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Vertical distribution, life cycle, and developmental characteristics of mesopelagic calanoid copepod *Gaidius variabilis* (Aetideidae) in the Oyashio region, western North Pacific Ocean.

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Abstract

Vertical distribution, life cycle, and developmental characteristics of the mesopelagic copepod *Gaidius variabilis* in the Oyashio region were investigated by combining the analyses of field copepodite populations with laboratory-rearing data of egg hatching and naupliar development. Field samplings from five discrete depths between the surface and ≤ 2000 m were made approximately every month for one year. Most populations of *G. variabilis* occurred at 600-1000 m depth. A modest degree of reversed diel vertical migration behavior and some stage-specific depth-distribution patterns were noted. All copepodite stages were observed throughout the year, suggesting a year-round spawning of *G. variabilis*. From a prominent abundance peak of copepodite stage 1 (C1) seen in June-August, together with development times of eggs and nauplii obtained in laboratory-rearing experiments, the major spawning season was extrapolated to April-June, the phytoplankton bloom season. Tracing the peak abundance of each copepodite stage (distinguishing males and females for C4-C6), the generation lengths of males and females were deduced as 2 and 1 yr, respectively. All between-stage increments in terms of wet-, dry-, and ash-free dry weights were greatest in C3/C4, and least in C5/C6 for both males and females. The increments in C3/C4 and C4/C5 were greater for males than for females, reflecting a longer stage duration of the males. These weights did not increase in C5/C6 males, possibly because feeding ceased in C6 males. These results of *G. variabilis* are compared with those of some mesopelagic copepods previously reported from other regions.

Introduction

In the subarctic Pacific, the life histories and associated vertical distribution patterns of oceanic calanoid copepods have been studied extensively for large grazers, such as *Neocalanus* spp., *Eucalanus bungii*, and *Metridia pacifica* (Miller et al. 1984; Batchelder 1985; Miller and Clemons 1988; Kobari and Ikeda 1999), because of their high abundance and importance as secondary producers. Except for these primarily epipelagic species, little data have been available for those living in meso- and bathypelagic zones in the subarctic Pacific until the recent studies on *Paraeuchaeta elongata* (Ozaki and Ikeda 1999) and *Pleuromamma scutullata* and *Heterorhabdus tanneri* (Yamaguchi and Ikeda 2000). Other than subarctic Pacific, presently available information about life cycle patterns of meso- and bathypelagic copepods include those of *P. elongata* (Morioka 1975; Ikeda and Hirakawa 1996) and *Scolecithricella minor* (Yamaguchi et al. 1999) in the Japan Sea, *Chiridius armatus* in the Norwegian and Swedish fjords (Matthews 1964; Bakke and Valderhaug 1978; Båmstedt 1988), *Euchaeta norvegica* in the Norwegian fjords (Wiborg 1954; Båmstedt and Matthews 1975; Bakke 1977), *Euchaeta* spp. in the northeastern North Atlantic (Mauchline 1994), *Pleuromamma gracilis* in the Adriatic Sea (Shmeleva and Kovalev 1974), *Pleuromamma robusta* in the North Atlantic (Park 1997), and *Microcalanus pygmaeus* and *Ctenocalanus citer* in the Weddell Sea (Schnack-Schiel and Mizdalski 1994).

Gaidius variabilis Brodsky (Aetideidae) is a medium-sized oceanic calanoid copepod distributed in the mesopelagic zone of the subarctic Pacific, Bering Sea, Okhotsk Sea, and Japan Sea (cf. Brodsky 1950). Studies have shown that *G. variabilis* is abundant at 100-500 m depth in the Bering Sea (Minoda 1971), 300-2000 m depth in the Japan Sea (Sazhin and Vinogradov 1979), and 400-1400 m in the western subarctic Pacific and Okhotsk Sea (Yamaguchi et al. 1998). *G. variabilis* is one of the important prey items of mesopelagic gonostomatid and myctophid fishes in the western subarctic Pacific, according to Gordon et al. (1985). Feeding habits of copepods belonging to the family Aetideidae have been considered as omnivores/detritivores (Arashkevich 1969; Alvarez and Matthews 1975; Falkenhaus et al. 1997a). All these results suggest the possibly important role of *G. variabilis* in the mesopelagic trophodynamics in the subarctic Pacific.

The present study aims to evaluate vertical distribution, life cycle, and developmental characteristics of *Gaidius variabilis* in the Oyashio region (western

subarctic Pacific) by combining analysis of seasonal field data with laboratory-rearing experiments. The present results are compared with congener species in other seas and with shallow-living copepods.

Materials and methods

Field samplings

Samples were collected at nearly monthly intervals from 4 September 1996 through 5 October 1997 on board the T.S. “Oshoro-Mar” and T.S. “Hokusei-Mar” of the Faculty of Fisheries of Hokkaido University, R.V. “Tansei-Mar” of the Ocean Research Institute of Tokyo University, R.V. “Hokko-Mar” of the Hokkaido National Fisheries Research Institute, and R.V. “Hokushin-Mar” of the Kushiro Fisheries Experimental Station (Table 1). All samplings were conducted between 41°30'–42°30'N and 145°00'–146°00'E in the Oyashio region off southeastern Hokkaido (hereafter referred to as Site H) (Fig. 1).

Zooplankton were collected with a closing net designed by Kawamura (1989) (60-cm mouth diameter, 0.1-mm mesh) equipped with a Rigosha flowmeter in the mouth of the net, and a TSK Depth Distance Recorder (Tsurumi Seiki, Yokohama, Japan) or RMD Depth meter (Rigosha, Tokyo, Japan) on a suspender rope. The net was towed vertically at 1 m s⁻¹ through five discrete depth strata: 0–the bottom of thermocline (Th), Th–250, 250–500, 500–1000, and 1000–≤2000 m (Table 1). When we failed to obtain this complete set of discrete depth series, missing depth stratum data were interpolated using data from the most recent samplings before and after the sampling date (see Table 1). Most samplings were conducted at night. To investigate the diel vertical migration patterns, a set of day-night samplings were conducted on 8 December 1996, 11 April 1997, and 5 October 1997 (Table 1). After collection, zooplankton samples were preserved immediately in a 5% formalin-seawater buffered with borax. Temperature and salinity were determined with a CTD system (Neil Brown, General Oceanics, Miami, USA or Sea Bird Electronics, Washington, USA) at each zooplankton sampling. Chlorophyll a concentration data at Site H were supplied by Drs. A. Tsuda, H. Saito, and H. Kasai of the Hokkaido National Fisheries Research Institute.

Identification and enumeration

In the land laboratory, *Gaidius variabilis* were sorted from the samples and counted under a dissecting microscope. Congeneric species (*G. brevispinus* and *G. tenuispinus*) were also found in the present materials, but the abundance of these congeneric species were much less than that of *G. variabilis* (<5%). Descriptions of the development stages other than adults are not available for this species. To identify the pre-adult copepodite stages, we referred to descriptions of other species of the family Aetideidae, i.e. *Chiridius armatus* and *Bradyidius bradyi* (Matthews 1964), and *Chiridius gracilis* (MacLellan and Shih 1974). Based on the presence of a fifth swimming leg (males) or not (females), identification of males and females was made for Copepodite stage 4 (C4) to adults (C6).

The mesh size of the nets used (0.10 mm) in this study was small enough to retain the C1 through adult stages of *Gaidius variabilis* (diagonal distance of the mesh is 0.14 mm, as compared with the prosome width of 0.20 mm for C1).

Depth where population resided

To make a quantitative comparison possible, the depth where 50% of the population resided (D50%) was calculated (cf. Pennak 1943). Additional calculations were made at depths where 25% (D25%) and 75% (D75%) of the population occurred.

