of replicates are in parentheses. To analyse the body allometry, the power regression model was used  $Y = a \cdot X^b$ , where  $Y$  is DW or AFDW ( $\mu\text{g}$ ) and  $X$  is PL (mm). F, female; M = male.

### Proportion of growth

The results of the PG at each copepodid stage, treating the adult value as 100%, are shown in fig. 4. As previously mentioned, PG also showed sex differences in C5/C6. For all weights (DW and AFDW) and species, the PG was the largest in females at C5/C6. Thus, more than half of the PGs were observed at C5/C6. In contrast, in males, the PGs were small at C5; the PGs were the largest at C4/C5, rather than those at C5/C6.

TABLE IV

Regression statistics for body allometry of *Gaetanus tenuispinus* (Sars G.O., 1900)

|                  | DW-PL   | AFDW-PL |
|------------------|---------|---------|
| Constant ( $a$ ) | 6.31    | 5.71    |
| Power ( $b$ )    | 3.42    | 3.39    |
| $r^2$            | 0.99    | 0.99    |
| $p$              | <0.0001 | <0.0001 |

TABLE V

Summary of prosome length (PL), dry weight (DW), and ash-free dry weight (AFDW) data of *Gaetanus brevispinus* (Sars G.O., 1900)

| Stage | PL (mm)                 | DW ( $\mu\text{g}$ )      | AFDW ( $\mu\text{g}$ )    |
|-------|-------------------------|---------------------------|---------------------------|
| C1    | 1.03 $\pm$ 0.02<br>(10) | 9.27 $\pm$ 0.58<br>(5)    | 8.61 $\pm$ 0.73<br>(5)    |
| C2    | 1.35 $\pm$ 0.02<br>(10) | 14.51 $\pm$ 1.33<br>(5)   | 13.20 $\pm$ 1.38<br>(5)   |
| C3    | 1.85 $\pm$ 0.03<br>(10) | 50.23 $\pm$ 3.83<br>(5)   | 45.05 $\pm$ 3.37<br>(5)   |
| C4F   | 2.47 $\pm$ 0.04<br>(10) | 108.63 $\pm$ 11.48<br>(5) | 97.02 $\pm$ 11.79<br>(5)  |
| C4M   | 2.44 $\pm$ 0.03<br>(10) | 113.17 $\pm$ 9.98<br>(5)  | 98.15 $\pm$ 9.57<br>(5)   |
| C5F   | 3.12 $\pm$ 0.04<br>(10) | 284.65 $\pm$ 26.07<br>(5) | 234.12 $\pm$ 27.37<br>(5) |
| C5M   | 3.08 $\pm$ 0.06<br>(10) | 317.15 $\pm$ 56.60<br>(5) | 247.83 $\pm$ 48.11<br>(5) |
| C6F   | 3.83 $\pm$ 0.09<br>(10) | 557.75 $\pm$ 39.01<br>(5) | 474.80 $\pm$ 38.01<br>(5) |
| C6M   | 3.07 $\pm$ 0.06<br>(10) | 345.35 $\pm$ 54.89<br>(5) | 304.10 $\pm$ 47.34<br>(5) |

Values are represented as mean  $\pm$  1 SD. The numbers of replicates are in parentheses. To analyse the body allometry, the power regression model was used  $Y = a \cdot X^b$ , where  $Y$  is DW or AFDW ( $\mu\text{g}$ ) and  $X$  is PL (mm). F, female; M, male.

## DISCUSSION

## Length, weights, and organic contents

This study established length (PL)-weight (DW and AFDW) equations for five aetideid copepod species in the Arctic Ocean. In the inter-species comparison, weights at the same PLs were the largest for *Chiridius obtusifrons*, followed by the genus *Aetideopsis* spp., whereas *Gaetanus* spp. was the lightest (fig. 1). In the Arctic Ocean, the vertical distribution of these aetideid copepods varied with species, from shallow to deep in the order of *C. obtusifrons* (shallowest) < *G.*

