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LIFE HISTORY AND PRODUCTION OF PELAGIC MYSIDS AND DECAPODS IN THE
OYASHIO REGION, JAPAN

BY

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Short title: LIFE HISTORY OF PELAGIC MYSIDS AND DECAPODS

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ABSTRACT

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Pelagic Mysidacea and Decapoda have important roles in marine ecosystems. However, information on their life histories is extremely limited. This study aimed to evaluate the life cycles of pelagic Mysidacea and Decapoda in the Oyashio region, Japan. Production of the four dominant species was estimated by combining body mass (DM) data and abundance data. Mysidacea belonging to 5 species from 5 genera occurred in the study area. Their abundance and biomass ranged between 11.7-50.1 ind. m⁻² and 1.2-7.9 g WM (Wet Mass) m⁻², respectively. Decapoda belonged to 6 species from 6 genera, and their abundance and biomass ranged between 9.0-17.3 ind. m⁻² and 3.0-17.3 g WM m⁻², respectively. Based on body length histograms, there were two to four cohorts for the three dominant mysids and one dominant decapod on each sampling date. Life histories of the two numerically dominant mysids (*Eucopia australis* and *Boreomysis californica*) followed similar patterns: recruitment of young in May, strong growth from April to June, and a longevity of three years. Life cycles of the two minor species (the mysid *Meterythrope microphthalmus* and the decapod *Hymenodora frontalis*) were not clear because of their low abundance. The timing of recruitment of the young and the strong juvenile growth for the two dominant mysids corresponds with the season when their prey is abundant. The annual production of the dominant mysid species was 14.0 mg DM m⁻² (*B. californica*) and 191.8 mg DM m⁻² (*E. australis*). Annual *P/B* (Production/Biomass) ratios ranged between 0.242 (*H. frontalis*) and 0.643 (*M. microphthalmus*). Compared with other regions, the Oyashio region showed high production and low *P/B* ratios. The high production in the Oyashio region may be related to the high biomass of these species. Because of the low temperature conditions (3°C), pelagic mysids and decapods in the Oyashio region may have slower growth, longer generation times and lower *P/B* ratios than in other oceans.

INTRODUCTION

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Pelagic Mysidacea and Decapoda are classified either as micronekton by strong swimming ability, or macrozooplankton by body size (Marshall, 1954). There are about 1000 species of Mysidacea that have been described from the world oceans, and about 200 species have been reported to occur in waters off Japan (Fukuoka, 2001). Most Mysidacea inhabit the coastal zone or benthopelagic layer, with a few species living in the pelagic zone, and ca. 50 mysids have been reported from the meso- and bathypelagic zone of the North Pacific (Mauchline & Murano, 1977). There are about 2600 species of Decapoda that have been described worldwide. Pelagic shrimp comprise ca. 270 species, which are found from coastal to oceanic regions and from the surface to deep-sea waters. About 120 species have been reported from waters around Japan (Iwasaki, 2001). Pelagic Mysidacea and Decapoda feed mainly on mesozooplankton (Foxton & Roe, 1974; Mauchline, 1980; Heffernan & Hopkins, 1981; Burghart et al., 2010), and are preyed upon by various large fishes (Mauchline & Gordon, 1980; Astthorsson, 1985; Gordon & Duncan, 1987). Thus, they have an important trophic role in marine ecosystems. The ecologies of pelagic Mysidacea and Decapoda have been summarized by Mauchline (1980) and Omori (1974), respectively.

From waters off Japan, Mysidacea and Decapoda are reported to be a food item of Pacific cod *Gadus macrocephalus* Tilesius, 1810 in the Doto area (eastern Hokkaido), flathead flounder *Hippoglossoides dubius* Schmidt, 1904 in Funka Bay, and walleye pollock *Theragra chalcogramma* (Pallas, 1814) in the Doto area and the Sea of Japan (Yamamura et al., 1993; Kooka et al., 1997; Yamamura et al., 2002; Kimura et al., 2004). The biomass of crustacean micronekton in the Oyashio region is 10% of that of mesozooplankton, yet is greater than that of fish micronekton (Ikeda et al., 2008). This information suggests that the crustacean micronekton may have an important role in the marine ecosystems in waters off Japan. Previous studies on the ecology of pelagic Mysidacea and Decapoda around Japan

66 report on vertical and horizontal distribution (Aizawa, 1974) and the biology and ecology of
67 the sergestid shrimp *Sergia lucens* (an important fishery target) in Suruga Bay (Omori,
68 1969). However, information on life history is limited to only one mysid in the Japan Sea
69 (Ikeda, 1992), and one decapod in Suruga Bay (Omori, 1969). Thus, despite the importance
70 of crustacean micronekton, information on their life history is scarce.

71 The present study aimed to evaluate community structure and life cycles of dominant
72 crustacean micronekton of Mysidacea and Decapoda in the Oyashio region, western subarctic
73 Pacific. To accurately evaluate life histories of these animals, samples were collected using a
74 fine mesh net (0.35 mm) that effectively captured small individuals and caused less damage
75 to larger individuals. In addition to population structure, production was estimated by
76 combining life history data and body mass data. The results were compared with information
77 from other regions, and the biological features of the crustacean micronekton in the Oyashio
78 region are discussed.

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MATERIAL AND METHODS

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Field sampling

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Zooplankton samples (oblique tow of Bongo nets [70 cm mouth diameter, 0.35 mm
mesh size] from 1000 m depth) were collected at Site H (41°22'N-41°32'N
145°41'E-146°10'E, fig. 1) in the Oyashio region at one to four month intervals from August
2002 to August 2003. Vertical tows of a Norpac net (45 cm mouth diameter, 0.33 mm mesh
size) from 500 m to surface and 150 m to surface were also conducted on each sampling
occasion. After collection, all the samples were preserved immediately in 5% borax-buffered
formalin-seawater. Temperature and salinity data were collected in conjunction with all
zooplankton samples using a CTD (SBE-9 plus, Sea Bird Electronics). Water samples for
chlorophyll *a* were collected with Niskin bottles from 12 depths between 0 and 150 m,

91 filtered through Whatman GF/F filters, extracted in 90% acetone in the dark for 24 hours, and
92 processed using a Turner Design fluorometer.

93

94 Identification and body length measurement

95 From Bongo net samples, Mysidacea and Decapoda were sorted from the entire
96 sample and enumerated with the aid of a dissecting microscope. Species identifications were
97 based on Chihara & Murano (1996), Li (1964), Murano (1999) and Hayashi (2007, 2009).
98 Based on morphology, individuals were sorted by developmental stage. Five stages were
99 identified: larvae, juvenile, adult male, adult female and ovigerous female.

100 For all specimens, body length (BL: distance between the tip of the rostrum and the
101 distal uropod endopodite of the straightened body) were measured with the aid of an ocular
102 micrometer with the precision of 0.25 mm. To evaluate generation length of Mysidacea and
103 Decapoda, cohort analysis was used to separate the normal distribution of BL frequency at
104 each sampling date. Cohort analysis was based on BL histograms using 1 mm bins.
105 Separation of the normal distribution of BL was done using MS-Excel solver (Aizawa &
106 Takiguchi, 1999).

107 Based on mean BL of each cohort, growth in BL was expressed with the von
108 Bertalanffy equation:

$$109 \quad BL_t = BL_{max}(1 - e^{-K[t-t_0]}) \quad (1)$$

110 where, t is age (year), BL_t is BL (mm) at age t . The Von Bertalanffy equation includes 3
111 parameters (BL_{max} , K and t_0), BL_{max} is maximum BL, K is growth factor and t_0 is age when the
112 BL is 0. Analysis of the von Bertalanffy equation was also conducted using MS-Excel solver
113 (Gorie, 2001).

114

115 Mass measurements

116 Mass measurements were conducted in the laboratory on land. Norpac net samples
117 composed of mesozooplankton were filtered through pre-weighed 100 µm mesh, and wet
118 mass (WM) was measured with an electronic balance. WM for 150-500 m was determined by
119 subtracting the 0-150 m WM data (g WM m⁻²) from the 0-500 m data. WM of Mysidacea and
120 Decapoda was measured for each species based on Bongo net samples.