Body length and weight

Prosome length (PL) of each copepodite stage was measured to the nearest 0.05 mm under a dissecting microscope fitted with an eye-piece micrometer. Wet weight (WW) of specimens was determined after rinsing the preserved specimens briefly with distilled water and blotting them on filter paper (cf. Omori and Ikeda 1984). The specimens were then placed in a drying oven (60°C) for 5 h, and the dry weight (DW) was measured. Ash weight (ASH) was determined by weighing the specimens before and after incineration at 480°C for 5 h. From these data, water content (WATER, % of WW) and ash-free dry weight (AFDW, % of DW) were estimated using the following equations: $\text{WATER} = (\text{WW} - \text{DW}) \times 100 / \text{WW}$, and $\text{AFDW} = (\text{DW} - \text{ASH}) \times 100 / \text{DW}$. Samples were weighed with a microbalance (Mettler Toledo MT5) to a precision of 1 μg .

Laboratory experiments

Live adult females of *Gaidius variabilis* were collected at a station (42°00'N, 141°30'E; bottom about 500 m deep) off Cape Esan, northwestern Pacific, on 15 July and 3 August 1997 with vertical hauls of an 80-cm ring net (0.33-mm mesh) from near the bottom to the surface. Concurrently, seawater was collected from 300 m depth with 20-liter Van-Dorn bottles and used for the following experiments. Upon retrieval of the net, the adult females were sorted and placed in 20-liter plastic containers filled with chilled seawater (about 2°C) and transported to the shore laboratory. At the laboratory, several batches of 10 to 20 females each were placed in a 500-ml polyethylene cylinder with a mesh (0.33-mm) bottom (to prevent eggs from being consumed by the females), which was suspended in 1000-ml glass beakers filled with 800-ml of Whatman GF/F filtered seawater. The experiment was run at 0.5, 3, 5, and 10°C in the dark. As food, a mixture of laboratory cultures of microalgae (*Heterocapsa triquetra*, *Chaetoceros gracilis*, and *Pavlova* sp.) were provided at a final concentration of $>2.0 \times 10^3$ cells ml⁻¹. To estimate clutch size, spawning interval, and number of successive spawning, 10 females were reared individually at 5°C in a separate experiment. The beakers were inspected daily for eggs. Upon release, individual eggs were transferred carefully into a 10-ml glass vial filled with the filtered seawater and incubated at 0.5, 3, 5, or 10°C. The development of nauplius stage 1 was followed up to the C1 stage by collecting their molts.

Results

Hydrography

The Oyashio is a western boundary current of the subarctic circulation in the North Pacific that flows southwestward along the Kuril Islands and Hokkaido until it reaches the east coast of northern Honshu, Japan, where it turns east at about 40°N (cf. Kono 1997). The Site H of this study is located at the southern end of the Oyashio. Over the study period, surface temperatures ranged from 2°C (March to April 1997) to 18°C (September to October 1996 and 1997) (Fig. 2a). Surface temperatures above 10°C occurred from September to November 1996 and from June to October 1997, when the thermocline was well established at 20-50 m depth. Temperatures below 3°C occurred from February to April 1997, when the top 150 m water column was well mixed vertically. Seasonal temperature changes decreased with increasing depth. Below 300 m depth, temperatures remained below 3.5°C throughout the year.

Surface salinity ranged seasonally from 32.2 to 34.1‰. Relatively high surface salinities (>33.5‰) occurred from December 1996 to January 1997 (Fig. 2b). Oyashio Water, characterized by salinities between 33.0 and 33.5‰ and temperatures lower than 3°C (Hanawa and Mitsudera 1987), was observed at 0-150 m from February to April 1997. Less saline water (<33.0‰) recorded near the surface during other months is considered to be derived from the Okhotsk Sea (Kono, personal communications). Salinity below 500 m depth changed only slightly throughout the year (range: 34.0-34.5).

Phytoplankton biomass, estimated as chlorophyll a concentrations, showed a drastic seasonality (Fig. 2c). Chlorophyll a concentrations at the surface were about 0.4 mg m⁻³ from August 1996 to the end of March 1997, then increased rapidly to >9 mg m⁻³ in May 1997, where concentrations above 2 mg m⁻³ extended down to 50 m depth. Surface chlorophyll a concentrations decreased to 2 mg m⁻³ by the end of June and were less than 1 mg m⁻³ toward the end of 1997. Chlorophyll a concentrations below 100 m depth were <0.2 mg m⁻³ throughout the year.

Vertical distribution

Most *Gaidius variabilis* populations were distributed below 500 m depth throughout the year. Day-night vertical distributions observed on 8 December 1996, 11 April, and 5 October 1997 exhibited a nocturnal descent pattern on all occasions (Fig. 3a). The magnitude of diel vertical migration of the entire population ranged from 80 m in October (daytime D50% = 990 m, and nighttime D50% = 1070 m) to 260 m in December (daytime D50% = 885 m, and nighttime D50% = 1145 m). Over the entire study period, the nighttime depths of D50% for the whole population ranged from 611 m (23 June 1997) to 1145 m (8 December 1996), but seasonal variations in the nighttime D50% were not significant ($p=0.65$, one-way ANOVA) (annual mean nighttime D50% = 812 [± 184 , 1 SD] m, Fig. 3a).

Between-stage differences in the nighttime D50% were significant ($p=0.006$, one-way ANOVA, Fig. 3b). The differences between females and males were not significant in C4 and C5 ($p=0.51$, Wilcoxon two-sample test), but significant in C6 ($p=0.01$), so the data for both sexes were separated only for C6 in Fig. 3b. The occurrence of C2 was the deepest (annual mean nighttime D50% = 983 [± 304] m), and the depth of occurrence became gradually shallower from C2 to C6F. The C6F

occurred at the shallowest depth, with its annual mean nighttime D50% of 646 (± 232) m. The magnitude of ontogenetic vertical migration was calculated as 337 m (983 m of C2 minus 646 m of C6F). The C6M was distributed deeper than C6F (annual mean = 782 [± 180] m).

Abundance/population structure

The C1 stage of *Gaidius variabilis* occurred throughout the year, but they were most abundant from 23 June to 17 August 1997 and very few in December-May (Fig. 4). Assuming the repetition of the same annual cycle, a sequential development of the major C1 population seen in June-August could be traced; i.e. developing to C2 in September-October and then C3 in October-December. The seasonal variations in abundance were less pronounced in C4 to C6. Combined data of females and males may obscure the developmental sequence from C4 to C6. For further analysis see “Life cycle” in the Discussion section.

Sex ratios of C4-C6 differed; females dominated in C4 and C6 (annual mean female:male ratio = 1.63:1 for C4, 4.45:1 for C6), and males dominated in C5 (0.78:1). Integrated sex ratio over C4-C6 was nearly equal (0.97:1).

Abundance data were converted to biomass (bottom panel of Fig. 4), combining the individual number and DW of each copepodite stage mentioned below (DW, Table 2). The biomass of *Gaidius variabilis* varied seasonally from 95 to 351 mg DW m⁻², with an annual mean of 221 mg DW m⁻². Biomass fractions of C1-C5 were greater than those of adults (annual mean 64 [± 9] %) (Fig. 4).

Body length and weight

All PL, WW, DW, and AFDW increased progressively from C1 to C3 (Table 2). After C4, sexual differences in these parameters became evident. The WW, DW, and AFDW of males were much greater than those of females at C4 and C5, but the reverse was the case at C6.

To analyze the body allometry, a power regression model was adopted; $W = aL^b$ (or $\log_{10} W = b \cdot \log_{10} L + \log_{10} a$), where W is WW, DW, or AFDW (all in μg), L is PL (mm), and a and b are fitted constants. The data of *Gaidius variabilis* closely fitted the regression model ($r^2 = 0.98-0.99$, Table 2), resulting in constant b (power) values of 3.14-3.32. Water contents ranged from 66.0% (C5M) to 78.4% of WW

(C5F). Water contents differed significantly between stages ($p < 0.0001$, one-way ANOVA). Subsequent analysis showed greater water contents in females than males ($p < 0.001$, Fisher's PLSD). AFDW ranged from 69.7% (C3) to 88.5% of DW (C5M), and also differed significantly between stages ($p < 0.0001$, one-way ANOVA). AFDW was greater in late copepodite stages than in early copepodite stages ($p < 0.001$, Fisher's PLSD).