TABLE VI

Regression statistics for body allometry of *Gaetanus brevispinus* (Sars G.O., 1900)

|                  | DW-PL   | AFDW-PL |
|------------------|---------|---------|
| Constant ( $a$ ) | 6.66    | 6.24    |
| Power ( $b$ )    | 3.31    | 3.22    |
| $r^2$            | 0.99    | 0.99    |
| $p$              | <0.0001 | <0.0001 |



TABLE VII

Summary of prosome length (PL), dry weight (DW), and ash-free dry weight (AFDW) data of *Aetideopsis multiserrata* (Wolfenden, 1904)

| Stage | PL (mm)                 | DW ( $\mu\text{g}$ )      | AFDW ( $\mu\text{g}$ )    |
|-------|-------------------------|---------------------------|---------------------------|
| C1    | 0.73 $\pm$ 0.02<br>(10) | 2.78 $\pm$ 0.27<br>(5)    | 2.68 $\pm$ 0.25<br>(4)    |
| C2    | 0.98 $\pm$ 0.03<br>(10) | 5.81 $\pm$ 0.58<br>(5)    | 5.60 $\pm$ 0.57<br>(5)    |
| C3    | 1.20 $\pm$ 0.03<br>(10) | 11.36 $\pm$ 1.73<br>(5)   | 10.35 $\pm$ 1.66<br>(5)   |
| C4F   | 1.58 $\pm$ 0.04<br>(10) | 30.82 $\pm$ 6.78<br>(5)   | 27.67 $\pm$ 5.88<br>(5)   |
| C4M   | 1.59 $\pm$ 0.03<br>(10) | 37.42 $\pm$ 4.13<br>(5)   | 33.07 $\pm$ 4.24<br>(5)   |
| C5F   | 2.08 $\pm$ 0.07<br>(10) | 108.83 $\pm$ 15.02<br>(5) | 89.00 $\pm$ 11.85<br>(5)  |
| C5M   | 2.13 $\pm$ 0.07<br>(10) | 98.68 $\pm$ 29.60<br>(5)  | 85.60 $\pm$ 27.74<br>(5)  |
| C6F   | 2.64 $\pm$ 0.10<br>(10) | 273.77 $\pm$ 93.21<br>(5) | 232.90 $\pm$ 82.77<br>(5) |
| C6M   | 2.18 $\pm$ 0.04<br>(10) | 109.67 $\pm$ 13.39<br>(5) | 95.40 $\pm$ 12.31<br>(5)  |

Values are represented as mean  $\pm$  1 SD. The numbers of replicates are in parentheses. To analyse the body allometry, the power regression model was used  $Y = a \cdot X^b$ , where  $Y$  is DW or AFDW ( $\mu\text{g}$ ) and  $X$  is PL (mm). F, female; M, male.

*tenuispinus* < *G. brevispinus* < *A. multiserrata* < *A. rostrata* (deepest) (Richter, 1994; Laakmann et al., 2009a; Smoot & Hopcroft, 2017). This vertical distribution order was also observed for the SHEBA samples treated in this study (Koguchi et al., 2022). Notably, the weights were higher for shallower dwelling species under the same PL conditions within the same genus. Within the same stages, the organic content (% DW) was higher for the shallower dwelling species than for the deeper dwelling ones. This pattern was the most prominent, especially in the late copepodid stages (fig. 2). The weight per length and organic content

TABLE VIII

Regression statistics for body allometry data of *Aetideopsis multiserrata* (Wolfenden, 1904)

|                  | DW-PL   | AFDW-PL |
|------------------|---------|---------|
| Constant ( $a$ ) | 6.90    | 6.47    |
| Power ( $b$ )    | 3.61    | 3.49    |
| $r^2$            | 0.99    | 0.99    |
| $p$              | <0.0001 | <0.0001 |

