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Title	Life history and production of pelagic mysids and decapods in the Oyashio region, Japan
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Citation	Crustaceana, 86(4), 449-474 https://doi.org/10.1163/15685403-00003170
Issue Date	2013-04
Doc URL	http://hdl.handle.net/2115/52971
Туре	article (author version)
File Information	Chikugo-et-al.pdf



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2	LIFE HISTORY AND PRODUCTION OF PELAGIC MYSIDS AND DECAPODS IN THE
3	OYASHIO REGION, JAPAN
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5	BY
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ABSTRACT

Pelagic Mysidacea and Decapoda have important roles in marine ecosystems. 17 However, information on their life histories is extremely limited. This study aimed to 18 19 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 20 and abundance data. Mysidacea belonging to 5 species from 5 genera occurred in the study 21 area. Their abundance and biomass ranged between 11.7-50.1 ind. m⁻² and 1.2-7.9 g WM 22 (Wet Mass) m⁻², respectively. Decapoda belonged to 6 species from 6 genera , and their 23 abundance and biomass ranged between 9.0-17.3 ind. m⁻² and 3.0-17.3 g WM m⁻², 24 respectively. Based on body length histograms, there were two to four cohorts for the three 25 dominant mysids and one dominant decapod on each sampling date. Life histories of the two 26 27 numerically dominant mysids (Eucopia australis and Boreomysis californica) followed similar patterns: recruitment of young in May, strong growth from April to June, and a 28 longevity of three years. Life cycles of the two minor species (the mysid Meterythrops 29 30 microphthalma 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 31 dominant mysids corresponds with the season when their prey is abundant. The annual 32 production of the dominant mysid species was 14.0 mg DM m⁻² (*B. californica*) and 191.8 mg 33 DM m⁻² (E. australis). Annual P/B (Production/Biomass) ratios ranged between 0.242 (H. 34 frontalis) and 0.643 (M. microphthalma). Compared with other regions, the Oyashio region 35 showed high production and low P/B ratios. The high production in the Oyashio region may 36 be related to the high biomass of these species. Because of the low temperature conditions 37 (3°C), pelagic mysids and decapods in the Oyashio region may have slower growth, longer 38

39 generation times and lower P/B ratios than in other oceans.

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INTRODUCTION

42 Pelagic Mysidacea and Decapoda are classified either as micronekton by strong swimming ability, or macrozooplankton by body size (Marshall, 1954). There are about 1000 43 44 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 45 the coastal zone or benthopelagic layer, with a few species living in the pelagic zone, and ca. 46 50 mysids have been reported from the meso- and bathypelagic zone of the North Pacific 47 (Mauchline & Murano, 1977). There are about 2600 species of Decapoda that have been 48 49 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 50 51 reported from waters around Japan (Iwasaki, 2001). Pelagic Mysidacea and Decapoda feed 52 mainly on mesozooplankton (Foxton & Roe, 1974; Mauchline, 1980; Heffernan & Hopkins, 1981; Burghart et al., 2010), and are preved upon by various large fishes (Mauchline & 53 Gordon, 1980; Astthorsson, 1985; Gordon & Duncan, 1987). Thus, they have an important 54 55 trophic role in marine ecosystems. The ecologies of pelagic Mysidacea and Decapoda have been summarized by Mauchline (1980) and Omori (1974), respectively. 56

From waters off Japan, Mysidacea and Decapoda are reported to be a food item of 57 Pacific cod Gadus macrocephalus Tilesius, 1810 in the Doto area (eastern Hokkaido), 58 flathead flounder *Hippoglossoides dubius* Schmidt, 1904 in Funka Bay, and walleve pollock 59 60 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 61 crustacean micronekton in the Oyashio region is 10% of that of mesozooplankton, yet is 62 greater than that of fish micronekton (Ikeda et al., 2008). This information suggests that the 63 crustacean micronekton may have an important role in the marine ecosystems in waters off 64 Japan. Previous studies on the ecology of pelagic Mysidacea and Decapoda around Japan 65

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

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

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MATERIAL AND METHODS

Field sampling

Zooplankton samples (oblique tow of Bongo nets [70 cm mouth diameter, 0.35 mm 82 mesh size] from 1000 m depth) were collected at Site H (41°22'N-41°32'N 83 145°41'E-146°10'E, fig. 1) in the Oyashio region at one to four month intervals from August 84 2002 to August 2003. Vertical tows of a Norpac net (45 cm mouth diameter, 0.33 mm mesh 85 size) from 500 m to surface and 150 m to surface were also conducted on each sampling 86 occasion. After collection, all the samples were preserved immediately in 5% borax-buffered 87 formalin-seawater. Temperature and salinity data were collected in conjunction with all 88 zooplankton samples using a CTD (SBE-9 plus, Sea Bird Electronics). Water samples for 89 chlorophyll a were collected with Niskin bottles from 12 depths between 0 and 150 m, 90

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.