Spawning and early development

Adult females of *Gaidius variabilis* laid a batch of 4 to 23 spherical eggs (mean egg diameter = $325 [\pm 11, 1SD] \mu\text{m}$, $N=20$). The eggs were slightly heavier than seawater and sank to the bottom of the containers. The spawning interval was 5 to 19 days, and the maximum number of successive spawning observed was five.

The egg hatching time was the longest at 0.5°C (7.9 d) and shortened consistently with increasing temperature (2.7 d at 10°C) (Table 3). Egg hatchability ranged from 33% to 89%. Naupliar development time was 29.2 d and 24.5 d at 5°C and 10°C , respectively (no data at 0.5 and 3°C). Successful survival from the N1 to C1 stages was 35% at 5°C , and 57% at 10°C . The relationship between development time (D , days) and temperature (T , $^\circ\text{C}$) was expressed by the Belehrádek equation: $D = a(T - \alpha)^b$, where a , b ($= -2.05$), and α are fitted constants (cf. McLaren et al. 1969; Corkett and McLaren 1970). Fitting the data to the Belehrádek equation yielded $D = 1394 (T + 12.066) - 2.05$ for egg hatching time, and $D = 10862 (T + 12.066) - 2.05$ for naupliar development time (Fig. 5).

Discussion

Vertical distribution

Diel vertical migration (DVM) is a behavioral characteristic known in many zooplankton, typically ascending to the surface layer at night and descending to depth during daylight hours, the so called 'normal' DVM (cf. review of Mauchline 1998). In contrast, *Gaidius variabilis* exhibited DVM in which the day-night patterns were reversed (Fig. 3a). Such a reverse DVM has been observed in some *Pseudocalanus*, *Calanus*, and *Sapphirina* species (Ohman et al. 1983; Bollens and Frost 1989; Chae and Nishida 1995). Both normal and reverse DVM behavior of zooplankton have been interpreted as avoidance from predators (Ohman et al. 1983; Ohman 1990; Lampert

1993). In the Oyashio region, *G. variabilis* have been reported as an important diet component of gonostomatid fishes (*Cyclothone atraria* and *C. pseudopallida*) and myctophid fishes (*Stenobrachius nannochir* and *Lampanyctus jordani*) (Gordon et al. 1985). Among these fishes, only *L. jordani* have a diel vertical migration (daytime: 400-700 m, nighttime: 60-700 m), and the other three are non-migrators residing at 400-700 m depth both day and night (Miya and Nemoto 1991; Watanabe et al. 1999). Compared with depth ranges of these predators, *G. variabilis* are distributed slightly deeper (annual mean night D50%: 812 m), so the daytime ascending behavior of *G. variabilis* apparently is not explainable by the predator-avoidance hypothesis. From the viewpoint of food availability, aetideid copepods including *G. variabilis* are omnivores/detritivores and fecal pellets are frequently found in their guts (Arashkevich 1969; Minoda 1971; Harding 1974; Greene 1985, 1988; Falkenhaus et al. 1997a), implying that their upward migration may be advantageous to increase energy gain by feeding when prey items are more abundant in the upper layers. Clearly, more information is needed about the vertical distribution pattern of the prey of *G. variabilis*, and the diel feeding rhythm of predatory mesopelagic fishes (if any) to interpret the reverse DVM of *G. variabilis* from the viewpoint of adaptive significance.

Information about ontogenetic vertical migration (OVM) of mesopelagic copepods is currently limited to only a few species belonging to the families Euchaetidae (Morioka 1975; Binet 1977) and Aetideidae (Richter 1994; Falkenhaus et al. 1997a). Although the magnitude of OVM and stage-specific depth distribution differ greatly between species, developmental ascent is a common characteristic of these copepods. For *Gaidius variabilis* studied here, the developmental ascent was seen from C2 to C6 females (Fig. 3b). Eggs and nauplii of *G. variabilis* were not collected in the present study, but judging from the data of C1 and C6, their distribution may be estimated as within 500-1000 m depth. Assuming this, the magnitude of the entire OVM of *G. variabilis* calculated in this study (337 m) is much less than that of OVM (500- >1000 m) for large grazing *Neocalanus* copepods in the subarctic Pacific (Miller et al. 1984; Kobari and Ikeda 1999).

Life cycle

The occurrence throughout the year of C1 and C6 adults suggests a continuous spawning of *Gaidius variabilis* in the Oyashio region. From the Belehrádek relation

between temperature and egg hatching time and naupliar development established in this study (Fig. 5), the likely spawning time for the abundance peak of C1 in June-August (Fig. 4) can be estimated. Designating a habitat temperature of 2.5°C (the temperature at ca. 800 m depth where the most of the population resided throughout the year, cf. Figs. 2 and 3), the Belehrádek equations (Fig. 5) predict the development time as 5.7 d for eggs and 44.8 d for naupliar stages, i.e. development from eggs to C1 is $5.7+44.8=50.5$ d. Thus, it is estimated that a large spawning of *G. variabilis* took place in April-June 1997 to form the peak of C1 in June-August 1997. It is calculated that development time from eggs to C3 is ca 6 mo (C3 dominated in October-December, Fig. 4).

The development sequence of the peak could be traced up to C3, but was obscured beyond C3 (Fig. 4). We consider that the development times of C4-C6 are different between males and females, and these differences are masking the developmental sequences beyond C3. For this reason, the accumulation pattern of body organic matter of *Gaidius variabilis* was different between males and females, and males have significantly greater accumulation than females in C4 and C5 (see “Characteristics of eggs and body allometry” below). Sexual differences in development time have been noted previously in other copepods; *Euchaeta norvegica* in Loch Etive (Hopkins 1982), *Metridia longa* in Balsfjorden (Tande and Grønvik 1983), and *Pseudocalanus acuspes* in Balsfjorden (Norrbín 1994).

The population structure of C4-C6 *Gaidius variabilis* was re-analyzed by separating females and males (Fig. 6). In females, C4 dominated in September-December 1996 (0.42-0.52 of the total C4-C6), C5 in January-March 1997 (0.38-0.40), and C6 in May-June 1997 (0.64-0.65). In males, C4 dominated in March-April 1997 (0.61-0.72), C5 in August-October 1997 (0.74-0.78), and C6 in December 1996-February 1997 (0.25-0.28). Thus, the development of C3 to C6 females takes 6-7 mo (October-June), while C3 to C6 males takes 14-15 mo (October-December of the next year, as shown by arrows in Fig. 4). Combining the development time from eggs to C3 mentioned above (6 mo), the generation time is now estimated as 12-13 mo for the females and 20-21 mo for the males. Taking into account large marginal errors due to a long sampling gap (ca. 1 mo) of this study, the generation time of *G. variabilis* is approximately one yr for females and 2 yr for males. The observed maturation of females well in advance of males (=proterogyny) in *G. variabilis* appears to be a new

development pattern for marine planktonic copepods, and adaptive significance of proterogyny in mesopelagic environments is a subject for future research.