121 For the dominant species; three species of Mysidacea (*Eucopia australis* Dana, 1852,
122 *Boreomysis californica* Ortmann, 1894 and *Meterythrops microphthalma* W. Tattersall, 1951)
123 and one species of Decapoda (*Hymenodora frontalis* Rathbun, 1902), BL-mass relationships
124 and BL-water or BL-organic contents were evaluated. For each species, WM, dry mass (DM)
125 and ash-free dry mass (AFDM) were determined for 42 individuals from various BL and
126 developmental stages. An aluminum pan was combusted at 480°C for 3 hours to remove
127 organic matter and weighed with a precision of 1 µg using a microbalance (Mettler
128 Electronics). WM was determined from preserved specimens after rinsing briefly in distilled
129 water and blotting on aluminum pan. Specimens were dried in a drying oven (60°C) for 6
130 hours, and the DM was measured. Ash was determined after incineration at 480°C for 6 hours.
131 AFDM was determined by subtracting Ash from DM (AFDM = DM - Ash). Relationship
132 between BL and body mass is expressed by the following equation:

$$133 \quad \text{Log}_{10}[\text{WM, DM or AFDM (mg)}] = a \times \text{Log}_{10}[\text{BL (mm)}] + b \quad (2)$$

134 where a and b are fitted constants. Water content (Water: %WM = 100 x [WM - DM] / WM)
135 and AFDM content (AFDM: %DM = 100 x [DM - Ash] / DM) were also calculated.

136

137 Production estimation

138 Based on the mean BL of each cohort, individual DM (W , mg DM ind.⁻¹) was
139 calculated based on the BL-DM equation. Growth of individual DM with time was expressed
140 with the equation ($\text{Log}_{10}W = at + b$, where a and b are fitted constants, and t is year). Based

141 on the normal distribution of the BL histogram, abundance (N , ind. m^{-2}) of each cohort was
142 determined. On the premise of a steady mortality across the cohorts, temporal changes in
143 abundance with time were expressed with the equation ($\text{Log}_{10}N = at + b$, where a and b are
144 fitted constants, and t is year). Production (P , mg DM m^{-2}) can be calculated using the
145 following formula (Omori & Ikeda, 1984):

$$146 \quad P = \frac{1}{2} \sum_{i=1}^n (N_{i-1} + N_i)(W_i - W_{i-1}) \quad (3)$$

147 where i is month. Using the above two equations, temporal changes in individual DM (W)
148 and abundance (N) were calculated by month. Based on these monthly data, annual
149 production (P) and annual mean biomass (B) were calculated for each cohort. The annual P
150 and annual mean B for each cohort of a given species thus computed were summed to yield
151 respective values for the entire population of the species. Based on these values, annual P/B
152 (Production/Biomass) ratios were also calculated.

153

154 RESULTS

155 Hydrography

156 Temporal changes in temperature, salinity, chlorophyll a , mesozooplankton biomass
157 and their depth distribution from August 2002 through August 2003 are shown in fig. 2.
158 Temperature showed seasonal variations above 200 m depth from $<1^{\circ}\text{C}$ (February to March)
159 to $>7^{\circ}\text{C}$ (August) (fig. 2A). Temperature below 300 m was stable around 3°C throughout the
160 year. Salinity ranged from 33.0 to 34.2. Salinity was lowest near the surface and increased
161 with increasing depth. Salinity below 300 m depth had little seasonal variation (fig. 2B).
162 Chlorophyll a varied between 26.8 and 52.6 $\text{mg } m^{-2}$ and showed little seasonality.
163 Mesozooplankton biomass varied between 34.6 and 493.9 $\text{g WM } m^{-2}$ with maximum values
164 between April and June (fig. 2C). During the peak season for mesozooplankton biomass
165 (April-June), their depth distribution also changed. During the rest of the year 25% of the

166 zooplankton biomass was in the 0-150 m depth range and the remaining 75% was in the
167 150-500 m depth layer. During the period from April to June the biomass in the 0-150 m
168 depth range increased and reached >50% (fig. 2D).

169

170 Community structure

171 Mysidacea belonging to 5 genera 5 species occurred in the Oyashio region (table I).
172 Their abundance varied between 11.7 and 50.1 ind. m⁻². The dominant Mysidacea species
173 were *Eucopia australis*, *Boreomysis californica* and *Meterythrops microphthalma*, which
174 accounted for 74-100% of the total abundance of Mysidacea. In terms of biomass, Mysidacea
175 ranged between 1.2 and 7.9 g WM m⁻², and was also dominated by the numerically abundant
176 species. Decapoda belonged to 6 genera 6 species, and their abundance ranged between 9.0
177 and 17.3 ind. m⁻² (table I). The numerically dominant species was *Hymenodora frontalis*, but
178 their contribution to total decapod abundance was below 42%. For decapods, the most
179 abundant category was small individuals which could not be identified to species (40-76%).
180 Decapoda biomass ranged between 3.0 and 17.3 g WM m⁻², and was dominated by low
181 numbers of large-sized *Bentheogennema borealis* (Rathbun, 1902) (30-98%).

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183 Water and AFDM (=organic) contents

184 Results on WM, DM, and AFDM of the three dominant mysids and one decapod
185 species are shown in fig. 3. For all species, there were highly significant correlations between
186 body mass and BL. These relationships were well expressed with power regressions ($r^2 =$
187 0.91-0.99, $p < 0.0001$) (table II). Differences among life stages (juvenile, adult male, adult
188 female, ovigerous female) did not affect these relationships (fig. 3A-D) so the regressions are
189 based on all juvenile-adult data combined. The biomass of eggs and larvae was not included
190 in the juvenile-adult regressions (fig. 3A-C). Water and AFDM contents of Mysidacea were

191 72.0-90.6%WM and 61.9-90.0%DM, respectively. As the animals grew from juvenile to adult,
192 water content decreased while AFDM content increased (fig. 3E-G). In contrast, eggs and
193 larvae of Mysidacea were characterized by low water content (below 74.4%WM) and high
194 AFDM (above 90.3%DM) content. Water content of the decapod *H. frontalis* was
195 64.5-80.3%WM, substantially lower than the values for Mysidacea (fig. 3H). However,
196 AFDM contents of *H. frontalis* (79.2-92.8%DM) were higher than those of Mysidacea.

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198

Population structure

199 Based on the BL histogram, there were two to four cohorts for the three dominant
200 mysids and one dominant decapod species on each sampling date (fig. 4). For *E. frontalis*, the
201 smallest juveniles were dominant in May 2003. This cohort was traceable and grew to 30 mm
202 BL during two years, at which point they were considered mature. Their generation length
203 was considered to be three years (fig. 4A). For *B. californica* the smallest juveniles were also
204 seen in May 2003. This cohort was traceable to maturity over two years, and their generation
205 length was also estimated to be three years (fig. 4B). The smallest *M. microphthalmma*
206 juveniles were observed in October 2002. Tracing the growth of this cohort suggested that
207 they matured after two years. However, low abundance of this species prevented an
208 estimation of longevity (fig. 4C). Because of low abundance, cohorts of the decapod *H.*
209 *frontalis* could not be separated within a single sampling date. Thus, cohort analysis of this
210 species was made for three consecutive periods: August-October 2002, February-March 2003
211 and May-June 2003. The smallest juveniles were observed in August-October. This cohort
212 had matured after two years and certain individuals were present during the third year.
213 However, their longevity could not be determined because of the low abundance (fig. 4D).

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215

Life history and production

216 Based on the BL histogram, growth by the main cohort of three three mysids and one
217 decapod was expressed using the von Bertalanffy equation (fig. 5A-D). In detail, there was
218 seasonality with growth where results for individuals were higher or lower than the von
219 Bertalanffy curves. For the two numerically dominant mysids: *E. australis* and *B. californica*,
220 their BL was higher during April to June, and lower during October to February relative to
221 the von Bertalanffy curves (fig. 5A, B). Applying BL-DM equations (table II), growth in
222 individual DM for each cohort was expressed by log-DM and linear-date regressions ($r^2 =$
223 $0.90-0.97$, $p < 0.0001$, fig. 5A-D). The number of individuals (N : ind. m^{-2}) included in each
224 cohort decreased with time and was expressed by log-abundance and linear-time regressions
225 (fig. 5E-H). Production of the four dominant species increased with time. Annual production
226 ranged between $14.0 \text{ mg DM } m^{-2}$ (*B. californica*) and $191.8 \text{ mg DM } m^{-2}$ (*E. australis*). Annual
227 P/B ratios ranged from 0.242 (*H. frontalis*) to 0.643 (*M. microphthalmalma*).