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Identification and body length measurement

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

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

Based on mean BL of each cohort, growth in BL was expressed with the vonBertalanffy equation:

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$$BL_t = BL_{max}(1 - e^{-K[t-tO]})$$
 (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).

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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 μ m 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.

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

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 $Log_{10}[WM, DM \text{ or } AFDM (mg)] = a \ge Log_{10}[BL (mm)] + b$ (2)

where *a* and *b* are fitted constants. Water content (Water: %WM = $100 \times [WM - DM] / WM$) and AFDM content (AFDM: %DM = $100 \times [DM - Ash] / DM$) were also calculated.

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Production estimation

Based on the mean BL of each cohort, individual DM (*W*, mg DM ind.⁻¹) was calculated based on the BL-DM equation. Growth of individual DM with time was expressed with the equation $(\text{Log}_{10}W = at + b)$, where *a* and *b* are fitted constants, and *t* is year). Based on the normal distribution of the BL histogram, abundance (N, ind. m⁻²) of each cohort was determined. On the premise of a steady mortality across the cohorts, temporal changes in abundance with time were expressed with the equation ($\text{Log}_{10}N = at + b$, where a and b are fitted constants, and t is year). Production (P, mg DM m⁻²) can be calculated using the following formula (Omori & Ikeda, 1984):

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

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RESULTS

Hydrography

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

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

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Community structure

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

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Water and AFDM (=organic) contents

Results on WM, DM, and AFDM of the three dominant mysids and one decapod species are shown in fig. 3. For all species, there were highly significant correlations between body mass and BL. These relationships were well expressed with power regressions ($r^2 =$ 0.91-0.99, p < 0.0001) (table II). Differences among life stages (juvenile, adult male, adult female, ovigerous female) did not affect these relationships (fig. 3A-D) so the regressions are based on all juvenile-adult data combined. The biomass of eggs and larvae was not included in the juvenile-adult regressions (fig. 3A-C). Water and AFDM contents of Mysidacea were 72.0-90.6%WM and 61.9-90.0%DM, respectively. As the animals grew from juvenile to adult,
water content decreased while AFDM content increased (fig. 3E-G). In contrast, eggs and
larvae of Mysidacea were characterized by low water content (below 74.4%WM) and high
AFDM (above 90.3%DM) content. Water content of the decapod *H. frontalis* was
64.5-80.3%WM, substantially lower than the values for Mysidacea (fig. 3H). However,
AFDM contents of *H. frontalis* (79.2-92.8%DM) were higher than those of Mysidacea.

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Population structure

199 Based on the BL histogram, there were two to four cohorts for the three dominant mysids and one dominant decapod species on each sampling date (fig. 4). For *E. frontalis*, the 200 201 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 was considered to be three years (fig. 4A). For *B. californica* the smallest juveniles were also 203 204 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. microphthalma juveniles were observed in October 2002. Tracing the growth of this cohort suggested that 206 they matured after two years. However, low abundance of this species prevented an 207 estimation of longevity (fig. 4C). Because of low abundance, cohorts of the decapod H. 208 209 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 and May-June 2003. The smallest juveniles were observed in August-October. This cohort 211 had matured after two years and certain individuals were present during the third year. 212 213 However, their longevity could not be determined because of the low abundance (fig. 4D).

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Life history and production

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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 mg DM m ⁻² (<i>B. californica</i>) and 191.8 mg DM m ⁻² (<i>E. australis</i>). Annual
227	P/B ratios ranged from 0.242 (H. frontalis) to 0.643 (M. microphthalma).
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229	DISCUSSION
230	Abundance and biomass
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the highest biomass measured by the present study is remarkable (table III). These results
suggest that both Mysidacea and Decapoda in the Oyashio region have greater abundance and
biomass than in other regions.

