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

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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

28 Introduction

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

38 Some mesopelagic and bathypelagic copepods are known to exhibit a specialized OVM
39 pattern, being found at shallower depths as their developmental stages progress (i.e.,
40 developmental ascent) (Yamaguchi et al., 2004 and references therein). The approximate ranges
41 of this specialized OVM are reported to be 300-600 m (Yamaguchi et al., 2004), which is
42 comparable but opposite to the normal OVM patterns of the Calanidae copepods. Specialized
43 OVMs have been observed for a number of species (Morioka, 1975; Weikert and Koppelman,
44 1993; Richter, 1994; Falkenhaus et al., 1997; Yamaguchi et al., 2004). These species include both
45 suspension feeders (e.g., *Chiridius armatus*, *Chiridius obtusifrons*, *Gaetanus variabilis*, *Lucicutia*
46 *longicauda*, *Metridia asymmetrica*, and *Metridia curticauda*) and predatory feeders (e.g.,
47 *Paraeuchaeta elongata*, *Paraeuchaeta birostrata*, and *Paraeuchaeta rubra*) (Ohtsuka and
48 Nishida, 1997). The driver for this specialized OVM pattern in meso- and bathypelagic copepods
49 is poorly understood, especially since limited information on these species is available. Whether
50 the specialized OVMs of meso- and bathypelagic copepods are related to season is unknown.

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

55

56 Methods

57 The data or samples from two previous expeditions were available for detailed
58 examination. In the western Arctic Ocean, the samples had been collected during the year-long
59 Surface Heat Budget of the Arctic Ocean (SHEBA) expedition (e.g., Ashjian et al., 2003).
60 Stratified vertical hauls from a 1 m² mouth area opening-closing net equipped with a 53 µm or
61 150 µm mesh were made from just above the sea floor and at shallower levels (e.g., 0–50 m, 50–
62 100 m, 100–200 m, 200–1,500 m, and 1,500–2,800 m) for daytime hours at 10-14 day intervals
63 (a total of 30 sampling dates) as the SHEBA ice station drifted through the Canada Basin to the
64 Mendeleyev Basin (74°41'N-80°15'N, 143°55'W-168°00'W) from 27 October 1997 to 29
65 September 1998 (Ashjian et al., 2003). Although these samples previously had been examined to
66 enumerate the dominant zooplankton types, less abundant species were under-quantified during
67 the original analysis. In the present analysis, whole samples (rather than splits) were re-examined
68 for the abundances of rarer species. In the western subarctic Pacific, samples were collected
69 during a study in the Oyashio region (41°30'N-42°30'N, 145°00'E-146°00'E; Yamaguchi and
70 Ikeda, 2002). Stratified vertical hauls with a 60-cm diameter opening-closing net equipped with
71 a 100 µm mesh were made down to 2,000 m (0–the bottom of thermocline (Th), Th–250 m, 250–
72 500 m, 500–1,000 m, 1,000–2,000 m) at monthly intervals (a total of 15 dates) from 4 September
73 1996 to 5 October 1997. For both studies, the samples were preserved with 4-5% buffered
74 formalin-seawater. The annual mean vertical profiles of temperature at each region were
75 calculated from CTD casts.

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

80
$$D_{50\%} = d_1 + d_2 \times \frac{50-p_1}{p_2}$$

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

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

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

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

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

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

103

104 Results

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

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

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

128 For both *P. glacialis* and *P. elongata*, the MIs of all life stages based on all three
129 measures (wet mass, dry mass, and ash free dry mass) were correlated with the annual mean $D_{50\%}$
130 of the post-moult stages ($r^2 = 0.686-0.847$, $p < 0.01$) (Fig. 2). The regressions between MI and $D_{50\%}$
131 in the form of power functions showed no differences between species (ANCOVA; $F_{1,42} = 0.004$,
132 $p = 0.95$) and units (ANCOVA; $F_{2,42} = 0.859$, $p = 0.43$) and showed no interaction between species
133 and units (ANCOVA; $F_{2,42} = 0.238$, $p = 0.79$); thus, based on all data for MI (%) and $D_{50\%}$ (m), the
134 overall regression was computed as:

135 $MI = 313329 D_{50\%}^{-1.414}$ ($r^2 = 0.648$, $p < 0.0001$).