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DISCUSSION

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Abundance and biomass

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Abundance and biomass of Mysidacea and Decapoda reported from various oceans are summarized in table III. Earlier studies sampled Mysidacea and Decapoda using IKMT or ORI nets, while more recent studies have used multi-opening and closing net sampling systems such as RMT and MOCNESS. To make quantitative comparisons possible, standardization of abundance and biomass data obtained from different sampling methods is required. Mesh sizes of nets in table III ranged between 0.2 mm and 4.5 mm. The Bongo net used in the present study has a smaller diameter (70 cm) and smaller net mesh size (0.35 mm). Greater abundances in this study may reflect effective collection of smaller individuals due to the smaller mesh size. However, the biomass found by the present study was also greater than that of the other regions. Even considering net avoidance due to smaller net diameter (70 cm),

241 the highest biomass measured by the present study is remarkable (table III). These results
242 suggest that both Mysidacea and Decapoda in the Oyashio region have greater abundance and
243 biomass than in other regions.

244 Geographical distribution of standing stock of Mysidacea and Decapoda is known to
245 vary in parallel with the biomass of the epipelagic mesozooplankton (Aizawa, 1974; Omori,
246 1974). This is considered to result from crustacean micronekton relying on epipelagic
247 mesozooplankton as food. Biomass ratios between mesozooplankton and crustacean
248 micronekton are known to be indices of ecological efficiency for the region (Blackburn,
249 1977). Within the studies in table III, values in the subarctic North Pacific Ocean and Bering
250 Sea by Nishikawa et al. (2001) may be based on similar fauna to the Oyashio region (cf.
251 Mauchline & Murano, 1977), although individuals were not identified to species. Compared
252 with the same fauna, the biomass of this study was higher than that of Nishikawa et al. (2001).
253 It indicates that the abundance and biomass of crustacean micronekton are higher in the
254 Oyashio region than elsewhere in the subarctic Pacific. This may be because the Oyashio
255 region is close to coastal areas, which are characterized by high primary production (Saito et
256 al., 1998; Kasai et al., 2002). Thus, the food supply for mesopelagic micronekton is expected
257 to be higher in the Oyashio region than in the oceanic region studied by Nishikawa et al.
258 (2001).

259

260 Water and AFDM (=organic) contents

261 Since most of the deep-sea crustacean micronekton have minimal diel vertical
262 migration, they may be less important for vertical material transport, but still function to
263 deposit organic material in the deep-sea throughout their long life history (Vinogradov, 1997).
264 Because of high pressure, low temperature, and presence of the oxygen minimum layer, the
265 deep-sea may not be a suitable environment for many living resources. However,

266 physiological studies on crustacean micronekton have revealed that they have adapted
267 effectively to such environments (Childress, 1977). Deep-sea crustacean micronekton have
268 larger body sizes compared to epipelagic species. This is due to the high water content of
269 deep-sea species. For instance, the water content of the decapod *Gnathophausia ingens*
270 (Dohrn, 1870) is known to be as high as 90%WM (Childress & Nygaard, 1974).
271 Consequently, the high water content of crustacean micronekton may yield high growth rate
272 per unit mass under food-limited deep-sea conditions. Specific gravity with nearly water may
273 serve an energetic function, since nearly neutral buoyancy would require less swimming
274 activity (Childress & Nygaard, 1974).

275 Water and AFDM contents of congener species of Mysidacea and Decapoda in this
276 study are summarized in table IV. Water and AFDM content values from this study
277 correspond well with values from previous studies. The decapods *Hymenodora* spp.
278 consistently show lower water content and higher AFDM content than the three mysids (table
279 IV). There is little change in water and AFDM contents throughout development from
280 juvenile to male or female, which agrees well with the previous study (Båmstedt, 1978).
281 While seasonality in water and AFDM contents of crustacean micronekton has been reported
282 (Båmstedt, 1988), measurements based on various seasons during this study do not confirm
283 this effect.

284 There are two remarkable findings from the water and AFDM contents analyses in
285 the present study. Firstly, water and AFDM contents of eggs and larvae showed low water
286 and high AFDM which was quite different from juveniles and adults (fig. 3E-G). Secondly,
287 water and AFDM content values from this study showed relatively higher water and lower
288 AFDM contents than the values previously reported for the same genera (table IV). The
289 former findings may reflect the fact that eggs and larvae contain large amount of yolk. The
290 high nutrition provided for early life stages may function as a survival strategy under

291 food-limited deep-sea conditions (e.g. K-strategy species). The latter finding of this study is
292 considered to be an artifact of the use of formalin to preserve the samples. Long storage in
293 formalin leads to inevitable loss of organic material such as protein and oil (Hopkins, 1968;
294 Fudge, 1968). Thus, it should be noted that the following production estimation discussed
295 below may somewhat underestimate actual production.

296

297

Life history and production

298 According to Mauchline (1972), the effect of latitude and depth on life history of
299 crustacean micronekton is summarized as: slower growth rate, larger body size and longer
300 generation length with increasing latitudes and depths. Generation length of bathypelagic
301 Mysidacea is expected to be 3-7 times longer than for the epipelagic species. The low
302 temperature in the bathypelagic zone and the high latitudes may result in, slower growth rates,
303 longer longevity and larger body sizes. Bathypelagic species have larger eggs than epipelagic
304 species. For bathypelagic species, longer generation length may imply that a long time is
305 spent in a sexually mature condition. This may be important for finding mates given the low
306 population density of the deep-sea.

307

Comparisons of life history parameters of four congener mysids and decapods in this
308 study are shown in table V. Life history in the Oyashio region is characterized by longer
309 generation length and smaller minimum maturity size within the congener species. This may
310 result partially from the low habitat temperature (3°C), consistent with the theory that lower
311 temperatures lead to increased longevity. The smaller size at maturity may function to
312 provide a longer period to seek a breeding partner, as suggested by Mauchline (1972).
313 However, the low temperature alone could not explain the slower growth rate of *M.*
314 *microphthalma* in the southern Japan Sea. This is considered to be caused by the lack of
315 predatory micronekton which is a special characteristic of the mesopelagic layer of the Japan

316 Sea (Ikeda, 1992).

317 Within the four species examined in this study, the large-body sized decapod *H.*
318 *frontalis* had the longest generation length (>45 months) (fig. 4D, table V). The family
319 Hoplophoridae, to which *Hymenodora* belongs is divided into two groups based on egg size,
320 and *Hymenodora* is considered to have very large eggs (Omori, 1974). The relative mass of
321 the fertilized egg to body mass is 13.2% for *H. frontalis*. This value is higher than for other
322 species, thus *Hymenodora* is a typical K-strategy species, having a few large eggs which
323 contain a large amount of yolk (Omori, 1974). According to Omori (1974), *H. frontalis* and *H.*
324 *glacialis*, which reach a maximum BL of 40-60 mm, may require two to three years to mature
325 and may live for five to eight years. In the present study, use of the smaller diameter of the
326 sampling gear may have impacted the quantitative collection of large, low density individuals.
327 Because of this, longevity could not be evaluated in this study. Future collection using
328 sampling gear with a larger mouth opening, such as a mid-water trawl, may allow for more
329 accurate evaluation of the longevity of *H. frontalis*.

330 As a feature of life history in the Oyashio region, the presence of clear seasonality
331 should be noted: i.e. recruitment of young and large BL growth of the two numerically
332 dominant Mysidacea species are observed during April to June (fig. 4A, B), recruitment of
333 young for the two numerically minor species was seen in August to October (fig. 4C, D).
334 According to Mauchline (1988), all mesopelagic crustacean micronekton in the Rockall
335 Trough have seasonality in reproduction, while bathypelagic species reproduce throughout
336 the year (no seasonality). The fact that all four species in this study showed clear seasonality
337 in recruitment of young suggests that they all have seasonality in reproduction. The presence
338 of seasonality in reproduction of crustacean micronekton in the Oyashio region would be a
339 special feature of this region, which has a clear spring phytoplankton bloom (Saito et al.,
340 1998; Kasai et al., 2002). Differences in the timing of recruitment of young between the two

341 dominant species and the two minor species may be attributed to differences in feeding habits
342 or depth distribution. The season (April to June) of the recruitment of young and greater
343 growth of two dominant mysids corresponds with the season when their prey
344 (mesozooplankton, mainly copepods) is abundant (fig. 2C). Using this abundant food,
345 juveniles may achieve substantially greater growth and adults can reproduce.

