



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

BY

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ABSTRACT

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 wet mass (WM) m⁻², respectively. Six species from 6 genera belonged to Decapoda, 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 *Meterythrops 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 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 production/biomass (*P/B*) ratios ranged between 0.242 (*H. frontalis*) and 0.643 (*M. microphthalma*). 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.

RÉSUMÉ

Les Mysidacés et les Décapodes pélagiques ont un rôle important dans les écosystèmes marins. Cependant, les informations sur leur histoire de vie sont extrêmement limitées. Cette étude a pour but d'évaluer les cycles de vie des Mysidacés et des Décapodes dans la région de Oyashio, Japon.

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La production des quatre espèces dominantes a été estimée en combinant les données de poids du corps (DM) et d'abondance. Les Mysidacés appartiennent à 5 espèces des 5 genres présents dans la zone étudiée. Leur abondance et biomasse s'étendent respectivement, entre 11,7-50,1 ind. m^{-2} et 1,2-7,9 g WM (Poids Frais). Les décapodes appartiennent à 6 espèces de 6 genres, et leur abondance et biomasse s'étendent respectivement entre 9,0-17,3 ind. m^{-2} et 3,0-17,3 g WM m^{-2} . Sur la base des histogrammes de longueur du corps, il y a eu deux à quatre cohortes pour les trois mysidacés dominants et un décapode dominant dans chaque échantillonnage. L'histoire de vie des deux mysidacés numériquement dominants (*Eucopia australis* et *Boreomysis californica*) suivent le même modèle : recrutement des jeunes en mai, forte croissance d'avril à juin, et une longévité de trois ans. Le cycle de vie des deux espèces mineures (le mysidacé *Meterythrops microphthalmus* et le décapode *Hymenodora frontalis*) n'a pas été clair à cause de leur faible abondance. Le moment du recrutement pour les jeunes et la forte croissance des juvéniles pour les deux mysidacés dominants correspondent avec la saison d'abondance des proies. La production annuelle des espèces dominantes de mysidacés a été de 14,0 mg DM m^{-2} (*B. californica*) et 191,8 mg DM m^{-2} (*E. australis*). Le ratio annuel *P/B* (Production/Biomasse) s'échelonne entre 0,242 (*H. frontalis*) et 0,643 (*M. microphthalmus*). Par comparaison aux autres régions, la région d'Oyashio a montré une production élevée et un ratio *P/B* faible. La forte production de la région d'Oyashio pourrait être reliée à la forte biomasse de ces espèces. A cause des conditions de température basses (3°C), les mysidacés et les décapodes pélagiques de la région de Oyashio pourraient avoir une croissance plus lente, un temps de génération plus long et un ratio *P/B* plus faible que dans les autres océans.

INTRODUCTION

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 15 000 species of Decapoda that have been described worldwide (De Grave et al., 2009). 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 the Pacific cod *Gadus macrocephalus* Tilesius, 1810 in the Doto area (eastern Hokkaido), the flathead flounder *Hippoglossoides dubius* Schmidt, 1904 in Funka Bay, and the walleye pollock *Theragra chalcogramma* (Pallas, 1814) in the Doto

area and the Sea of Japan (Yamamura et al., 1993, 2002; Kooka et al., 1997; Kimura et al., 2004). The biomass of crustacean micronekton in the Oyashio region is 10% of that of mesozooplankton, yet this 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 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 crustacean micronekton of Mysidacea and Decapoda in the Oyashio region, western subarctic Pacific. To accurately evaluate life histories of these animals, samples were collected using a fine mesh net (0.335 mm) that effectively captured small individuals and caused less damage to larger individuals. In addition to population structure, production was estimated by combining life history data and body mass data. The results were compared with information from other regions, and the biological features of the crustacean micronekton in the Oyashio region are discussed.

MATERIAL AND METHODS

Field sampling

Zooplankton samples (oblique tow of Bongo nets (70 cm mouth diameter, 0.335 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, 0.335 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, filtered through Whatman GF/F filters, extracted in 90% acetone in the dark for 24 hours, and processed using a Turner Design fluorometer.