136

137 Discussion

138 Day-night differences in depth distributions

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

155

156 Ontogenetic vertical migration (OVM)

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

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

167 avoid predation pressure in surface layers during the food-scarce season, when little food is
168 available to mitigate the risk of predation (Miller et al., 1984; Conover, 1988). Even for
169 *Paraeuchaeta* spp., the early life stages (eggs, nauplii, and early copepodids) may be vulnerable
170 to predation in the surface layers and thus avoid predation by remaining deeper. In addition, the
171 ovigerous (egg-carrying) *Paraeuchaeta* C6F do not perform DVM and remain in a deeper layer
172 throughout the day, presumably to avoid predation while carrying eggs (Bollens and Frost, 1991;
173 Vestheim et al., 2001). Since the fecundity of *Paraeuchaeta* spp. is low (*K*-selection) (Mauchline,
174 1998; Auel, 2004), remaining in a deeper layer during the reproductive (C6F/M) and early
175 developmental stages (C1, C2), when vulnerable to predation, may be an adaptive trait to reduce
176 mortality due to predation. In the Arctic Ocean, recent ice melt is expected to increase visual
177 predation pressure from pelagic fish by increasing light penetration in the open ocean (Varpe et
178 al., 2015; Langbehn and Varpe, 2017; Kaartvedt and Titelman, 2018). From this point of view,
179 the predation-induced OVM pattern of the Arctic *P. glacialis* may be altered in the environmental
180 conditions of the near future, but it is of note that the OVM pattern was strong even for the
181 subarctic *P. elongata*.

182

183 Moulting increments (MI)

184 For both *P. glacialis* and *P. elongata*, the MIs were greatest at the transition from C4 to C5 (Fig.
185 1b). This observation contrasts with a previous study in the Japan Sea in which the MI of *P.*
186 *elongata* was reported to peak at an earlier stage transition (C3/C4) and at a higher MI (550% in
187 DM) (Morioka, 1975; Ikeda and Hirakawa, 1996) than seen here. This regional difference in stage
188 specific maximum MI may have occurred because the C3 stage was found at the shallowest depth
189 in the Japan Sea (Morioka, 1975), while stages C3-C5 were found at shallowest depths for both
190 species and regions studied here. The negative mass growth in E/N (Fig. 1b) likely occurred
191 because the naupliar development of *Paraeuchaeta* spp. does not require food (Ikeda and
192 Hirakawa, 1996; Ozaki and Ikeda, 1997). The observed limited mass growth of the older male
193 stages C5M/C6M of both species (Fig. 1b) may result from cessation of feeding accompanied by
194 degeneration of the feeding appendages in C6M of *Paraeuchaeta* spp. (Campbell, 1934) (Fig. 1b).