346 Production and P/B ratios from this study were compared with those of mysids in
347 other waters (Mediterranean) (table VI). Compared with the values in the Mediterranean,
348 high production and low P/B ratios were the case in the Oyashio region. The high production
349 in the Oyashio region may result from high biomass in the region (table III). Since the values
350 in the Mediterranean are based on benthopelagic species under high temperature conditions
351 (9.8-11.2°C) (Cartes et al., 2001), they may have shorter generation lengths and higher P/B
352 ratios. Because of the extremely low temperature conditions (3°C) in the Oyashio region,
353 crustacean micronekton may have slower growth, longer generation length and lower P/B
354 ratios than in other oceans.

355 For P/B ratios of invertebrates, Banse & Mosher (1980) reported the equation: $P/B =$
356 $0.65 M_s^{-0.37}$, where M_s is caloric content (kcal) of mature individuals living under 5-20°C
357 temperature conditions. By using previously reported values for caloric contents of
358 Mysidacea and Decapoda as 4178-7533 cal g⁻¹ DM (Mauchline, 1980), the P/B ratios of the
359 four species in this study are predicted to be 0.51-2.19, which is greater than the estimates
360 obtained from this study (0.24-0.64). This discrepancy may be partly because the temperature
361 range of the above formula (5-20°C) is much higher than in the Oyashio region (3°C). It also
362 should be noted that the formula by Banse & Mosher (1980) is based on the coastal or neritic
363 species living under sufficient food conditions, and there is a wide range in precision of
364 prediction using this method (50-200%). The low temperature conditions (3°C) in the deep
365 Oyashio region are considered to be a reason that crustacean micronekton in this region have

366 lower *P/B* ratios than other regions. For the low *P/B* ratio of mysids under low habitat
367 temperature, similar situation was reported for Antarctic mysids (Siegel &
368 Muhlenhardt-Siegel, 1998).

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512 **Figure Legends**

513 Fig. 1. Location of sampling station (Site H) in the western subarctic Pacific. Depth contours
514 (2000, 4000, 6000 and 8000 m) are superimposed.

515 Fig. 2. Temporal changes in: A, temperature; B, salinity; C, chlorophyll *a* and
516 mesozooplankton wet mass; and, D, depth distribution of mesozooplankton wet
517 mass; at Site H from August 2002 to August 2003.

518 Fig. 3. Relationships between masses (WM, DM and AFDM) and body lengths of: A,
519 *Eucopia australis* Dana, 1852; B, *Boreomysis californica* Ortmann, 1894; C,
520 *Meterythrops microphthalma* W. Tattersall, 1951; and, D, *Hymenodora frontalis*
521 Rathbun, 1902. Half-solid, open and solid symbols denote juveniles, females and
522 males, respectively. For A-C, eggs or larvae were also measured. Developmental
523 changes in water content (%WM, triangles) and AFDM content (%DM, circles) of:
524 E, *E. australis*; F, *B. californica*; G, *M. microphthalma*; and, H, *H. frontalis*. For
525 juveniles to adults, regressions are shown with solid lines. *: $p < 0.05$, ***: $p <$
526 0.0001.

527 Fig. 4. Temporal changes in body length composition of: A, *Eucopia australis* Dana, 1852; B,
528 *Boreomysis californica* Ortmann, 1894; C, *Meterythrops microphthalma* W.
529 Tattersall, 1951; and, D, *Hymenodora frontalis* Rathbun, 1902; at Site H from
530 August 2002 to August 2003. Number of individuals measured for each histogram is
531 shown in parentheses. For D, data from several months were combined due to low
532 abundance of this species. Dashed lines indicate estimated growth of each cohort.

533 Fig. 5. Estimated growth curve for body length (open symbols) and dry mass (solid symbols)
534 of: A, *Eucopia australis* Dana, 1852; B, *Boreomysis californica* Ortmann, 1894; C,
535 *Meterythrops microphthalma* W. Tattersall, 1951; and, D, *Hymenodora frontalis*
536 Rathbun, 1902; at Site H. Abundance of each cohort (open symbols) from body

537 length histogram (cf. Fig. 4) and estimated production (solid lines) of: E, *E.*
538 *australis*; F, *B. californica*; G, *M. microphthalma*; and, H, *H. frontalis*. Symbols and
539 bars in A-D indicate means and standard deviations for each cohort. Annual
540 production and *P/B* (Production/Biomass) ratios are also shown for E-H. *t*: time
541 (year).

TABLE I

Temporal changes in abundance (ind. m⁻²) and biomass (mg WM m⁻²) of Mysidacea and Decapoda at Site H during August 2002 to August 2003. Values in the parentheses indicate percentage composition.

Taxa	2002		2003		9 Oct.		11 Feb.		13 Mar.		11-12 May		21 May		4-28 June		23 Aug.	
	ind. m ⁻²	mg WM m ⁻²	ind. m ⁻²	mg WM m ⁻²	ind. m ⁻²	mg WM m ⁻²	ind. m ⁻²	mg WM m ⁻²	ind. m ⁻²	mg WM m ⁻²	ind. m ⁻²	mg WM m ⁻²	ind. m ⁻²	mg WM m ⁻²	ind. m ⁻²	mg WM m ⁻²	ind. m ⁻²	mg WM m ⁻²
<i>Mysidacea</i>																		
<i>Ectopia australis</i> Dana, 1852	9.10 (46.0)	4286.0 (83.2)	24.18 (79.0)	4394.7 (91.0)	14.98 (37.6)	2960.9 (37.6)	14.83 (47.2)	5686.5 (90.4)	7.72 (15.4)	1937.9 (55.2)	6.81 (57.9)	2280.3 (85.6)	9.77 (25.5)	965.7 (78.2)				
<i>Boreomysis californica</i> Ortmann, 1894	7.10 (35.9)	362.9 (7.0)	6.12 (20.0)	367.6 (7.6)	11.24 (40.6)	376.4 (4.8)	7.41 (23.6)	498.1 (7.9)	6.89 (13.8)	351.0 (10.0)	3.45 (29.4)	220.2 (8.3)	6.51 (17.1)	92.6 (7.5)				
<i>Meterothrops micropthalma</i> W. Tattersall, 1951	0.42 (2.1)	6.0 (0.1)	-	-	0.58 (2.1)	4.1 (0.1)	0.93 (3.0)	31.2 (0.5)	32.87 (65.6)	91.2 (26.0)	1.00 (8.5)	42.0 (1.6)	21.98 (57.4)	176.2 (14.3)				
<i>Gnathophausia gigas</i> W.-Stuhm, 1875	0.34 (1.7)	457.2 (8.9)	0.31 (1.0)	68.6 (1.4)	0.58 (2.1)	4538.2 (57.6)	-	-	0.62 (1.2)	269.8 (7.7)	0.49 (4.1)	121.0 (4.5)	-	-				
<i>Acanthomysis dimorpha</i> Li, 1936	1.23 (6.2)	12.6 (0.2)	1.23 (4.0)	1.0 (0.0)	-	-	0.18 (0.6)	1.5 (0.0)	0.32 (0.6)	2.6 (0.1)	-	-	-	-				
Juveniles (unidentified)	1.57 (7.9)	26.7 (0.5)	-	-	0.29 (1.0)	3.00 (0.0)	8.06 (25.7)	73.3 (1.2)	1.67 (3.3)	35.1 (1.0)	-	-	-	-				
Total Mysidacea	19.76	5151.4	30.61	4830.9	27.66	7882.6	31.41	6290.6	50.10	3508.6	11.74	2663.6	38.26	1234.5				
<i>Decapoda</i>																		
<i>Hymenodora frontalis</i> Rathbun, 1902	2.99 (26.1)	2348.4 (31.9)	4.90 (42.1)	1099.1 (23.3)	4.61 (40.0)	983.6 (32.4)	2.86 (24.3)	2009.0 (22.2)	3.27 (19.0)	1256.7 (22.8)	2.51 (17.4)	2250.8 (26.3)	-	-				
<i>Bentheogammarus borealis</i> (Rathbun, 1902)	0.47	3528.2	1.56	13161.8	0.29	925.1	1.34	6211.9	0.46	2257.1	0.49	3570.7	3.26	8475.5				
<i>Sergestes similis</i> Hansen, 1903	0.21 (1.8)	319.0 (4.3)	1.53 (13.2)	1649.8 (35.0)	0.86 (7.5)	910.9 (30.0)	0.35 (3.0)	576.6 (6.4)	(2.6)	1494.5 (27.1)	(3.4)	2461.9 (28.7)	-	-				
<i>Gennadas propinquus</i> Rathbun, 1906	0.13 (1.1)	113.1 (9.6)	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Sergia japonica</i> Bate, 1881	0.13 (1.1)	707.9 (9.6)	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Acanthephyra quadrispinosa</i> Kemp, 1939	-	-	0.15 (1.5)	46.7 (0.3)	-	-	-	-	-	-	-	-	-	-				
Juveniles (unidentified)	7.50 (65.6)	340.9 (4.6)	4.59 (39.5)	170.2 (3.6)	5.76 (50.0)	219.9 (7.2)	7.24 (61.4)	233.5 (2.6)	12.42 (72.0)	506.3 (9.2)	10.92 (75.7)	287.4 (3.4)	5.70 (63.6)	143.3 (1.7)				
Total Decapoda	11.43	7357.4	11.63	4715.8	11.52	3039.4	11.79	9031.0	17.25	5514.6	14.44	8570.8	8.95	8618.9				