244 Geographical distribution of standing stock of Mysidacea and Decapoda is known to vary in parallel with the biomass of the epipelagic mesozooplankton (Aizawa, 1974; Omori, 245 1974). This is considered to result from crustacean micronekton relying on epipelagic 246 mesozooplankton as food. Biomass ratios between mesozooplankton and crustacean 247 micronekton are known to be indices of ecological efficiency for the region (Blackburn, 248 249 1977). Within the studies in table III, values in the subarctic North Pacific Ocean and Bering Sea by Nishikawa et al. (2001) may be based on similar fauna to the Oyashio region (cf. 250 251 Mauchline & Murano, 1977), although individuals were not identified to species. Compared 252with the same fauna, the biomass of this study was higher than that of Nishikawa et al. (2001). It indicates that the abundance and biomass of crustacean micronekton are higher in the 253 Oyashio region than elsewhere in the subarctic Pacific. This may be because the Oyashio 254255 region is close to coastal areas, which are characterized by high primary production (Saito et al., 1998; Kasai et al., 2002). Thus, the food supply for mesopelagic micronekton is expected 256 to be higher in the Oyashio region than in the oceanic region studied by Nishikawa et al. 257 (2001). 258

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Water and AFDM (=organic) contents

Since most of the deep-sea crustacean micronekton have minimal diel vertical migration, they may be less important for vertical material transport, but still function to deposit organic material in the deep-sea throughout their long life history (Vinogradov, 1997). Because of high pressure, low temperature, and presence of the oxygen minimum layer, the 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 effectively to such environments (Childress, 1977). Deep-sea crustacean micronekton have 267 larger body sizes compared to epipelagic species. This is due to the high water content of 268 269 deep-sea species. For instance, the water content of the decapod Gnathophausia ingens (Dohrn, 1870) is known to be as high as 90%WM (Childress & Nygaard, 1974). 270 Consequently, the high water content of crustacean micronekton may yield high growth rate 271 per unit mass under food-limited deep-sea conditions. Specific gravity with nearly water may 272 serve an energetic function, since nearly neutral buoyancy would require less swimming 273 274 activity (Childress & Nygaard, 1974).

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

There are two remarkable findings from the water and AFDM contents analyses in the present study. Firstly, water and AFDM contents of eggs and larvae showed low water and high AFDM which was quite different from juveniles and adults (fig. 3E-G). Secondly, water and AFDM content values from this study showed relatively higher water and lower AFDM contents than the values previously reported for the same genera (table IV). The former findings may reflect the fact that eggs and larvae contain large amount of yolk. The high nutrition provided for early life stages may function as a survival strategy under food-limited deep-sea conditions (e.g. K-strategy species). The latter finding of this study is
considered to be an artifact of the use of formalin to preserve the samples. Long storage in
formalin leads to inevitable loss of organic material such as protein and oil (Hopkins, 1968;
Fudge, 1968). Thus, it should be noted that the following production estimation discussed
below may somewhat underestimate actual production.

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Life history and production

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

Comparisons of life history parameters of four congener mysids and decapods in this 307 study are shown in table V. Life history in the Oyashio region is characterized by longer 308 309 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 temperatures lead to increased longevity. The smaller size at maturity may function to 311 provide a longer period to seek a breeding partner, as suggested by Mauchline (1972). 312 However, the low temperature alone could not explain the slower growth rate of M. 313 microphthalma in the southern Japan Sea. This is considered to be caused by the lack of 314 predatory micronekton which is a special characteristic of the mesopelagic layer of the Japan 315

316 Sea (Ikeda, 1992).

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

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

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

Production and P/B ratios from this study were compared with those of mysids in 346 other waters (Mediterranean) (table VI). Compared with the values in the Mediterranean, 347 high production and low P/B ratios were the case in the Oyashio region. The high production 348 349 in the Oyashio region may result from high biomass in the region (table III). Since the values in the Mediterranean are based on benthopelagic species under high temperature conditions 350 (9.8-11.2°C) (Cartes et al., 2001), they may have shorter generation lengths and higher P/B351 352 ratios. Because of the extremely low temperature conditions (3°C) in the Oyashio region, crustacean micronekton may have slower growth, longer generation length and lower P/B353 ratios than in other oceans. 354

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

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

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ACKNOWLEDGEMENTS

We thank Dr. Tracy Shaw for her critical reading and constructive comments on an earlier draft of the manuscript. We are grateful to the captain, officers, crews and researchers on board T/S "Oshoro-Maru" and "Ushio-Maru", Hokkaido University for their great effort during field sampling. We would like to thank Ms. Nao Kanazawa who kindly sorted the mysids and decapods used in this study. This study was supported by Grant-in-Aid for Scientific Research (A) 24248032 and Grant-in-Aid for Scientific Research on Innovative Areas 24110005 from the Japan Society for the Promotion of Science (JSPS).