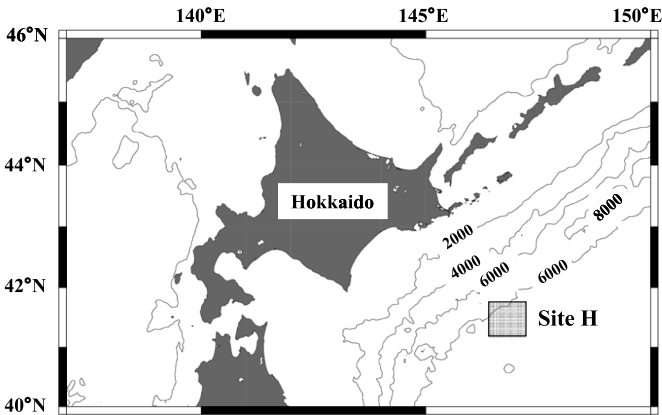


Fig. 1. Location of sampling station (Site H) in the western subarctic Pacific. Depth contours (2000, 4000, 6000 and 8000 m) are superimposed.

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 Von Bertalanffy equation:

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

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

Mass measurements

Mass measurements were conducted in the laboratory on land. Norpac net samples composed of mesozooplankton were filtered through pre-weighed 100 μm

mesh, and wet mass (WM) was measured with an electronic balance. WM for 150-500 m was determined by subtracting the 0-150 m WM data (g WM m⁻²) from the 0-500 m data. WM of Mysidacea and Decapoda was measured for each species based on Bongo net samples.

For the dominant species; three species of Mysidacea (*Eucopia australis* Dana, 1852, *Boreomysis californica* Ortmann, 1894 and *Meterythropus microphthalmus* W. Tattersall, 1951) and one species of Decapoda (*Hymenodora frontalis* Rathbun, 1902), BL-mass relationships 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 developmental stages. An aluminum pan was combusted at 480°C for 3 h to remove 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 water and blotting on aluminum pan. Specimens were dried in a drying oven (60°C) for 6 h, and the DM was measured. Ash was determined after incineration at 480°C for 6 h. AFDM was determined by subtracting Ash from DM (AFDM = DM - Ash). Relationship between BL and body mass is expressed by the following equation:

$$\log_{10}(\text{WM, DM or AFDM (mg)}) = a \times \log_{10}(\text{BL (mm)}) + b \quad (2)$$

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

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 ($\log_{10} W = at + b$, 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 ($\log_{10} N = at + b$, 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):

$$P = 0.5 \sum_{i=1}^n (N_{i-1} + N_i)(W_i - W_{i-1}) \quad (3)$$

where i is month. Using the above two equations, temporal changes in individual DM (W) and abundance (N) were calculated by month. Based on these monthly data, annual production (P) and annual mean biomass (B) were calculated for each

cohort. The annual P and annual mean B for each cohort of a given species thus computed were summed to yield respective values for the entire population of the species. Based on these values, annual production/biomass (P/B) ratios were also calculated.

RESULTS

Hydrography

Temporal changes in temperature, salinity, chlorophyll a , mesozooplankton biomass and their depth distribution from August 2002 through August 2003 are shown in fig. 2. Temperature showed seasonal variations above 200 m depth from $<1^{\circ}\text{C}$ (February to March) to $>7^{\circ}\text{C}$ (August) (fig. 2A). Temperature below 300 m was stable around 3°C throughout the year. Salinity ranged from 33.0 to 34.2. Salinity was lowest near the surface and increased 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. Mesozooplankton biomass varied between 34.6 and 493.9 g WM m^{-2} with maximum values 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 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).

Community structure

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

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

Taxa and species	2002						2003									
	9-10 August		9 October		11 February		13 March		11-12 May		21 May		4-28 June		23 August	
	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>Eucopia australis</i> Dana, 1852	9.10 (46.0)	4286.0 (83.2)	6.69 (44.8)	3303.5 (84.6)	24.18 (79.0)	4394.7 (91.0)	14.98 (54.2)	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)	7.24 (48.5)	548.3 (14.0)	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 microphthalma</i> W. Tattersall, 1951	0.42 (2.1)	6.0 (0.1)	0.69 (4.7)	49.0 (1.3)	- (-)	- (-)	0.58 (2.1)	4.1 (0.1)	0.93 (3.0)	31.2 (0.5)	32.87 (65.6)	912.2 (26.0)	1.00 (8.5)	42.0 (1.6)	21.98 (57.4)	176.2 (14.3)
<i>Gnathophausia gigas</i> W.-Suhm, 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)	0.15 (1.0)	1.0 (0.0)	- (-)	- (-)	- (-)	- (-)	0.18 (0.6)	1.5 (0.0)	0.31 (0.6)	2.6 (0.1)	- (-)	- (-)	- (-)	- (-)