TABLE II

Regression statistics between masses (Y : WM, DM, and AFDM in mg) and total length (X : mm) of *Eucopia australis* Dana, 1852, *Boreomysis californica* Ortmann, 1894, *Meterythrope microphthalma* W. Tattersall, 1951 and *Hymenodora frontalis* Rathbun, 1902 at Site H. ***: $p < 0.0001$.

Species	Unit	Regression model			
		$\log_{10}Y = a \cdot \log_{10}X + b$		n	r^2
		a	b		
<i>Eucopia australis</i>	WM	3.10	1.01	42	0.96***
	DM	3.34	1.00	42	0.93***
	AFDM	3.42	1.00	42	0.91***
<i>Boreomysis californica</i>	WM	3.43	1.01	42	0.98***
	DM	3.51	1.00	42	0.98***
	AFDM	3.54	1.00	42	0.98***
<i>Meterythrope microphthalma</i>	WM	3.05	1.03	42	0.99***
	DM	3.30	1.00	42	0.99***
	AFDM	3.37	1.00	42	0.98***
<i>Hymenodora frontalis</i>	WM	3.02	1.02	42	0.99***
	DM	3.16	1.00	42	0.97***
	AFDM	3.14	1.00	42	0.96***

TABLE III

Comparison on abundance and biomass of Mysidacea and Decapoda from various oceans. *: for comparison, dry mass data were converted to wet mass (WM) using water contents of this study (cf. table IV).

Taxa	Depth range (m)	Abundance (ind. m ⁻²)	Biomass (mg WM m ⁻²)	Sampling gear	References
Mysidacea					
Oyashio region	0-1000	11.7-50.1	1234-7883	Bongo net (0.35)	This study
Kosterfjorden	0-200	3.0	125*	Conical net (0.40)	Båmstedt (1988)
NE Atlantic	1900-5430	0.930	-	RMT8 (4.5)	Hargreaves & Murano (1996)
Western subarctic Pacific	0-1000	10.7-10.8	1044-1164	RMT1+8 (4.5)	Nishikawa et al. (2001)
Central subarctic Pacific	0-1000	7.58-9.37	1426-1776	RMT1+8 (4.5)	Nishikawa et al. (2001)
Bering Sea	0-1000	12.7	1346	RMT1+8 (4.5)	Nishikawa et al. (2001)
Gulf of Alaska	0-1000	5.11-5.26	590-860	RMT1+8 (4.5)	Nishikawa et al. (2001)
Decapoda					
Oyashio region	0-1000	8.9-17.3	3039-17311	Bongo net (0.35)	This study
Arctic Osean	0-1500	6.1	-	Multinet (0.20)	Auel and Hagen (2002)
Kosterfjorden	0-200	4.0	200*	Conical net (0.40)	Båmstedt (1988)
Sagami Bay	0-1000	-	3220	ORI net (0.33)	Aizawa (1974)
Kuroshio region	0-1000	-	260-1240	ORI net (0.33)	Aizawa (1974)
North equatorial current	0-1000	-	190	ORI net (0.33)	Aizawa (1974)
Equatorial water	0-1000	-	660	ORI net (0.33)	Aizawa (1974)
Western subarctic Pacific	0-1000	5.4-6.6	1255-2615	RMT1+8 (4.5)	Nishikawa et al. (2001)
Central subarctic Pacific	0-1000	5.0-5.6	2840-3372	RMT1+8 (4.5)	Nishikawa et al. (2001)
Bering Sea	0-1000	5.9	1983	RMT1+8 (4.5)	Nishikawa et al. (2001)
Gulf of Alaska	0-1000	2.0-2.4	1347-1577	RMT1+8 (4.5)	Nishikawa et al. (2001)

TABLE IV

Comparison of Water and AFDM contents of three mysids (*Eucopia*, *Boreomysis*, *Meterythrops*) and one decapods (*Hymenodora*) from various oceans.

Taxa	Species	Location	Water (% WM)	AFDM (% DM)	References
Mysidacea					
	<i>Eucopia austoralis</i> Dana, 1852	Oyashio region	84.0	78.8	This study
	<i>Boreomysis californica</i> Ortmann, 1894	Oyashio region	85.8	78.4	This study
	<i>Boreomysis californica</i> Ortmann, 1894	Southern California	82.6	80.1	Childress & Nygaard (1974)
	<i>Boreomysis arctica</i> (Krøyer, 1861)	Korsfjorden	-	85.3	Båmstedt (1978)
	<i>Boreomysis arctica</i> (Krøyer, 1861)	Kosterfjorden	-	83.2	Båmstedt (1988)
	<i>Meterythrops microphthalma</i> W. Tattersall, 1951	Oyashio region	85.3	73.6	This study
	<i>Meterythrops microphthalma</i> W. Tattersall, 1951	Japan Sea	79.6	84.1	Ikeda (1991)
Decapoda					
	<i>Hymenodora frontalis</i> Rathbun, 1902	Oyashio region	72.5	88.6	This study
	<i>Hymenodora frontalis</i> Rathbun, 1902	Southern California	63.8	93.3	Childress & Nygaard (1974)

TABLE V

Comparison on generation length, minimum maturity size and maximum body size of three mysids (*Eucopia*, *Boreomysis*, *Meterythrope*) and one decapods (*Hymenodora*) from various oceans. For this study, data on habitat depths are from ^a: Murano (1999), ^b: Taniguchi (1969), ^c: Tattersall (1951) and ^d: Kikuchi & Omori (1985). BL: body length.