It is noted that the estimated major spawning season of *Gaidius variabilis* (April-June) was well synchronized with the phytoplankton bloom in the Oyashio region (Fig. 2c). Aetideid copepods are classified as omnivores/detritivores as mentioned above. Since diatoms are estimated to sink at a speed of approximately 175 m d⁻¹ in the subarctic Pacific, regardless of taxa, size, or morphology (Takahashi 1986), they may reach the depth of *G. variabilis* (800 m) live in 4.6 d (800/175). Since C6 females of *G. variabilis* are numerous in April-June (Fig. 6) active spawning may be induced by a large food (phytoplankton) supply from the upper layers. Matched timing of spawning and phytoplankton bloom has also been observed in a aetideid copepod *Chiridius armatus* in Malangen, northern Norway (Falkenhaus et al. 1997b). For epipelagic herbivorous copepods, food supply is an important mechanism which controls the magnitude of their spawning (Runge 1985; Hirche and Bohrer 1987; Peterson 1988).

There is no comparable information about the life cycle of *Gaidius* species. As a mesopelagic aetideid copepod, life cycles of *Chiridius armatus* have been studied intensively in the Norwegian and Swedish fjords, resulting in a half-year life cycle with an intense spawning in mid-winter and mid-summer in Korsfjorden (Bakke and Valderhaug 1978), or one-year life cycle with a main spawning in September-March in Raunefjorden (Matthews 1964). Båmstedt (1988) noted that the population of this species in Kosterfjorden western Sweden has one-year life cycle, which is similar to that described by Matthews (1964). The two-year generation time of male *G. variabilis* in the Oyashio region in the present study is thus longer than the 1-2 generations per year of *C. armatus* in the Norwegian and Swedish fjords. While different species make meaningful comparison impossible, dissimilar habitat temperatures between the fjords (5-8°C, cf. Falkenhaus et al. 1997b) and the Oyashio region (2-4°C, Fig. 2a) may be considered as one of the possible attributes.

Characteristics of eggs and body allometry

The spawning pattern of calanoid copepods is divided into two types: free spawner (or broadcast-spawner), and egg-sac spawner (or egg-brooding spawner). Among aetideid copepods, *Chiridius gracilis* and *Euchirella pseudopulchra* are egg-sac spawners

(MacLellan and Shih 1974; Ohman and Townsend 1998), and *Chiridius armatus* and *Aetideus armatus* are free spawners (Matthews 1964). *Gaidius variabilis* was demonstrated to be a free spawner in the present study.

The egg size of calanoid copepod is proportional to the body size of adult females. Mauchline (1998) presented the relationship between egg size and prosome length of adult females for free spawners as: $Y=0.032X+0.06$, where Y is egg diameter (mm), and X is prosome length (mm). From this relationship and $X=3.02$ mm for *Gaidius variabilis* females (Table 2), the egg diameter of *G. variabilis* is predicted as 0.16 mm, which is much smaller than the observed egg diameter (0.33 mm) in this study. This discrepancy may be due to the fact that the data Mauchline used are mainly of epipelagic copepods. In other studies, Mauchline (1991, 1995) noticed divergent egg sizes for deeper-living copepods from the relationship between egg size and body length, and demonstrated that within genus *Euchaeta* (all egg-sac spawners) the egg diameter increases with increasing depth of occurrence. Although data for egg diameter are extremely scarce for deeper-living free-spawning copepods, the present results of *G. variabilis* suggest that increasing egg diameter with depth of occurrence may also be the case for free-spawning copepods. According to Mauchline (1998), most free-spawning copepods release a batch of 3-50 eggs at discrete time intervals. The batch egg number observed for *G. variabilis* in this study (4 to 23) falls well within the general range of 3-50 eggs of free-spawning copepods summarized by Mauchline (1998).

Based the data on PL, WW, DW, and AFDW of C1 through C6 given in Table 2, the increments in terms of PL, WW, DW, and AFDW from premolt stages (increment= [postmolt size-premolt size]/ premolt size; cf. Mauchline 1998) were calculated for each copepodite stage (Fig. 7). The increment based on PL ranged from 0.11 for C5M/C6M to 0.42 for C3/C4M, and was less variable than increments based on weights (Fig. 7). The increments in terms of WW, DW, and AFDW paralleled each other well, and showed large differences between stages. The increments determined by weights increased progressively during development from C1 to C4, and showed a maximum in C3/C4M (increments in WW, DW, and AFDW were 1.95, 2.51, and 2.95, respectively). The increments based on weights were much greater for males than for females in C3/C4 and C4/C5, but reversed in C5/C6. Added to greater weight increments, C4 and C5 males contain less water than C4 and C5 females (Table 2),

suggesting that accumulation of dry matter in the body is more intensive for the former than the latter. In terms of AFDW, the C3/C4M and C4M/C5M are 1.4 and 1.8 times greater than the C3/C4F and C4F/C5F (Table 2). The negative increment (i.e. degrowth) seen in C5/C6 males (Fig. 7) may be due to the degeneration of feeding appendages of adult males *Gaidius variabilis* (Brodsky 1950), a common phenomenon seen in aetideid copepods (Matthews 1964; MacLellan and Shih 1974). Degeneration of feeding appendages implies that feeding ceases, therefore body organic matter is utilized for metabolism and production of spermatophores leading to the loss in weight.

As a mesopelagic copepod, between-stage increment has been calculated for *Paraeuchaeta elongata* in the Japan Sea by Ikeda and Hirakawa (1996). The increment patterns across copepodite stages of *P. elongata* are consistent with the patterns of *Gaidius variabilis* in that the increment is greatest at C3/C4, and least at C5M/C6M (*P. elongata* cease feeding at C6M like *G. variabilis*), but the former differs from the latter in that the greatest increment seen at C3/C4 is more marked (5.0 vs. 3.0) and differences in increments between males and females are not appreciable, except for C5/C6 (male>female for *G. variabilis*). In a recent study, the greatest increment is also found at C3/C4 (ca. 5.0) in another mesopelagic copepod *Heterorhabdus tanneri* (Yamaguchi and Ikeda 2000). Mauchline (1998) compiled increment data for DW of marine copepods (mostly of shallow-living species) and showed that increments tended to increase progressively with stage number in copepodites (only females) and reach the maximum around 2.0. Therefore, it seems there are some differences in organic-matter accumulation in the body between epipelagic and mesopelagic copepods, but this conclusion is still premature because of the paucity of data for mesopelagic copepods.

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Figure Legends

- Fig. 1.** The Oyashio region in the western subarctic Pacific Ocean (a), and the sampling site (“Site H”, shaded) in the Oyashio region (b). Depth contours (200, 1000, 3000, 5000, and 7000 m) are superimposed in (b).
- Fig. 2.** Seasonal changes in vertical profiles of temperature (°C) (a), salinity (‰) (b), and chlorophyll a (mg m⁻³) (c) at Site H. Note the depth scale of (c) is not the same as those of (a) and (b). Solid triangles on top abscissa denote sampling dates.
- Fig. 3.** *Gaidius variabilis*. Day/night and seasonal (a), and developmental (b) changes in vertical distribution at Site H. Bathymetric distribution of the population is defined as depths where the 50% of the population was distributed (D50%), and the vertical bars the range where 25-75% of the population (D25% and D75%) resided. Open and closed symbols in (a) indicate daytime and nighttime data, respectively.
- Fig. 4.** *Gaidius variabilis*. Seasonal changes in numerical abundance of each copepodite stage and biomass at Site H (integrated over 0-2000 m). x and horizontal broken line in each panel denote annual mean abundance. Arrows show estimated developmental sequences of cohorts (see text for details).
- Fig. 5.** *Gaidius variabilis*. The relationship between egg hatching time or naupliar development time (D) and temperature (T, °C) fitted to the Belehrádek function. Vertical bars represent 95% confidence intervals.
- Fig. 6.** *Gaidius variabilis*. Seasonal changes in the composition of C4, C5, and C6 in the total female and male populations at Site H. The estimated peak spawning season is denoted by the horizontal bar at the bottom of the figure (for details, see text).
- Fig. 7.** *Gaidius variabilis*. Between-stage increment based on prosome length (PL), wet weight (WW), dry weight (DW), or ash-free dry weight (AFDW).