TABLE I
(Continued)

Taxa and species	2002						2003									
	9-10 August		9 October		11 February		13 March		11-12 May		21 May		4-28 June		23 August	
	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>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)	4.87 (49.6)	177.1 (1.0)	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	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

Values in parentheses indicate percentage composition.

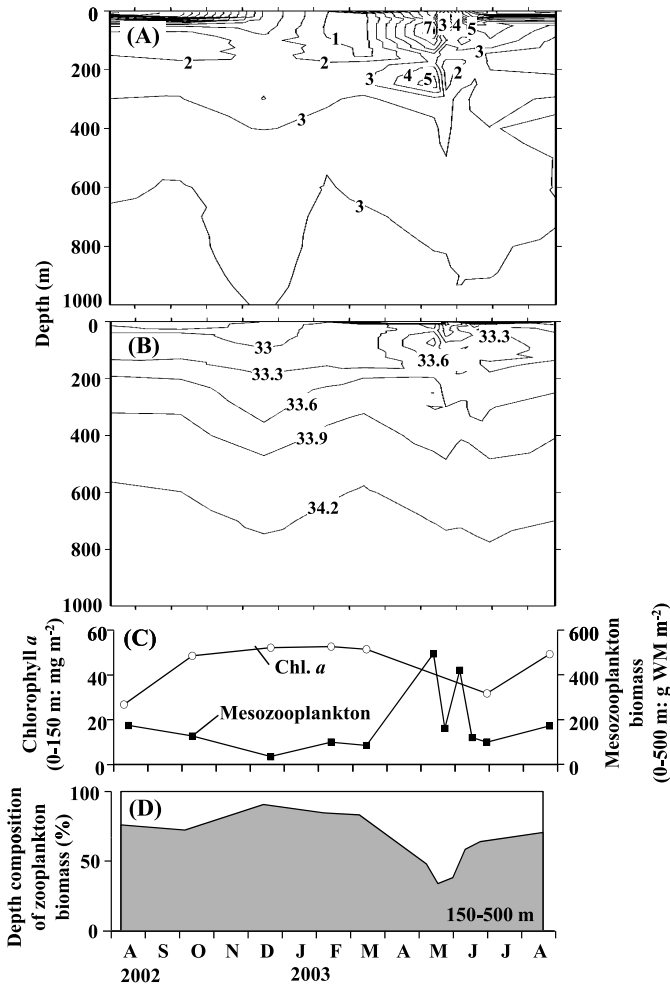


Fig. 2. Temporal changes at Site H from August 2002 to August 2003 in: A, temperature; B, salinity; C, chlorophyll *a* and mesozooplankton wet mass; D, depth distribution of mesozooplankton wet mass.