Taxa	Location	Habitat depth (m)	Habitat temp. (°C)	Generation length (month)	Minimum maturity size (BL: mm)	Maximum size (BL: mm)	References
Mysidacea							
<i>Eucopia austoralis</i> Dana, 1852	Oyashio region	>600 ^a	3	34	23.3	36	This study
<i>Eucopia grimaldii</i> Nouvel, 1942	Southern New England	-	-	-	32.0	32	Wigley & Burns (1971)
<i>Eucopia grimaldi</i>	Rockall Trough	1700	4	24?	25.0	37	Mauchline (1986, 1988)
<i>Eucopia unguiculata</i> (W.-Suhm, 1875)	Rockall Trough	900	8.5	24?	22.0	32	Mauchline (1986, 1988)
<i>Boreomysis californica</i> Ortmann, 1894	Oyashio region	350-2430 ^b	3	34	12.8	20.3	This study
<i>Boreomysis microps</i> G.O. Sars, 1883	Rockall Trough	1100-1700	4.0-7.0	12-24	15	24	Mauchline (1986, 1988)
<i>Boreomysis nobilis</i> G.O. Sars, 1885	Off Iceland	350-400	-	36	-	-	Astthorsson (1985)
<i>Boreomysis tridens</i> G.O. Sars, 1870	Southern New England	-	-	-	26.0	26	Wigley & Burns (1971)
<i>Meterythrope microphthalma</i> W. Tattersall, 1951	Oyashio region	360-1800 ^c	3	>24	7.0	18.9	This study
<i>Meterythrope microphthalma</i> W. Tattersall, 1951	Japan Sea	0-1000	<1	36-48	14.0	21	Ikeda (1992)
<i>Meterythrope picta</i> Holt & Tattersall, 1951	Rockall Trough	1500	4.5	15?	-	15	Mauchline (1988)
<i>Meterythrope robusta</i> S.I. Smith, 1879	Off Iceland	100-300	-	12-24	11.9	-	Astthorsson (1984)
<i>Meterythrope robusta</i> S.I. Smith, 1879	Gulf of Maine	110-150	-	-	8.5	12	Wigley & Burns (1971)
Decapoda							
<i>Hymenodora frontalis</i> Rathbun, 1902	Oyashio region	600-1000 ^d	3	>45	22.7	48	This study
<i>Hymenodora glacialis</i> Buchholz, 1874	Rockall Trough	1300-1700	3-3.5	?	29.0	62	Mauchline (1988)

TABLE VI

Comparison of production, *P/B* (Production/Biomass) ratio and generation length of mysids and decapods in the Oyashio region (this study), SE Bay of Biscay and Catalan Sea (Cartes et al., 2001).

Location Species	Production (mg DM m ⁻² year ⁻¹)	<i>P/B</i> ratio	Generation length (month)
Oyashio region			
<i>Eucopia austoralis</i> Dana, 1852	191.8	0.371	34
<i>Boreomysis californica</i> Ortmann, 1894	14	0.281	34
<i>Meterythroptis microphthalma</i> W. Tattersall, 1951	16.5	0.643	>24
<i>Hymenodora frontalis</i> Rathbun, 1902	123.5	0.242	>45
Mean		0.384	
SE Bay of Biscay			
<i>Boreomysis megalops</i> G.O. Sars, 1872	11.849	3.9	12
<i>Boreomysis arctica</i> (Krøyer, 1861)	0.927	7.9	6
Other mysids (4 species)	2.082 ± 2.263	6.1 ± 1.5	6.7 ± 1.2
Mean		5.2	
Catalan Sea			
<i>Boreomysis arctica</i> (Krøyer, 1861)	8.940	6.1	6
Other mysids (6 species)	0.485 ± 0.342	6.7 ± 3.7	9.8 ± 8.0
Mean		6.6	

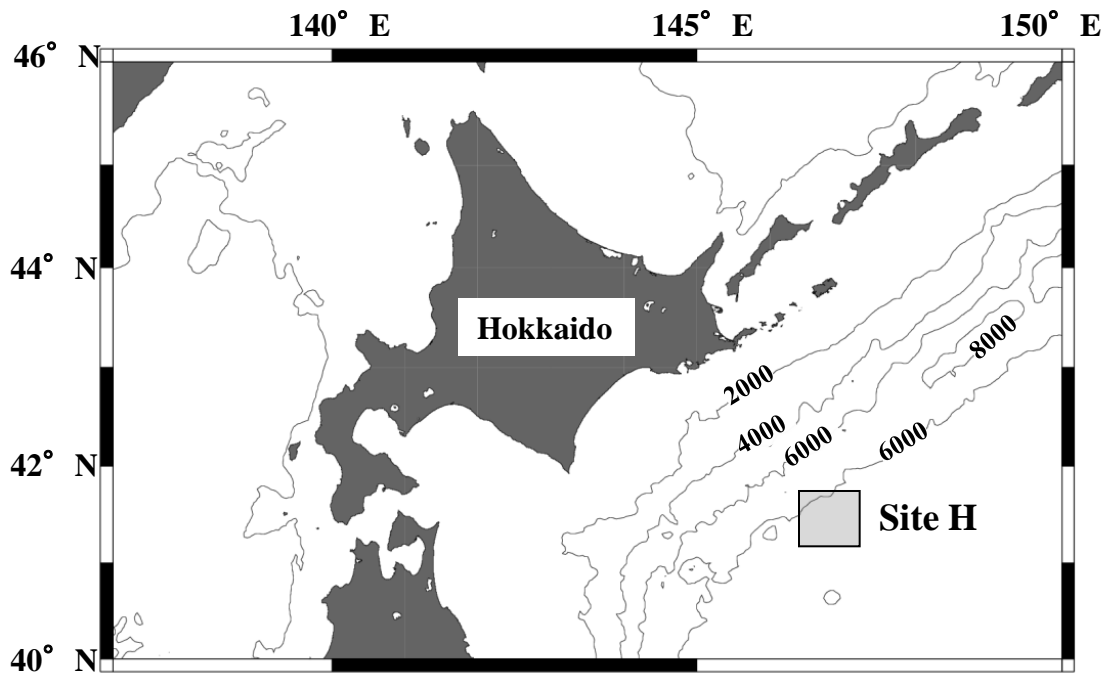


Fig. 1. (Chikugo et al.)

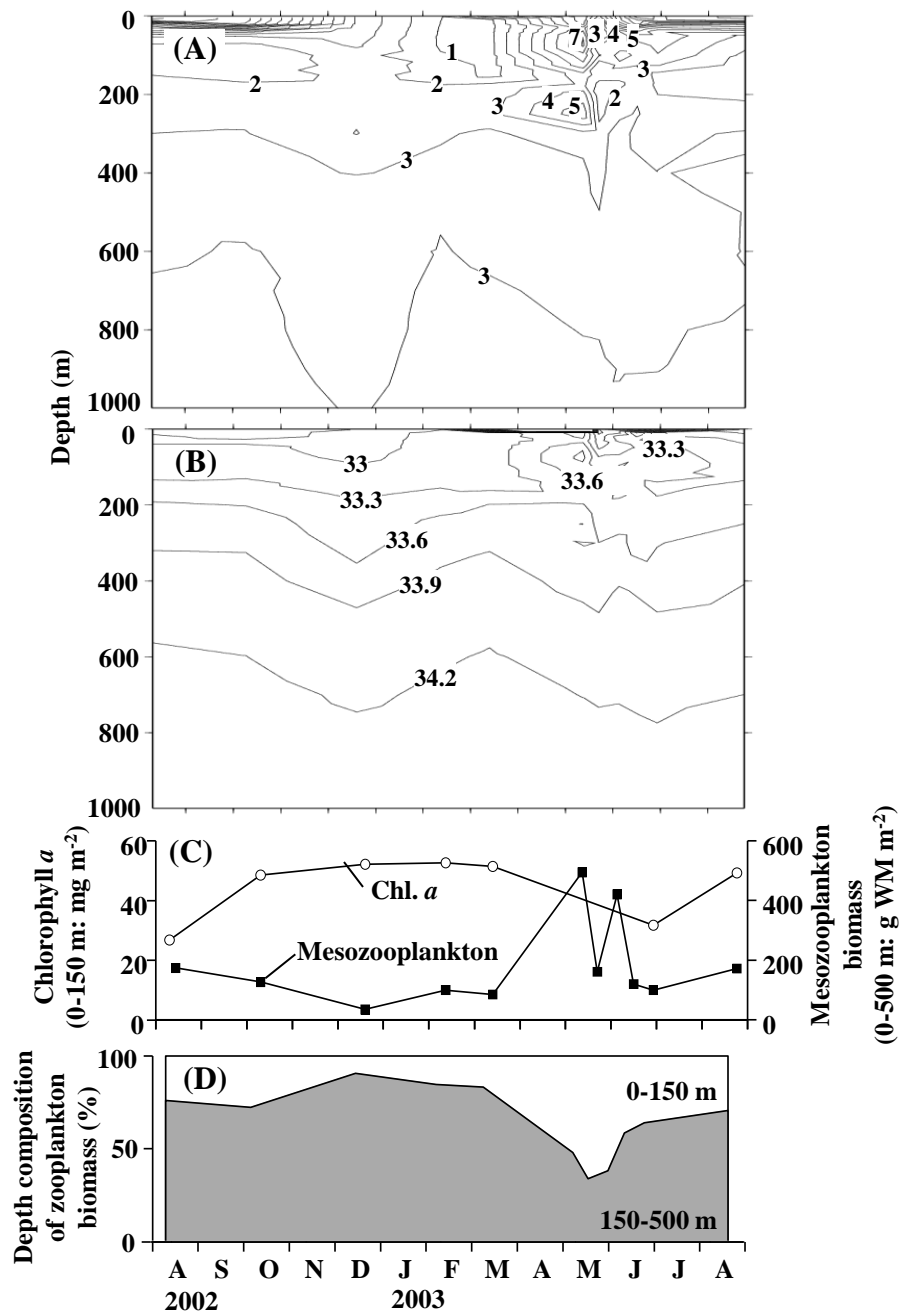


Fig. 2. (Chikugo et al.)