Table 1 *Gaidius variabilis* . Sampling data at Site H (Lat. 41°30'N-42°30'N, Long. 145°00'E-146°00'E) in the Oyashio region. Discrete sampling strata are: surface-thermocline (Th), Th-250, 250-500, 500-1000, and 1000-12000 m.

Date	Time (Local time)	Vessel
4 September 1996	1827-2023	<i>Oshoro-Marui</i>
19 September 1996	1737-1944	<i>Hokusei-Marui</i>
1 October 1996	2325-0205	<i>Hokusei-Marui</i>
8 December 1996	0110-0248, 0636-0850	<i>Hokushin-Marui</i>
13 January 1997	1000-1200	<i>Hokko-Marui</i>
20 February 1997	0230-0510*	<i>Hokushin-Marui</i>
17 March 1997	0055-0330	<i>Hokko-Marui</i>
11 April 1997	0240-0440, 0820-1030	<i>Hokusei-Marui</i>
6 May 1997	2335-0320**	<i>Hokko-Marui</i>
4 June 1997	1850-2009***	<i>Oshoro-Marui</i>
23 June 1997	2123-2326	<i>Hokusei-Marui</i>
2 July 1997	1953-2208	<i>Hokusei-Marui</i>
17 August 1997	1945-2139	<i>Oshoro-Marui</i>
26 August 1997	1010-1201	<i>Tansei-Marui</i>
5 October 1997	2045-2220, 1505-1715	<i>Hokusei-Marui</i>

Missing stratum: *500-1000, 1000-12000 m; **Th-250, 250-500 m; ***1000-<2000 m.

Table 2 *Gaidius variabilis*. Summary of prosome length (PL), wet weight (WW), dry weight (DW), ash-free dry weight (AFDW), water content (%WW), and AFDW (%DW). Values are mean $\pm$ 1SD; number of replicates in parentheses. For analyzing body allometry, the power regression model $W = a \cdot L^b$ was used, where W is WW, DW, or AFDW (μ g) and L is PL (mm). Water (%WW) and AFDW (%DW) were calculated and differences between stages were tested by one-way ANOVA and Fisher's PLSD. Any two stages not connected by underlining are significantly different (Fisher's PLSD, $p < 0.001$).

Copepodite stage	PL (mm)	WW (μ g)	DW (μ g)	AFDW (μ g)	Water (%WW)	AFDW (%DW)
C1	0.76 $\pm$ 0.03 (100)	24.92 $\pm$ 3.39 (2)	7.39 $\pm$ 1.13 (2)	5.32 $\pm$ 0.43 (2)	70.2 $\pm$ 3.4 (2)	72.9 $\pm$ 8.9 (2)
C2	1.07 $\pm$ 0.05 (100)	62.31 $\pm$ 9.07 (4)	16.67 $\pm$ 3.44 (4)	12.31 $\pm$ 1.79 (4)	73.4 $\pm$ 2.3 (4)	74.7 $\pm$ 5.5 (4)
C3	1.42 $\pm$ 0.02 (100)	161.6 $\pm$ 16.7 (4)	42.17 $\pm$ 5.75 (4)	29.19 $\pm$ 2.32 (4)	73.9 $\pm$ 2.9 (4)	69.7 $\pm$ 4.9 (4)
C4F	1.91 $\pm$ 0.04 (100)	458.6 $\pm$ 61.5 (4)	111.3 $\pm$ 22.9 (4)	84.38 $\pm$ 15.42 (4)	75.9 $\pm$ 2.3 (4)	76.1 $\pm$ 2.0 (4)
C4M	2.01 $\pm$ 0.15 (100)	476.1 $\pm$ 59.0 (4)	148.1 $\pm$ 12.3 (4)	115.4 $\pm$ 8.6 (4)	68.8 $\pm$ 1.2 (4)	78.0 $\pm$ 1.8 (4)
C5F	2.48 $\pm$ 0.07 (100)	1074 $\pm$ 208 (4)	233.4 $\pm$ 63.3 (4)	192.7 $\pm$ 55.0 (4)	78.4 $\pm$ 3.0 (4)	82.3 $\pm$ 1.9 (4)
C5M	2.43 $\pm$ 0.12 (100)	1198 $\pm$ 165 (4)	405.7 $\pm$ 49.4 (4)	359.0 $\pm$ 41.9 (4)	66.0 $\pm$ 3.0 (4)	88.5 $\pm$ 0.7 (4)
C6F	3.02 $\pm$ 0.07 (100)	1409 $\pm$ 451 (4)	451.6 $\pm$ 61.6 (4)	375.6 $\pm$ 53.4 (4)	77.9 $\pm$ 3.2 (4)	83.1 $\pm$ 1.2 (4)
C6M	2.68 $\pm$ 0.04 (100)	1190 $\pm$ 115 (4)	349.6 $\pm$ 13.5 (4)	304.5 $\pm$ 15.0 (4)	70.4 $\pm$ 2.6 (4)	87.1 $\pm$ 2.3 (4)
Regression statistics for body allometry						
	WW-PL	DW-PL	AFDW-PL	one-way ANOVA		
Constant (a)	56.283	15.479	11.125	df	8	8
Power (b)	3.135	3.169	3.320	F	9.6	9.9
r^2	0.990	0.982	0.978	p	<0.0001	<0.0001
				Fisher's PLSD	C5M C4M C1 C6M C2 C3 C4F C6F C5F	C3 C1 C2 C4F C4M C5F C6F C6M C5M

Table 3 *Gaidius variabilis* . A summary of rearing experiments on eggs and nauplii.

Values are means $\pm$ 1SD, -: no data. Number of specimens is in parentheses.

Temperature (°C)	Hatching time (d)	Hatchability (%)	Naupliar duration (d)	N1 to C1 survival (%)
0.5	7.9 $\pm$ 0.9 (7)	33	-	-
3	5.2 $\pm$ 0.5 (17)	89	-	-
5	4.0 $\pm$ 0.4 (20)	67	29.2 $\pm$ 2.6 (7)	35
10	2.7 $\pm$ 0.3 (7)	47	24.5 $\pm$ 0.6 (4)	57