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

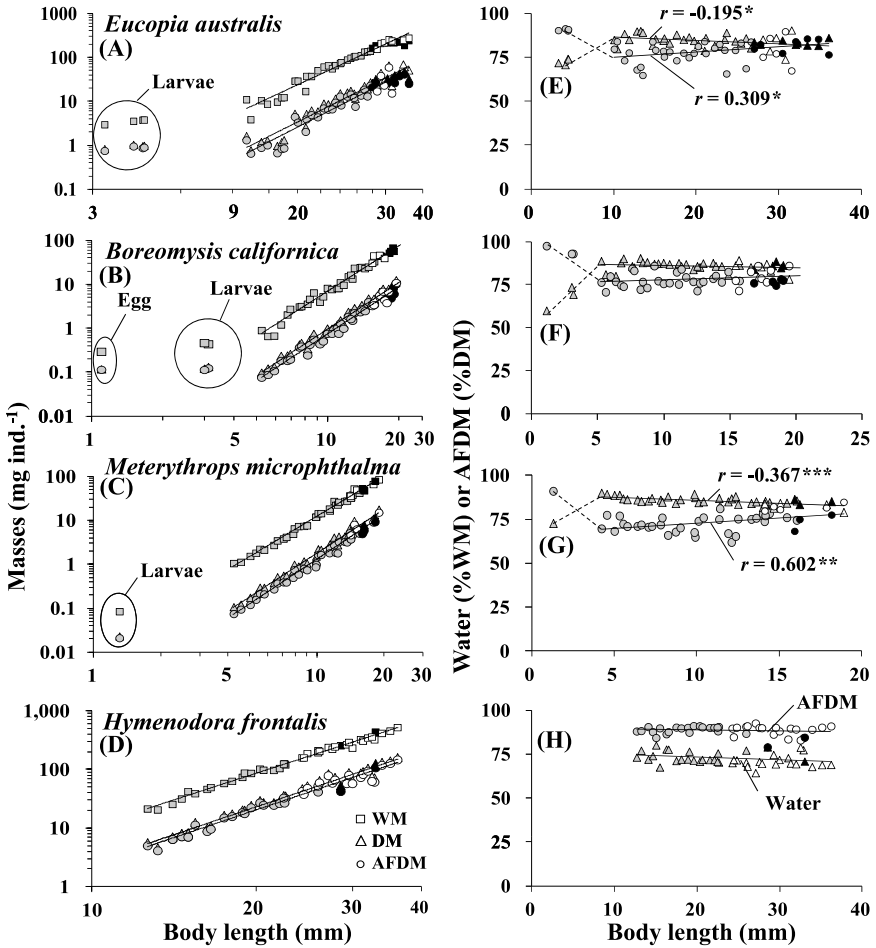


Fig. 3. Relationships between masses (WM, DM and AFDM) and body lengths of A, *Eucopeia australis* Dana, 1852; B, *Boreomysis californica* Ortmann, 1894; C, *Meterythropters microphthalma* W. Tattersall, 1951; D, *Hymenodora frontalis* Rathbun, 1902. Half-filled, open and filled symbols denote juveniles, females and males, respectively. For A-C, eggs or larvae were also measured. Developmental 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 juveniles to adults, regressions are shown with solid lines. * $p < 0.05$, *** $p < 0.0001$.

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.

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, *Meterythroptis microphthalma* W. Tattersall, 1951 and *Hymenodora frontalis* Rathbun, 1902 at Site H

Species	Unit	Regression model		n	r^2
		$\log_{10} Y = a \times \log_{10} X + b$			
		a	b		
<i>Eucopia australis</i> Dana, 1852	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> Ortmann, 1894	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>Meterythroptis microphthalma</i> W. Tattersall, 1951	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> Rathbun, 1902	WM	3.02	1.02	42	0.99***
	DM	3.16	1.00	42	0.97***
	AFDM	3.14	1.00	42	0.96***

*** $p < 0.0001$.

Population structure

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 smallest juveniles were dominant in May 2003. This cohort was traceable and grew to 30 mm 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 seen in May 2003. This cohort was traceable to maturity over two years, and their generation 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 they matured after two years. However, low abundance of this species prevented an estimation of longevity (fig. 4C). Because of low abundance, cohorts of the decapod *H. frontalis* could not be separated within a single sampling date. Thus, cohort analysis of this 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 had matured after two years and certain individuals were present during the third year. However, their longevity could not be determined because of the low abundance (fig. 4D).