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512 Figure Legends

- Fig. 1. Location of sampling station (Site H) in the western subarctic Pacific. Depth contours
 (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.
- Fig. 3. Relationships between masses (WM, DM and AFDM) and body lengths of: A, 518 Eucopia australis Dana, 1852; B. Boreomysis californica Ortmann, 1894; C. 519 520 Meterythrops microphthalma W. Tattersall, 1951; and, D, Hymenodora frontalis Rathbun, 1902. Half-solid, open and solid symbols denote juveniles, females and 521 males, respectively. For A-C, eggs or larvae were also measured. Developmental 522 523 changes in water content (%WM, triangles) and AFDM content (%DM, circles) of: E, E. australis; F, B. californica; G, M. microphthalma; and, H, H. frontalis. For 524 juveniles to adults, regressions are shown with solid lines. *: p < 0.05, ***: p <525 526 0.0001.
- Fig. 4. Temporal changes in body length composition of: A, *Eucopia australis* Dana, 1852; B, *Boreomysis californica* Ortmann, 1894; C, *Meterythrops microphthalma* W.
 Tattersall, 1951; and, D, *Hymenodora frontalis* Rathbun, 1902; at Site H from
 August 2002 to August 2003. Number of individuals measured for each histogram is
 shown in parentheses. For D, data from several months were combined due to low
 abundance of this species. Dashed lines indicate estimated growth of each cohort.
- Fig. 5. Estimated growth curve for body length (open symbols) and dry mass (solid symbols)
 of: A, *Eucopia australis* Dana, 1852; B, *Boreomysis californica* Ortmann, 1894; C, *Meterythrops microphthalma* W. Tattersall, 1951; and, D, *Hymenodora frontalis*Rathbun, 1902; at Site H. Abundance of each cohort (open symbols) from body

537length histogram (cf. Fig. 4) and estimated production (solid lines) of: E, E.538australis; F, B. californica; G, M. microphthalma; and, H, H. frontalis. Symbols and539bars in A-D indicate means and standard deviations for each cohort. Annual540production and P/B (Production/Biomass) ratios are also shown for E-H. t: time541(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.