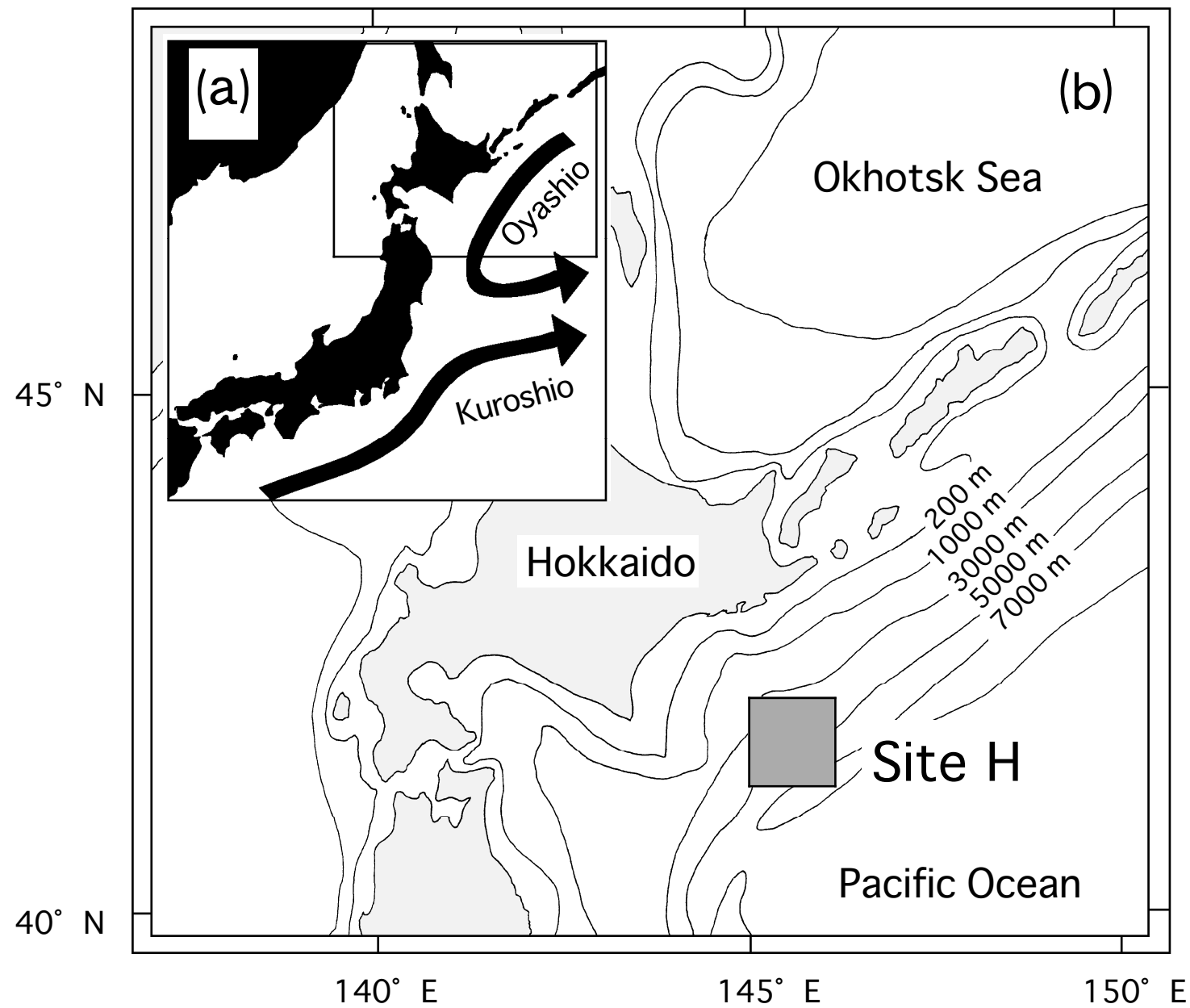


Fig. 1 (Yamaguchi and Ikeda 2000)

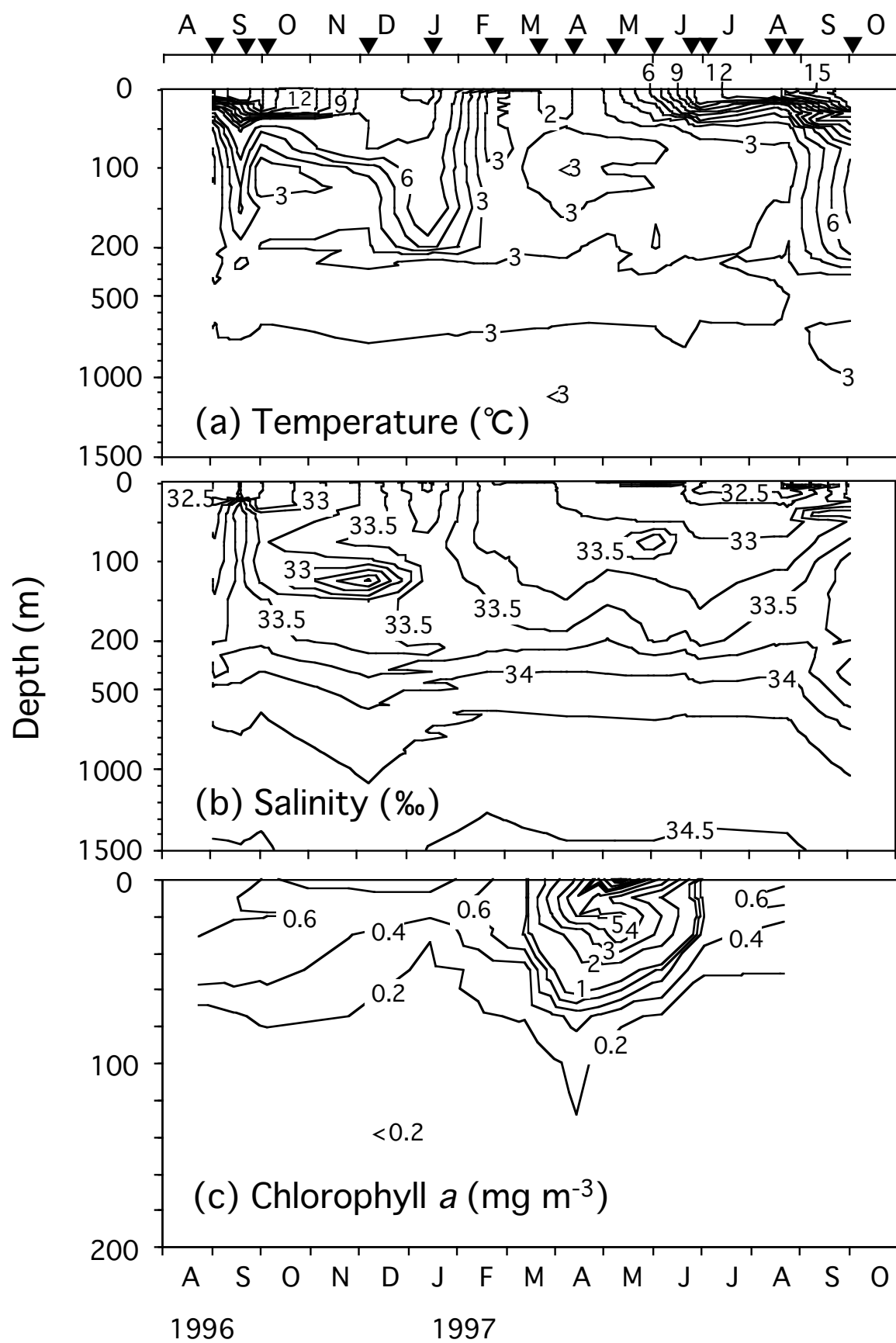


Fig. 2 (Yamaguchi and Ikeda 2000)