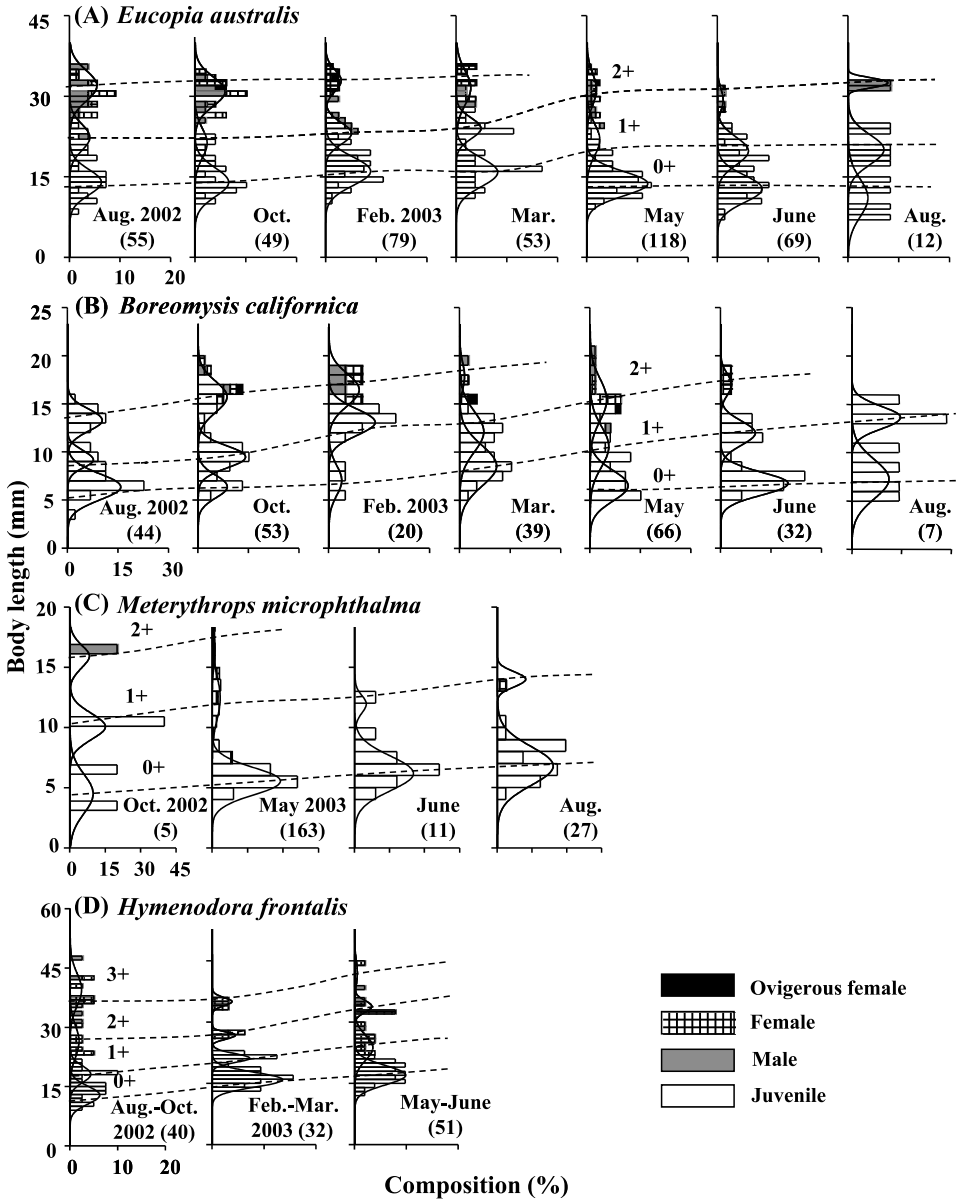


Fig. 4. Temporal changes at Site H from August 2002 to August 2003 in body length composition of A, *Eucopia australis* Dana, 1852; B, *Boreomysis californica* Ortmann, 1894; C, *Meterythropus microphthalmus* W. Tattersall, 1951; D, *Hymenodora frontalis* Rathbun, 1902. The number of individuals measured 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.

Life history and production

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

DISCUSSION

Abundance and biomass

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 (0.335 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), 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.

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, 1974). This is considered to result from crustacean micronekton relying on epipelagic mesozooplankton as food. Biomass ratios between