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	ď	2002 10 Aug	σ		1 2	003 Feb	13	Mar	1-11	7 May	110	Дау	86-4	entl	23	
1 a.v.a Species	ind. m ⁻²	mg WM m ⁻²	ind. m ⁻²	mg WM m ⁻²	ind. m ⁻²	mg WM m ⁻²	ind. m ⁻²	me WM m ⁻²	ind. m ⁻²	ng WM m ⁻²	ind. m ⁻² n	le WM m ⁻²	ind. m ⁻² r	me WM m ⁻²	ind. m ⁻² 1	ng WM m ⁻²
Mysidacea		D		2		2		2		2				2		
Eucopia australis Dana, 1852	9.10	4286.0	6.69	3303.5	24.18	4394.7	14.98	2960.9	14.83	5686.5	7.72	1937.9	6.81	2280.3	9.77	965.7
	(46.0)	(83.2)	(44.8)	(84.6)	(0.67)	(91.0)	(54.2)	(37.6)	(47.2)	(90.4)	(15.4)	(55.2)	(57.9)	(85.6)	(25.5)	(78.2)
Boreomysis californica Ortmann, 1894	7.10	362.9	7.24	548.3	6.12	367.6	11.24	376.4	7.41	498.1	6.89	351.0	3.45	220.2	6.51	92.6
	(35.9)	(0.7)	(48.5)	(14.0)	(20.0)	(1.6)	(40.6)	(4.8)	(23.6)	(6.7)	(13.8)	(10.0)	(29.4)	(8.3)	(17.1)	(7.5)
Meterythrops microphthalma W. Tattersall, 1951	0.42	6.0	0.69	49.0		ı	0.58	4.1	0.93	31.2	32.87	912.2	1.00	42.0	21.98	176.2
	(2.1)	(0.1)	(4.7)	(1.3)	-	(-)	(2.1)	(0.1)	(3.0)	(0.5)	(65.6)	(26.0)	(8.5)	(1.6)	(57.4)	(14.3)
Gnathophausia gigas WSuhm, 1875	0.34	457.2		,	0.31	68.6	0.58	4538.2	,	,	0.62	269.8	0.49	121.0		,
	(1.7)	(8.9)	-	-	(1.0)	(1.4)	(2.1)	(57.6)	-	(-)	(1.2)	(7.7)	(4.1)	(4.5)	(-)	-
Acanthomysis dimorpha Ii, 1936	1.23	12.6	0.15	1.0		,		,	0.18	1.5	0.32	2.6		,		,
	(6.2)	(0.2)	(1.0)	(0.0)	-	(-)	-	(-)	(0.6)	(0.0)	(0.6)	(0.1)	-	(-)	-	-
Juveniles (unidentified)	1.57	26.7	0.15	4.9	,	ı	0.29	3.00	8.06	73.3	1.67	35.1	,		,	ı
	(6.7)	(0.5)	(1.0)	(0.1)	-	(-)	(1.0)	(0.0)	(25.7)	(1.2)	(3.3)	(1.0)	-	(-)	-	-
Total Mysidacea	19.76	5151.4	14.93	3906.8	30.61	4830.9	27.66	7882.6	31.41	6290.6	50.10	3508.6	11.74	2663.6	38.26	1234.5
Decapoda																
Hymenodora frontalis Rathbun, 1902	2.99	2348.4	2.87	3035.9	4.90	1099.1	4.61	983.6	2.86	2009.0	3.27	1256.7	2.51	2250.8	,	ı
	(26.1)	(31.9)	(29.2)	(17.5)	(42.1)	(23.3)	(40.0)	(32.4)	(24.3)	(22.2)	(19.0)	(22.8)	(17.4)	(26.3)	-	-
Bentheogennema borealis (Rathbun, 1902)	0.47	3528.2	1.56	13161.8	0.61	1796.8	0.29	925.1	1.34	6211.9	0.46	2257.1	0.49	3570.7	3.26	8475.5
	(4.1)	(48.0)	(15.9)	(76.0)	(5.3)	(38.1)	(2.5)	(30.4)	(11.4)	(68.8)	(2.6)	(40.9)	(3.4)	(41.7)	(36.4)	(98.3)
Sergestes similis Hansen, 1903	0.21	319.0	0.37	889.0	1.53	1649.8	0.86	910.9	0.35	576.6	1.10	1494.5	0.52	2461.9		
	(1.8)	(4.3)	(3.8)	(5.1)	(13.2)	(35.0)	(7.5)	(30.0)	(3.0)	(6.4)	(6.4)	(27.1)	(3.6)	(28.7)	-	-
Gennadas propinquus Rathbun, 1906	0.13	113.1		ı		ı	,	ı	,	ı	,	ı		ı		ı
	(1.1)	(1.5)	-	(-)	-	(-)	-	-	•	(-)	-	(-)	-	(-)	-	-
Sergia japonica Bate, 1881	0.13	707.9		ı		ı	,	ı	,	ı		ı		ı		ı
	(1.1)	(9.6)	-	(-)	-	(-)	-	-	•	(-)	-	(-)	-	(-)	-	-
Acanthephyra quadrispinosa Kemp, 1939	·	ı	0.15	46.7		,		ı		·		ı		ı		ı
	(-)	÷	(1.5)	(0.3)	<u>-</u>	(-)	-	-	•	(-)	-	(-)	-	(-)	-	÷
Juveniles (unidentified)	7.50	340.9	4.87	177.1	4.59	170.2	5.76	219.9	7.24	233.5	12.42	506.3	10.92	287.4	5.70	143.3
	(65.6)	(4.6)	(49.6)	(1.0)	(39.5)	(3.6)	(50.0)	(7.2)	(61.4)	(2.6)	(72.0)	(9.2)	(75.7)	(3.4)	(63.6)	(1.7)
Total Decapoda	11.43	7357.4	9.82	17310.6	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 Click here to download Tab

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, *Meterythrops microphthalma* W. Tattersall, 1951 and *Hymenodora frontalis* Rathbun, 1902 at Site H. ***: *p* < 0.0001.