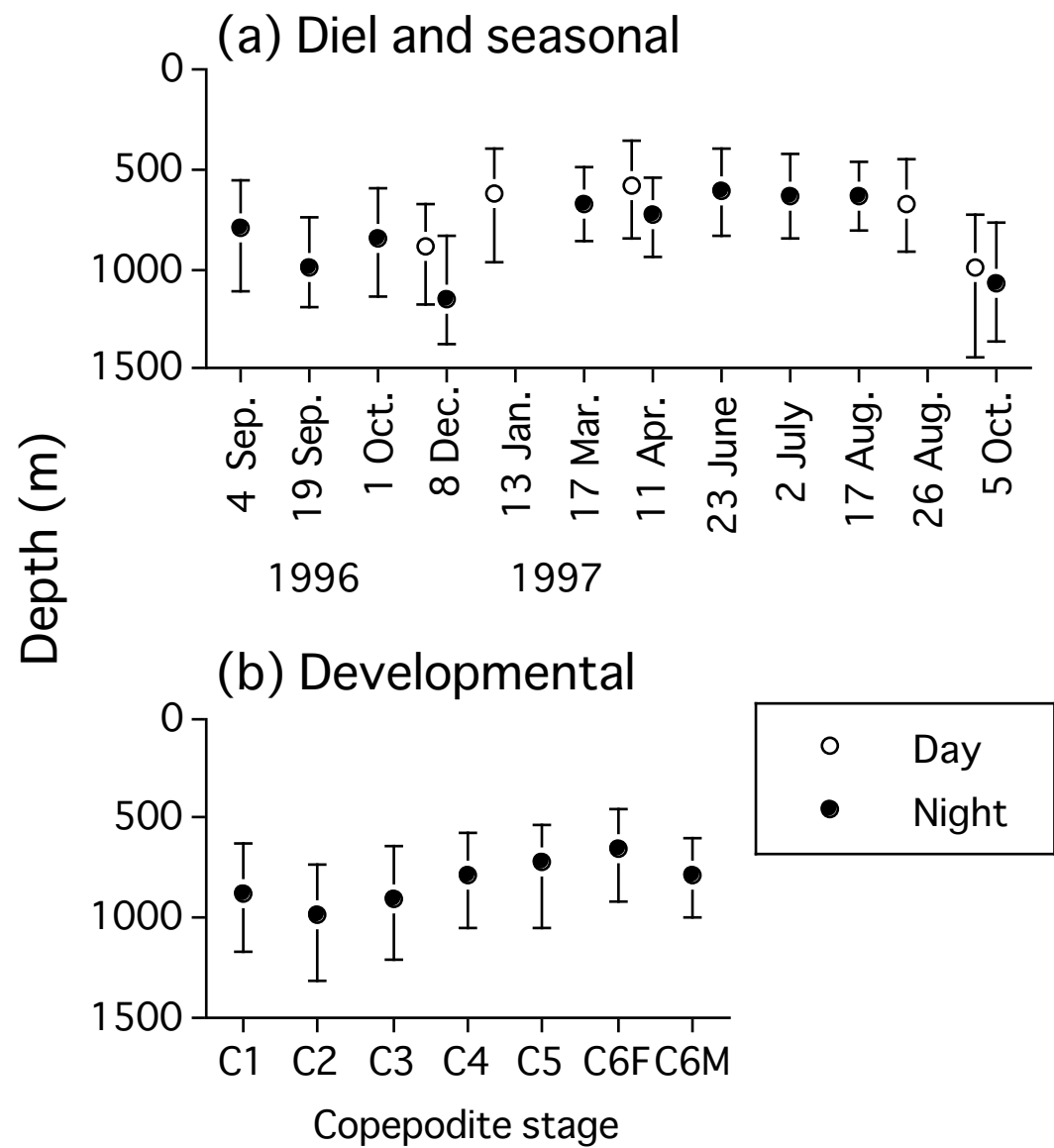


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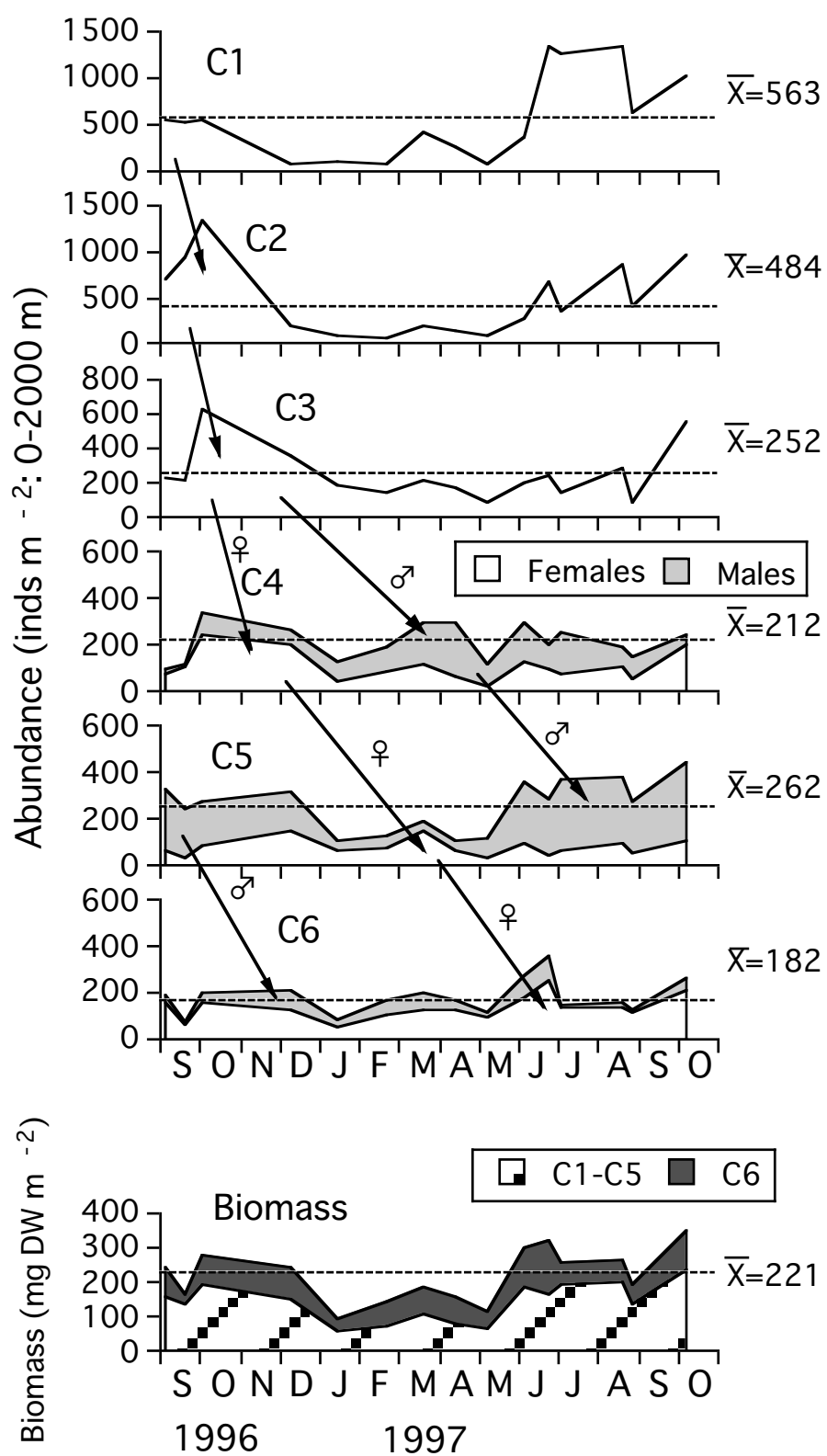


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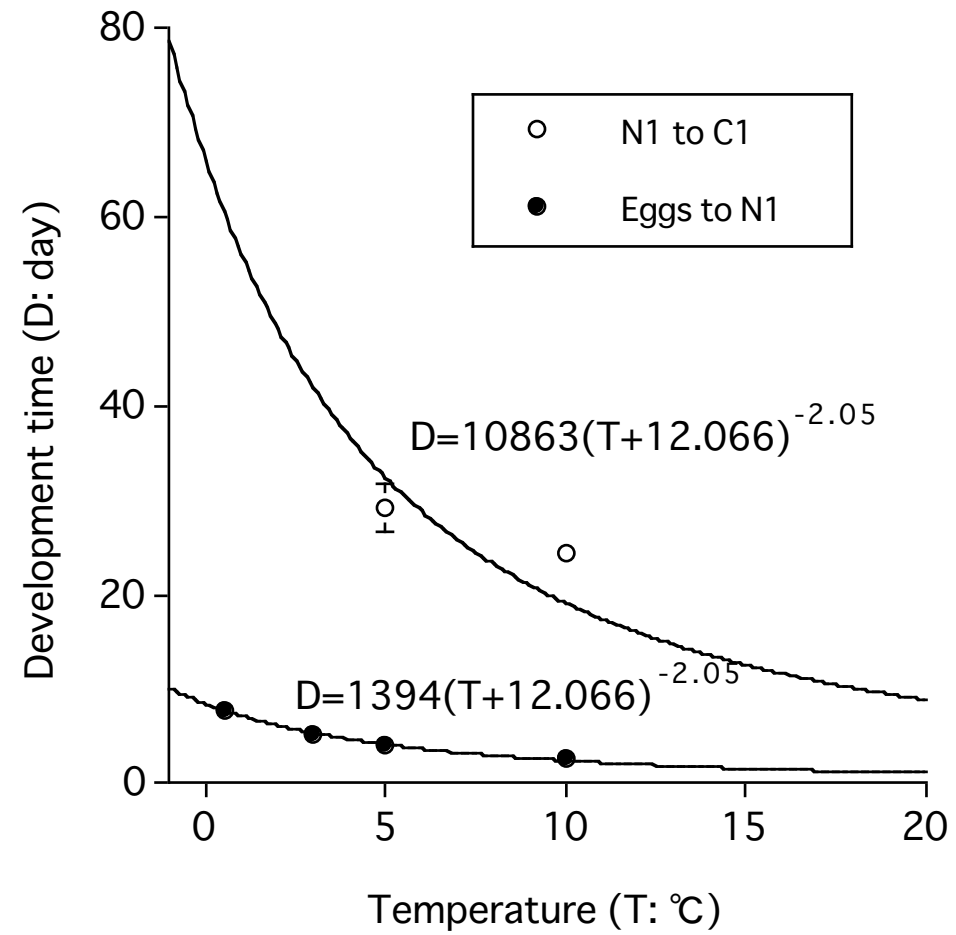