TABLE IX

Summary of prosome length (PL), dry weight (DW), and ash-free dry weight (AFDW) data of *Aetideopsis rostrata* Sars G.O., 1903

| Stage | PL (mm)                 | DW ( $\mu\text{g}$ )      | AFDW ( $\mu\text{g}$ )    |
|-------|-------------------------|---------------------------|---------------------------|
| C3    | 1.50 $\pm$ 0.05<br>(10) | 29.51 $\pm$ 4.50<br>(5)   | 26.20 $\pm$ 4.83<br>(5)   |
| C4F   | 1.98 $\pm$ 0.07<br>(10) | 83.02 $\pm$ 5.54<br>(5)   | 69.92 $\pm$ 4.22<br>(5)   |
| C4M   | 2.21 $\pm$ 0.05<br>(10) | 110.08 $\pm$ 13.33<br>(5) | 93.12 $\pm$ 11.79<br>(5)  |
| C5F   | 2.64 $\pm$ 0.19<br>(10) | 154.12 $\pm$ 33.73<br>(5) | 126.38 $\pm$ 31.41<br>(5) |
| C5M   | 3.09 $\pm$ 0.06<br>(10) | 335.83 $\pm$ 77.69<br>(5) | 284.07 $\pm$ 68.50<br>(5) |
| C6F   | 3.34 $\pm$ 0.07<br>(10) | 402.58 $\pm$ 38.59<br>(5) | 323.20 $\pm$ 36.35<br>(5) |
| C6M   | 3.34 $\pm$ 0.11<br>(5)  | 481.75 $\pm$ 88.66<br>(4) | 409.50 $\pm$ 79.65<br>(4) |

Values are represented as mean  $\pm$  1 SD. The numbers of replicates are in parentheses. To analyse the body allometry, the power regression model was used  $Y = a \cdot X^b$ , where  $Y$  is DW or AFDW ( $\mu\text{g}$ ) and  $X$  is PL (mm). F, female; M, male.

may reflect the nutritional conditions (Yamaguchi et al., 2019, 2020). Since food resources are limited in the deep sea and are supplied from the upper layer, the nutritional supply within the same genus is expected to be higher for shallower-dwelling species than for deep-dwelling species (Yamaguchi et al., 2002, 2019). Thus, the heavier weights per length and higher organic content observed in the shallow-dwelling species within the genera *Gaetanus* and *Aetideopsis* may reflect a greater food availability to the shallower-dwelling species than to the deeper-distributed species.

Ontogenetic changes in the organic content within species were common for Aetideidae, with high organic contents (90-95% DW) at early copepodid stages and a diminution during development toward approximately 85% DW in adult females (fig. 2). This reflects the lipid-rich eggs of Aetideidae. In the Arctic

TABLE X

Regression statistics for body allometry of *Aetideopsis rostrata* Sars G.O., 1903

|                  | DW-PL   | AFDW-PL |
|------------------|---------|---------|
| Constant ( $a$ ) | 7.84    | 7.05    |
| Power ( $b$ )    | 3.30    | 3.23    |
| $r^2$            | 0.99    | 0.98    |
| $p$              | <0.0001 | <0.0001 |