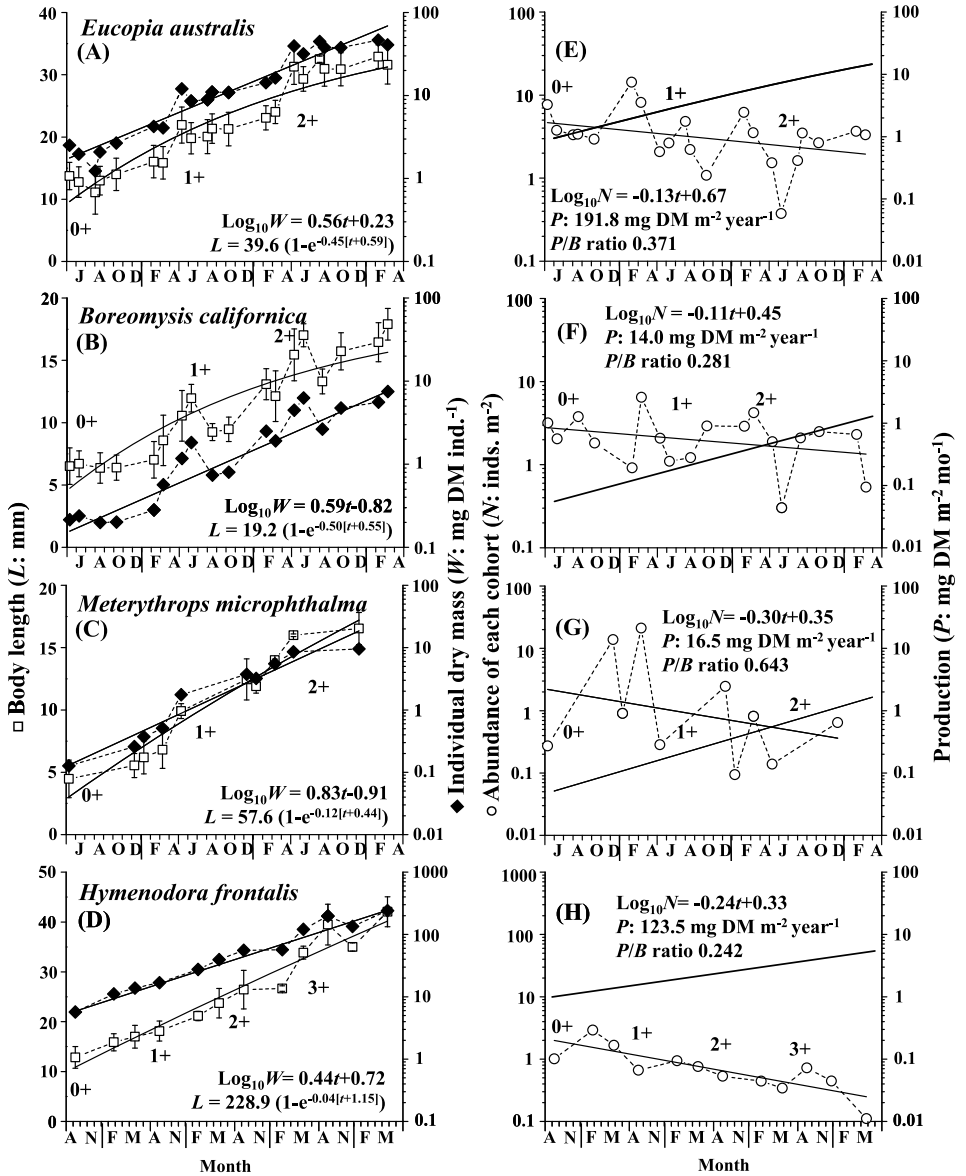


Fig. 5. Estimated growth curve for body length (open symbols) and dry mass (solid symbols) at Site H of A, *Eucopia australis* Dana, 1852; B, *Boreomysis californica* Ortmann, 1894; C, *Meterythroptis microphthalma* W. Tattersall, 1951; D, *Hymenodora frontalis* Rathbun, 1902. Abundance of each cohort (open symbols) from body length histogram (cf. fig. 4) and estimated production (solid lines) of: E, *E. australis*; F, *B. californica*; G, *M. microphthalma*; H, *H. frontalis*. Symbols and bars in A-D indicate means and standard deviations for each cohort. Annual production and production/biomass (P/B) ratios are also shown for E-H. t , time (year).