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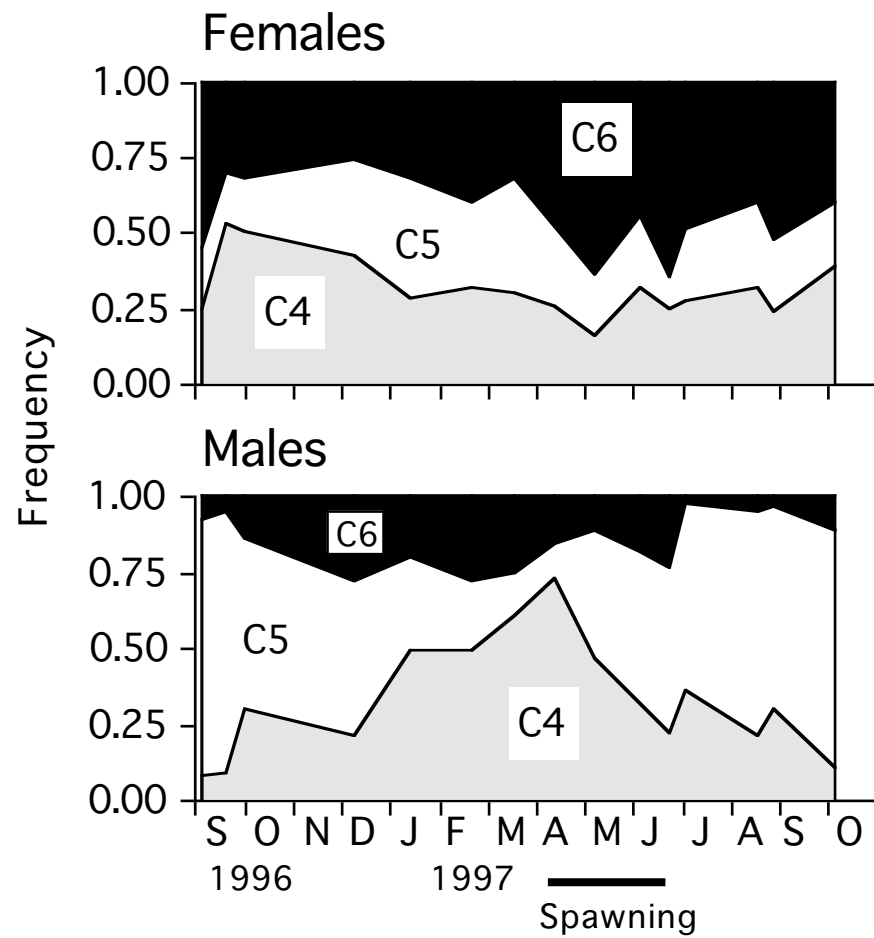


Fig. 6 (Yamaguchi and Ikeda 2000)

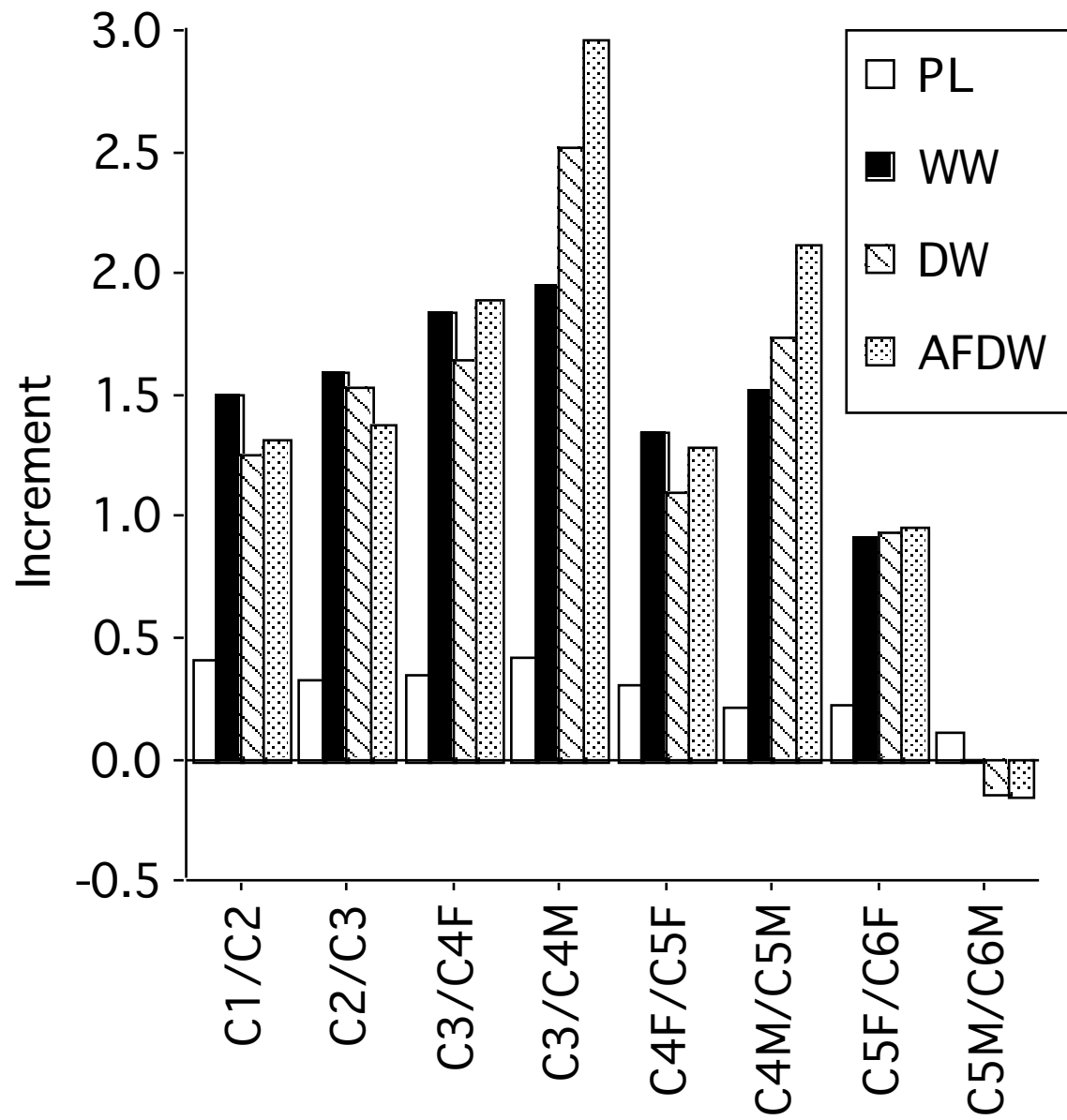


Fig. 7 (Yamaguchi and Ikeda 2000)