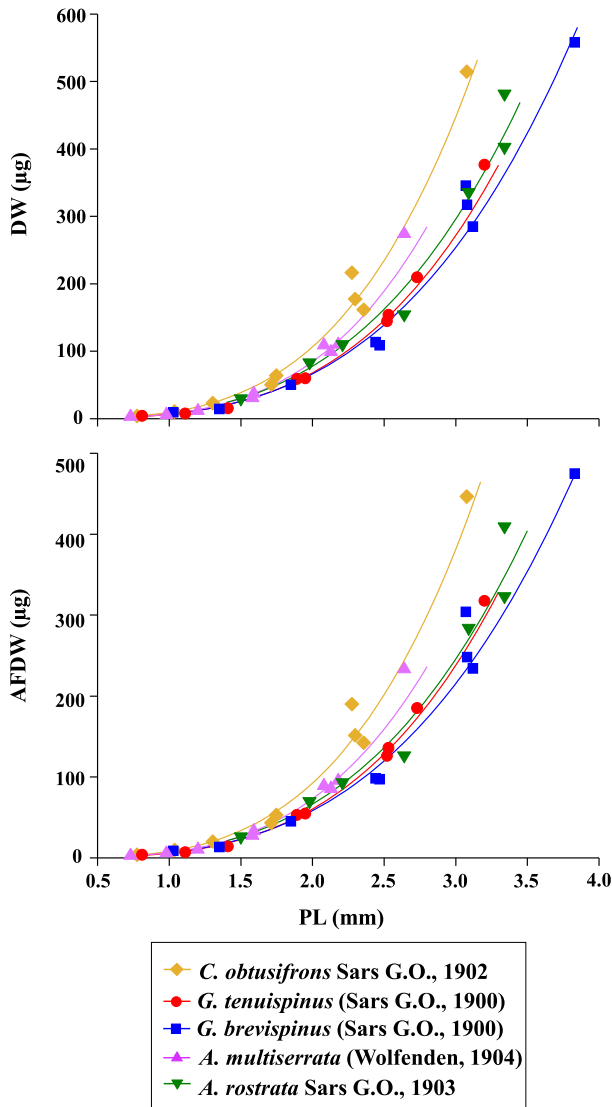


Fig. 1. Relationships between dry weight (DW) and prosome length (PL) (upper) and ash-free dry weight (AFDW) and PL (lower) for the five dominant aetideid copepods in the western Arctic Ocean: *Chiridius obtusifrons* Sars G.O., 1902, *Gaetanus tenuispinus* (Sars G.O., 1900), *Gaetanus brevispinus* (Sars G.O., 1900), *Aetideopsis multiserrata* (Wolfenden, 1904), and *Aetideopsis rostrata* Sars G.O., 1903. For details of the regressions, see tables II, IV, VI, VIII and X.

Ocean, the aetideid copepods spawn a small number of large eggs that are thought to be able to develop without feeding during the naupliar stage (Kosobokova et al., 2007). Naupliar development without feeding has been reported during the laboratory rearing of *Gaetanus variabilis* (Brodsky, 1950) (currently considered

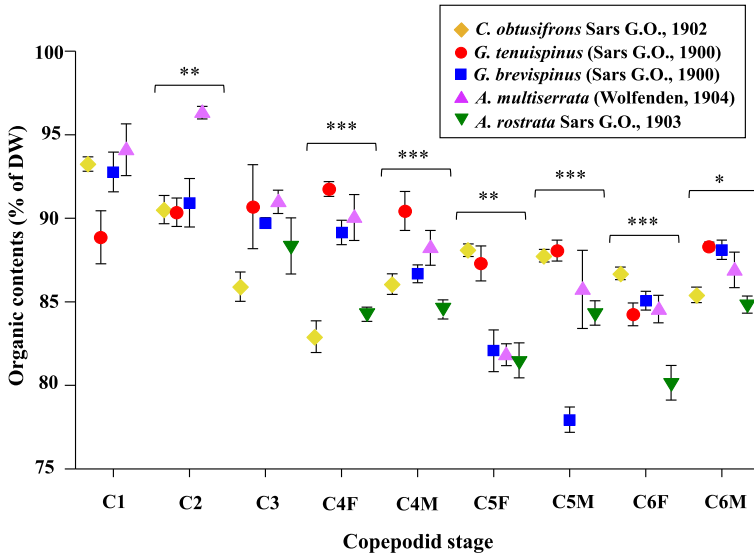


Fig. 2. Organic contents (% of DW) of the five dominant aetideid copepods in the western Arctic Ocean: *Chiridius obtusifrons* Sars G.O., 1902, *Gaetanus tenuispinus* (Sars G.O., 1900), *Gaetanus brevispinus* (Sars G.O., 1900), *Aetideopsis multiserrata* (Wolfenden, 1904), and *Aetideopsis rostrata* Sars G.O., 1903, at each copepodid stage. Symbols and bars represent means and standard errors, respectively. F, female; M, male. Inter-species differences were tested by one-way ANOVA for each stage. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

a synonym and referred to as *Gaetanus minutus* (Sars G.O., 1907)), a dominant aetideid copepod found in the mesopelagic zone of the western subarctic Pacific (Yamaguchi & Ikeda, 2000). As a reproduction characteristic of mesopelagic copepods, spawning with a small number of large-sized eggs rich in lipids is well documented (Mauchline, 1998). Hence, the high organic content in the early copepodid stages observed in this study may result from the residual organic content of lipid-rich eggs carried through the naupliar phase and into the early copepodids.