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

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Comparison on abundance and biomass of Mysidacea and Decapoda from various oceans. *: for comparison, dry mass data (nf tabla IV) f this + + • 1

Taxa	Depth range	Abundance	Biomass	Sampling gear	
Location	(m)	(ind. m ⁻²)	(mg WM m^{-2})	(mesh size: mm)	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	I	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	ı	Multinet (0.20)	Auel and Hagen (2002)
Kosterfjorden	0-200	4.0	200*	Conical net (0.40)	Båmstedt (1988)
Sagami Bay	0-1000	I	3220	ORI net (0.33)	Aizawa (1974)
Kuroshio region	0-1000	I	260-1240	ORI net (0.33)	Aizawa (1974)
North equatorial current	0-1000	ı	190	ORI net (0.33)	Aizawa (1974)
Equatorial water	0-1000	I	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			110
Comparison of Water and AFDM contents of three mysids	(Eucopia, Boreomysis various oceans.	, Meterythro	<i>ps</i>) and one o	decapods (<i>Hymenodora</i>) from
Taxa		Water	AFDM	4.PP
Species	Location	(W M)	(% DM)	References
Mysidacea				
Eucopia austoralis Dana, 1852	Oyashio region	84.0	78.8	This study
Boreomysis californica Ortmann, 1894	Oyashio region	85.8	78.4	This study
Boreomysis californica Ortmann, 1894	Southern California	82.6	80.1	Childress & Nygaard (1974)
Boreomysis arctica (Krøyer, 1861)	Korsfjorden	ı	85.3	Båmstedt (1978)
Boreomysis arctica (Krøyer, 1861)	Kosterfjorden	I	83.2	Båmstedt (1988)
Meterythrops microphthalma W. Tattersall, 1951	Oyashio region	85.3	73.6	This study
Meterythrops microphthalma W. Tattersall, 1951	Japan Sea	79.6	84.1	Ikeda (1991)
Decapoda				
Hymenodora frontalis Rathbun, 1902	Oyashio region	72.5	88.6	This study
Hymenodora frontalis Rathbun, 1902	Southern California	63.8	93.3	Childress & Nygaard (1974)

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

Taxa		Habitat	Habitat	Generation	Minimum maturity	Maximum	
Species	Location	depth (m)	temp. (°C)	length (month)) size (BL: mm)	size (BL: mm)	References
Mysidacea							
Eucopia austoralis Dana, 1852	Oyashio region	$>600^{a}$	3	34	23.3	36	This study
Eucopia grimaldii Nouvel, 1942	Southern New England	- [32.0	32	Wigley & Burns (1971)
Eucopia grimaldi	Rockall Trough	1700	4	24?	25.0	37	Mauchline (1986, 1988)
Eucopia unguiculata (WSuhm, 1875)	Rockall Trough	006	8.5	24?	22.0	32	Mauchline (1986, 1988)
Boreomysis californica Ortmann, 1894	Oyashio region	350-2430 ^b	3	34	12.8	20.3	This study
Boreomysis microps G.O. Sars, 1883	Rockall Trough	1100-1700	4.0-7.0	12-24	15	24	Mauchline (1986, 1988)
Boreomysis nobilis G.O. Sars, 1885	Off Iceland	350-400		36	,		Astthorsson (1985)
Boreomysis tridens G.O. Sars, 1870	Southern New England	- [26.0	26	Wigley & Burns (1971)
Meterythrops microphthalma W. Tattersall, 1951	Oyashio region	360-1800°	3	>24	7.0	18.9	This study
Meterythrops microphthalma W. Tattersall, 1951	Japan Sea	0-1000	$\overline{\vee}$	36-48	14.0	21	Ikeda (1992)
Meterythrops picta Holt & Tattersall, 1951	Rockall Trough	1500	4.5	15?	,	15	Mauchline (1988)
Meterythrops robusta S.I. Smith, 1879	Off Iceland	100-300		12-24	11.9		Astthorsson (1984)
Meterythrops robusta S.I. Smith, 1879	Gulf of Maine	110-150			8.5	12	Wigley & Burns (1971)
Decapoda							
Hymenodora frontalis Rathbun, 1902	Oyashio region	600-1000 ^d	3	>45	22.7	48	This study
Hymenodora glacialis Buchholz, 1874	Rockall Trough	1300-1700	3-3.5	è	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	Production	P/B ratio	Generation length
Species	$(mg DM m^{-2} year^{-1})$		(month)
Oyashio region			
Eucopia austoralis Dana, 1852	191.8	0.371	34
Boreomysis californica Ortmann, 1894	14	0.281	34
Meterythrops microphthalma W. Tattersall, 1951	16.5	0.643	>24
Hymenodora frontalis Rathbun, 1902	123.5	0.242	>45
Mean		0.384	
SE Bay of Biscay			
Boreomysis megalops G.O. Sars, 1872	11.849	3.9	12
Boreomysis arctica (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			
Boreomysis arctica (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.)



Composition (%)

Fig. 4. (Chikugo et al.)



Fig. 5. (Chikugo et al.)



Fig. 5. (Chikugo et al.)