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

200

201 Relationship between MI and OVM

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

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

220

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316 Figure captions

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

326

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

331

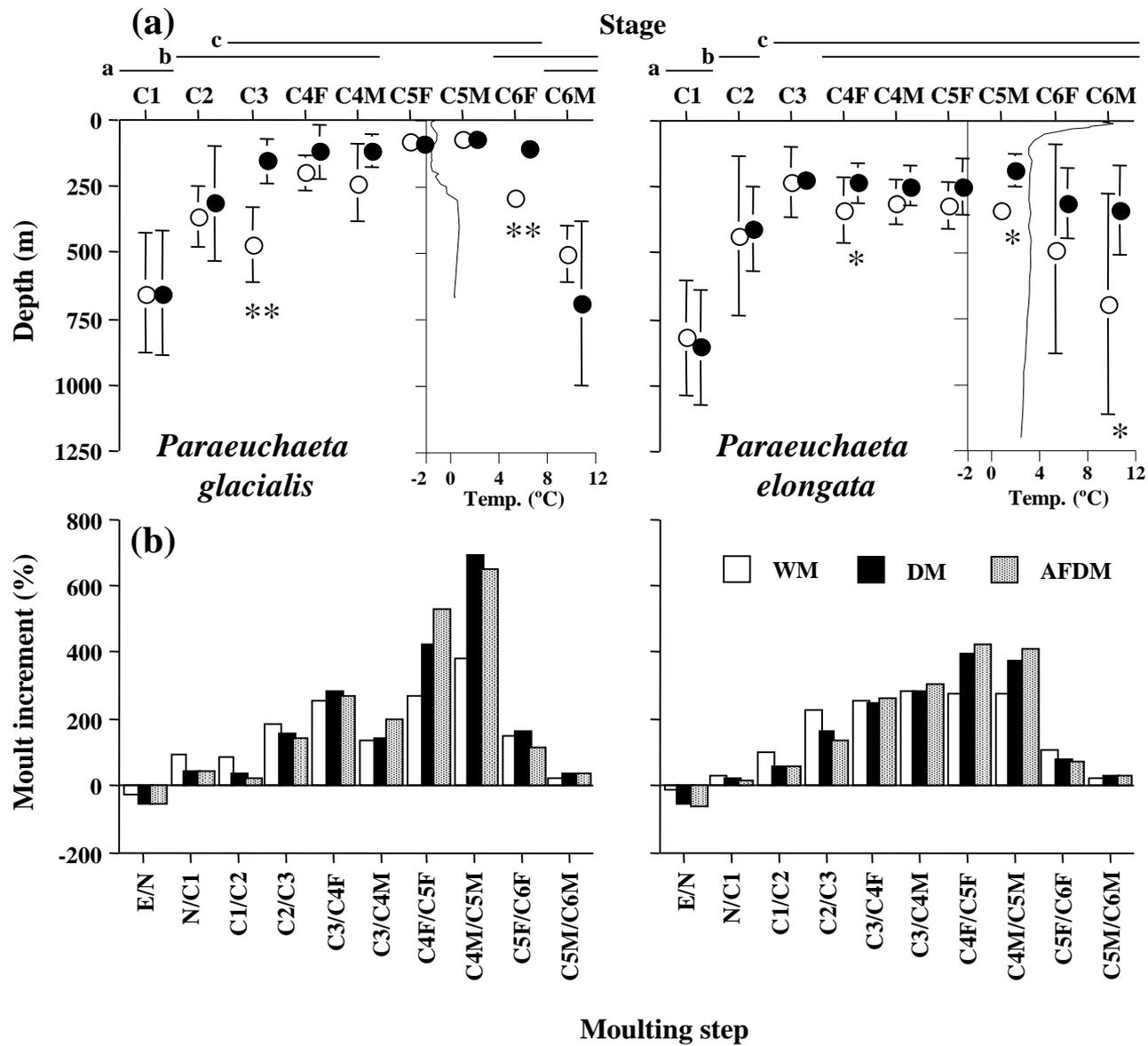


Fig. 1

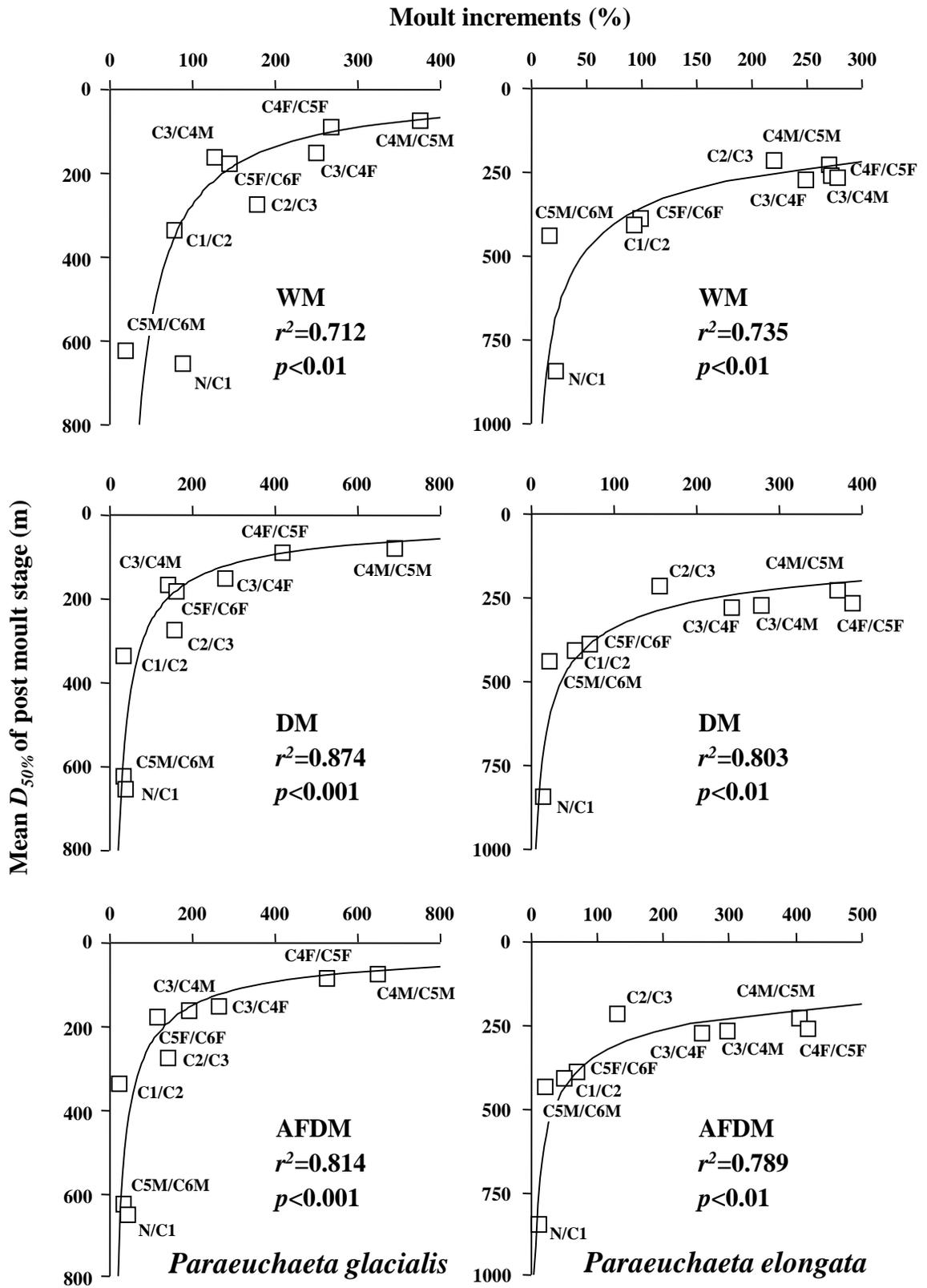


Fig. 2