#### Moult increment / proportion of growth

A common feature observed for the MI and PG of the five aetideid species was sexual differences at the C5/C6 stages. Thus, the MI was the greatest for females between C5/C6 but almost non-existent for males at the same stage (fig. 3). For PG, more than half of the growth of females occurred by C5/C6, especially of body weight, but showed extremely low proportions in males (fig. 4). These sex differences in weight growth may result from the degeneration of the feeding appendages and cessation of feeding in C6 male aetideid copepods (Ohtsuka & Huys, 2001; Yamaguchi et al., 2005, 2007). The longevity of the C6 males after

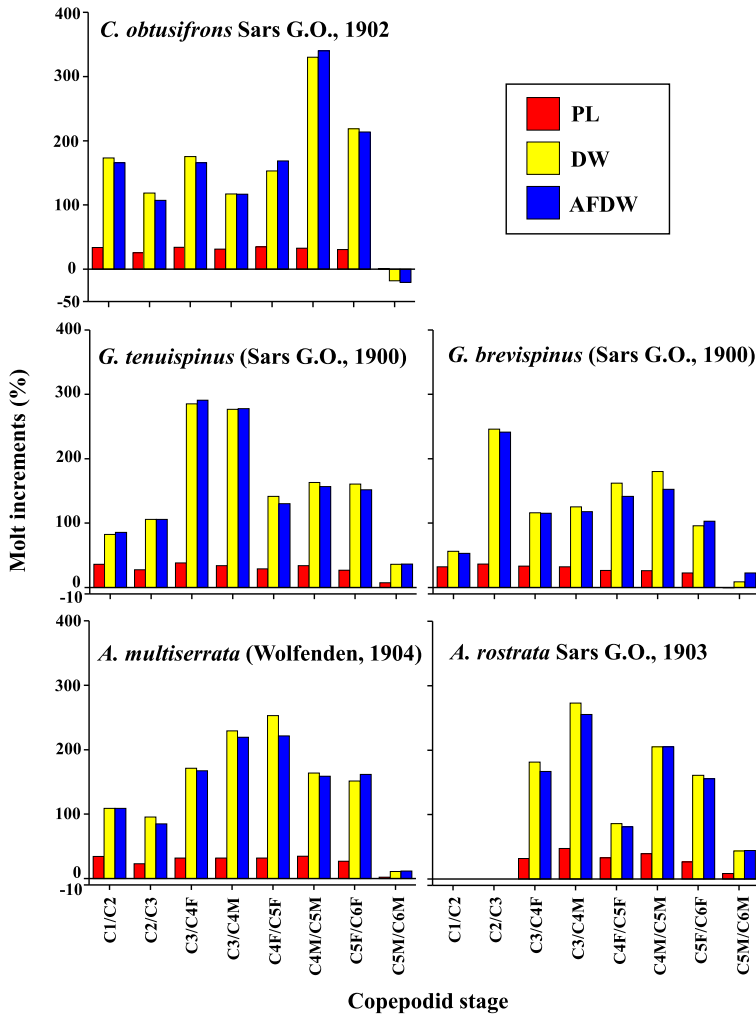


Fig. 3. Molt increments (MI) in prosome length (PL) and body weights (DW: dry weight, AFDW: ash-free dry weight) of the five dominant aetideid copepods in the western Arctic Ocean: *Chiridius obtusifrons* Sars G.O., 1902, *Gaetanus tenuispinus* (Sars G.O., 1900), *Gaetanus brevispinus* (Sars G.O., 1900), *Aetideopsis multiserrata* (Wolfenden, 1904), and *Aetideopsis rostrata* Sars G.O., 1903. F, female; M, male.

cessation of feeding is expected to be short. This is confirmed by the extremely low abundance of C6 males in the field populations (Yamaguchi & Ikeda, 2000). An extremely low abundance of C6 males in the field was also observed in the western Arctic Ocean in this study (Koguchi et al., 2022).