TABLE III
Comparison on abundance and biomass of Mysidacea and Decapoda from various oceans

Taxon and location	Depth range (m)	Abundance (ind. m ⁻²)	Biomass (mg WM m ⁻²)	Sampling gear (mesh size, mm)	Reference
Mysidacea					
Oyashio region	0-1000	11.7-50.1	1234-7883	Bongo net (0.335)	This study
Kosterfjorden	0-200	3.0	125*	Conical net (0.4)	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 (0.335)	This study
Arctic Ocean	0-200	6.1	–	Multinet (0.2)	Auel & Hagen (2002)
Kosterfjorden	0-1500	4.0	200*	Conical net (0.4)	Båmstedt (1988)
Sagami Bay	0-1000	–	3220	ORI net (0.33)	Aizawa (1974)
Kuroshio region	0-1000	–	26-1240	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	5.0-6.6	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)

* For comparison, dry mass data were converted to wet mass (WM) using water contents of this study (cf. table IV).

mesozooplankton and crustacean micronekton are known to be indices of ecological efficiency for the region (Blackburn, 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. Mauchline & Murano, 1977), although individuals were not identified to species. Compared with 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 Oyashio region than elsewhere in the subarctic Pacific. This may be because the Oyashio 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 to be higher in the Oyashio region than in the oceanic region studied by Nishikawa et al. (2001).

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, physiological studies on crustacean micronekton have revealed that they have adapted effectively to such environments (Childress, 1977). Deep-sea crustacean micronekton have larger body sizes compared to epipelagic species. This is due to the high water content of 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). Consequently, the high water content of crustacean micronekton may yield high growth rate per unit mass under food-limited deep-sea conditions. Specific gravity with nearly water may serve an energetic function, since nearly neutral buoyancy would require less swimming activity (Childress & Nygaard, 1974).

Water and AFDM contents of congener species of Mysidacea and Decapoda in this study are summarized in table IV. Water and AFDM content values from this study correspond well with values from previous studies. The decapods *Hymenodora* spp. consistently show lower water content and higher AFDM content than the three mysids (table IV). There is little change in water and AFDM contents throughout development from 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 (Båmstedt, 1988), measurements based on various seasons during this study do not confirm this effect.

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

TABLE IV

Comparison of water and AFDM content of three mysids (*Eucopia*, *Boreomysis*, *Meterythroptera*) and one decapod (*Hymenodora*) from various oceans

Taxon and species	Location	Water (%WM)	AFDM (%DM)	Reference
Mysidacea				
<i>Eucopia australis</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)	Kosterfjorden	–	85.3	Båmstedt (1978)
<i>Boreomysis arctica</i> (Krøyer, 1861)	Kosterfjorden	–	83.2	Båmstedt (1988)
<i>Meterythroptera microphtalma</i> W. Tattersall, 1951	Oyashio region	85.3	73.6	This study
<i>Meterythroptera microphtalma</i> W. Tattersall, 1951	Sea of Japan	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)

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.

Life history and production

According to Mauchline (1972), the effect of latitude and depth on life history of crustacean micronekton is summarized as: slower growth rate, larger body size

and longer generation length with increasing latitudes and depths. Generation length of bathypelagic Mysidacea is expected to be 3-7 times longer than for the epipelagic species. The low 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 species. For bathypelagic species, longer generation length may imply that a long time is spent in a sexually mature condition. This may be important for finding mates given the low population density of the deep-sea.

Comparisons of life history parameters of four congener mysids and decapods in this study are shown in table V. Life history in the Oyashio region is characterized by longer generation length and smaller minimum maturity size within the congener species. This may 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 provide a longer period to seek a breeding partner, as suggested by Mauchline (1972). However, the low temperature alone could not explain the slower growth rate of *M. microphthalma* in the southern Japan Sea. This is considered to be caused by the lack of predatory micronekton which is a special characteristic of the mesopelagic layer of the Japan Sea (Ikeda, 1992).

Within the four species examined in this study, the large-body sized decapod *H. frontalis* had the longest generation length (>45 months) (fig. 4D, table V). The family 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 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 contain a large amount of yolk (Omori, 1974). According to Omori (1974), *H. frontalis* and *H. 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 sampling gear may have impacted the quantitative collection of large, low density individuals. 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 accurate evaluation of the longevity of *H. frontalis*.