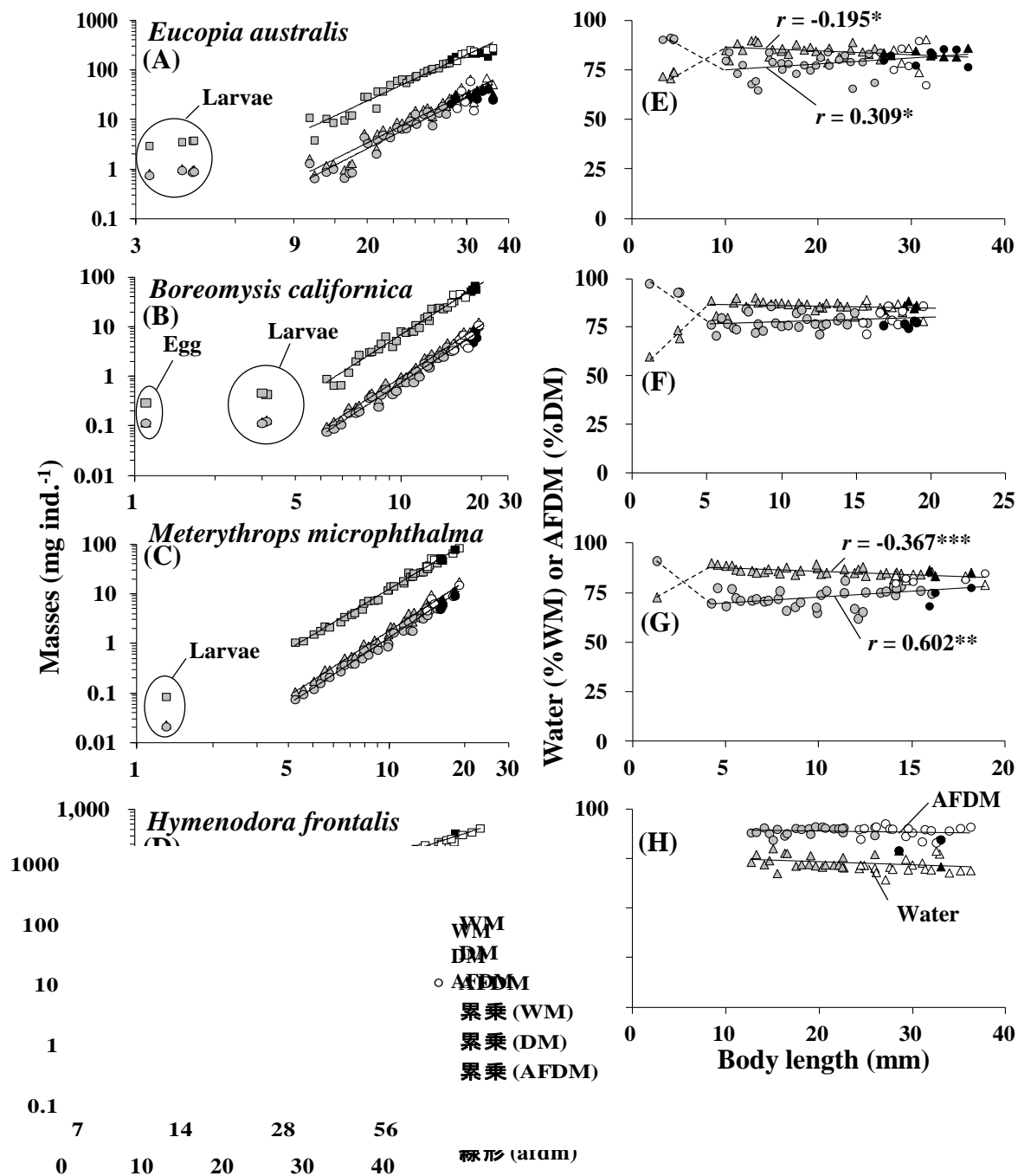


Fig. 3. (Chikugo et al.)

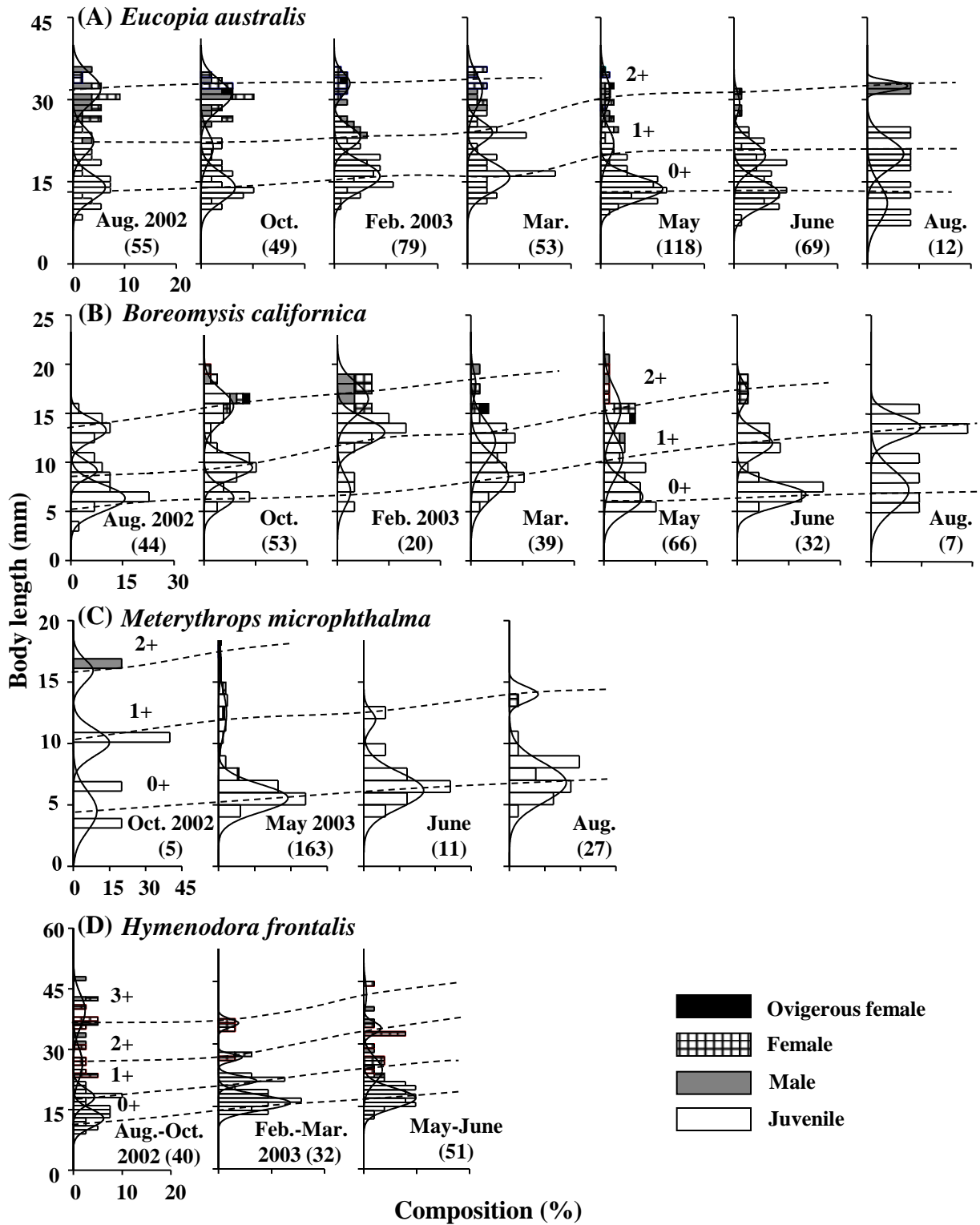


Fig. 4. (Chikugo et al.)