The PG in weight may depend on the time spent at each copepodid stage (Yamaguchi et al., 2020, 2022). Thus, females undergo more than half of the PG in their lifetime at the C5/C6 stage and are considered to spend a longer time at

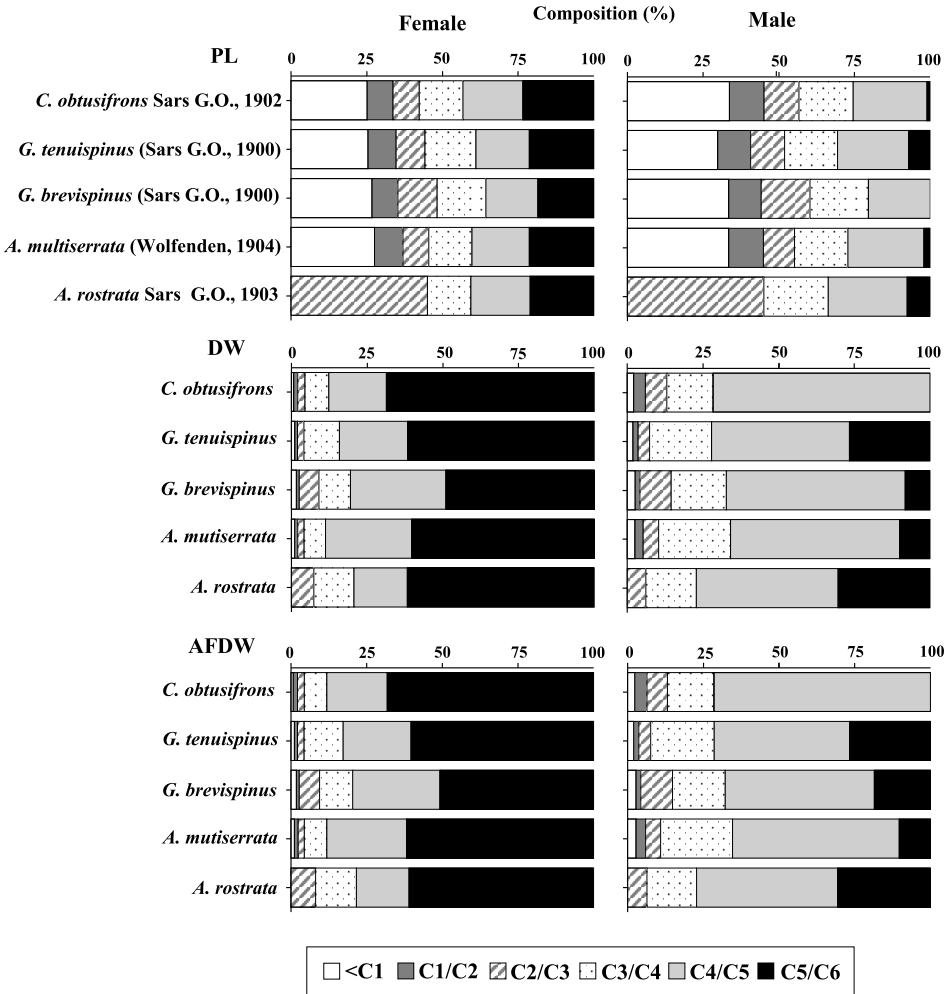


Fig. 4. The proportion of growth (PG) in prosome length (PL) and weights (dry weight (DW) and ash-free dry weight (AFDW)) at each stage, which is calculated by the C6 values as 100% for the five dominant arctideid copepods in the western Arctic Ocean: *Chiridius obtusifrons* Sars G.O., 1902, *Gaetanus tenuispinus* (Sars G.O., 1900), *Gaetanus brevispinus* (Sars G.O., 1900), *Aetideopsis mutiserrata* (Wolfenden, 1904), and *Aetideopsis rostrata* Sars G.O., 1903. Note that C1 and C2 were not available for *Aetideopsis rostrata*; their C2/C3 stage is treated as <math><C\_3</math>.

C6. In contrast, the highest PG was observed for males at C4/C5, suggesting that males spend a long time in the field at C5. These facts indicate that there are sex differences in the stages with the longest residence time: C6 in females and C5 in males. The longer time females spend at C6 may allow them to promptly adapt to the initiation of reproduction and changes in food availability (Yamaguchi & Ikeda, 2000; Yamaguchi et al., 2020).

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