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 dominant Mysidacea species are observed during April to June (fig. 4A, B), recruitment of young for the two numerically minor species was seen in August to October (fig. 4C, D). According to Mauchline (1988), all mesopelagic crustacean micronekton in the Rockall Trough have seasonality in reproduction, while bathypelagic species reproduce throughout the year (no seasonality). The

TABLE V
Comparison on generation length, minimum maturity size and maximum body size of three mysids (*Eucopia*, *Boreomysis*, *Meterythrops*) and one decapods (*Hymenodora*) from various oceans

Taxon and species	Location	Habitat depth (m)	Habitat temperature (°C)	Generation length (months)	Maturity size (BL, mm)		Reference
					Minimum	Maximum	
Mysidacea							
<i>Eucopia australis</i> Dana, 1852	Oyashio region	>600 ^a	3	34	23.3	36.0	This study
<i>Eucopia grimaldii</i> Nouvel, 1942	Southern New England	–	–	–	32.0	32.0	Wigley & Burns (1971)
<i>Eucopia grimaldii</i>	Rockall Trough	1700	4	24?	25.0	37.0	Mauchline (1986, 1988)
<i>Eucopia unguiculata</i> (W.-Suhm, 1875)	Rockall Trough	900	8.5	24?	22.0	32.0	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	15.0	24.0	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	26.0	Wigley & Burns (1971)
<i>Meterythrops microphthalma</i> W. Tattersall, 1951	Oyashio region	360-1800 ^c	3	>24	7.0	18.9	This study
<i>Meterythrops microphthalma</i> W. Tattersall, 1951	Sea of Japan	0-1000	<1	36-48	14.0	21.0	Ikeda (1992)

TABLE V
(Continued)

Taxon and species	Location	Habitat depth (m)	Habitat temperature (°C)	Generation length (months)	Maturity size (BL, mm)		Reference
					Minimum	Maximum	
<i>Meterythropis picta</i> Holt & Tattersall, 1951	Rockall Trough	1500	4.5	15?	-	15.0	Mauchline (1988)
<i>Meterythropis robusta</i> S. I. Smith, 1879	Off Iceland	100-300	-	12-24	11.9	-	Asthorsson (1984)
<i>Meterythropis robusta</i> S. I. Smith, 1879	Gulf of Maine	110-150	-	-	8.5	12.0	Wigley & Burns (1971)
Decapoda							
<i>Hymenodora frontalis</i> Rathbun, 1902	Oyashio region	600-1100 ^d	3	>45	22.7	48.0	This study
<i>Hymenodora glacialis</i> Buchholz, 1874	Rockall Trough	1300-1700	3-3.5	?	29.0	62.0	Mauchline (1988)

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.

TABLE VI

Comparison of production, production/biomass (P/B) 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 and species	Production (mg DM m ⁻² year ⁻¹)	P/B ratio	Generation length (months)
Oyashio region			
<i>Eucopeia australis</i> Dana, 1852	191.8	0.371	34
<i>Boreomysis californica</i> Ortmann, 1894	14	0.281	34
<i>Meterythroptis microphtalma</i> W. Tattersall, 1951	16.5	0.643	>24
<i>Hymenodora frontalis</i> Rathbun, 1902	123.5	0.242	>45
Mean		0.384	
SE Sea 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	

fact that all four species in this study showed clear seasonality in recruitment of young suggests that they all have seasonality in reproduction. The presence 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., 1998; Kasai et al., 2002). Differences in the timing of recruitment of young between the two 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 other waters (Mediterranean) (table VI). Compared with the values in the Mediterranean, high production and low P/B ratios were the case in the Oyashio region. The high production 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 (9.8–11.2°C) (Cartes et al., 2001), they may have shorter generation lengths and higher P/B 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/B ratios than in other oceans.

For P/B ratios of invertebrates, Banse & Mosher (1980) reported the equation: $P/B = 0.65M_s^{-0.37}$, where M_s is caloric content (kcal) of mature individuals living under 5-20°C temperature conditions. By using previously reported values for caloric contents of Mysidacea and Decapoda as 4178-7533 cal g⁻¹ DM (Mauchline, 1980), the P/B ratios of the four species in this study are predicted to be 0.51-2.19, which is greater than the estimates 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 should be noted that the formula by Banse & Mosher (1980) is based on the coastal or neritic species living under sufficient food conditions, and there is a wide range in the precision of prediction using this method (50-200%). The low temperature conditions (3°C) in the deep Oyashio region are considered to be a reason that crustacean micronekton in this region have lower P/B ratios than other regions. For the low P/B ratio of mysids under low habitat temperature, a similar situation was reported for Antarctic mysids (Siegel & Muhlenhardt-Siegel, 1998).

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