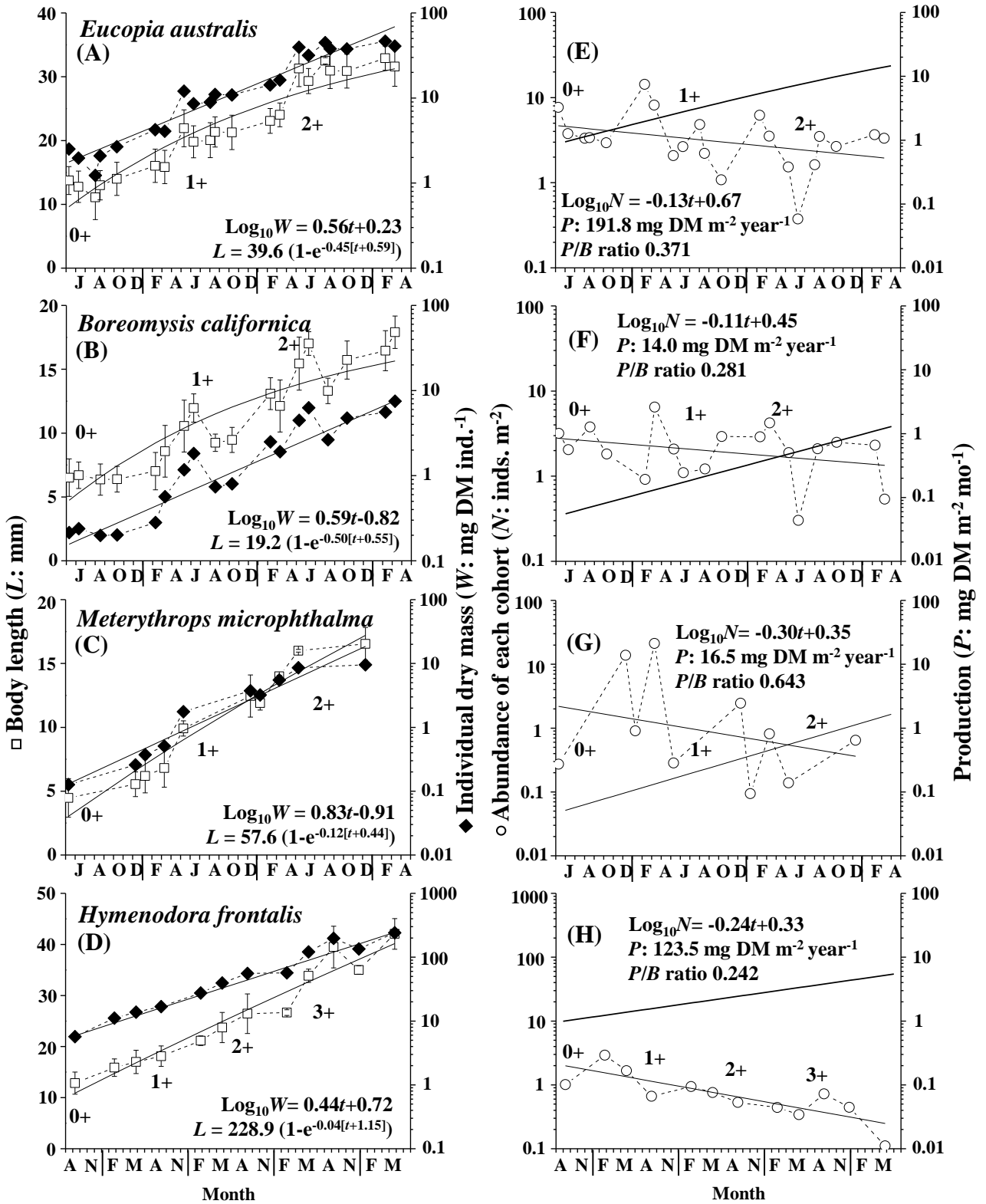


Fig. 5. (Chikugo et al.)

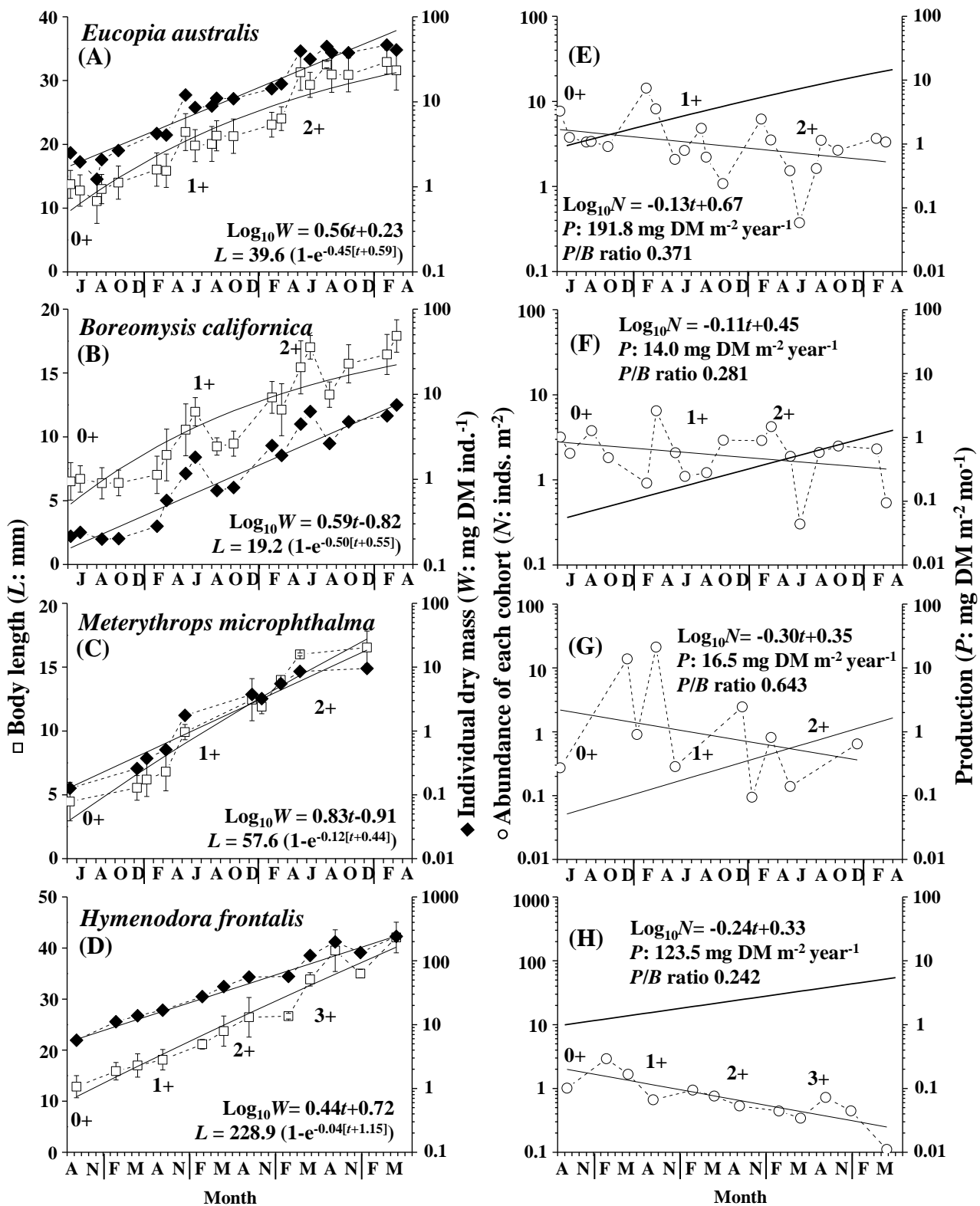


Fig. 5. (Chikugo et al.)