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Vertical distribution, life cycle and body allometry of two oceanic calanoid copepods (*Pleuromamma scutellata* and *Heterorhabdus tanneri*) in the Oyashio region, western North Pacific Ocean.

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Running head: Life cycle of *Pleuromamma* and *Heterorhabdus*

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Abstract. Diel and seasonal vertical distribution, life cycle and body allometry of *Pleuromamma scutullata* and *Heterorhabdus tanneri* were investigated in the Oyashio region during September 1996 through October 1997. Monthly samples were collected with 0.1 mm-mesh closing nets towed through five discrete depths between the surface and ≤ 2000 m. Copepodite stages 1 through 6 of *P. scutullata* and 3 through 6 of *H. tanneri* were collected effectively with the nets. Day-night samplings during December 1996, April and October 1997 revealed both species ascend at night. Seasonal differences in the vertical distribution patterns of both copepods were insignificant, and *P. scutullata* was distributed much shallower (250-500 m) than *H. tanneri* (600-850 m). By tracing the sequential changes in abundance peaks of each copepodite stage, both species are considered to produce one generation per year. The main reproduction season was estimated to occur in spring for *P. scutullata* and in winter for *H. tanneri*. The relationships between prosome length and wet weight, dry weight, and ash-free dry weight indicated that the increase in weight per molt was much greater in *H. tanneri* than in *P. scutullata*. These dissimilar features are discussed in relation to the dissimilar food habits of these two species and production cycle of food organisms in the Oyashio region.

Introduction

In the subarctic Pacific, the life histories of oceanic calanoid copepods have been studied extensively for large herbivorous species, such as *Neocalanus* spp., *Eucalanus bungii* and *Metridia pacifica* (Miller et al., 1984; Batchelder, 1985; Miller and Clemons, 1988). Excepting these species, little is known about life cycles of other oceanic copepods in the subarctic Pacific.

Pleuromamma scutullata Brodsky (Metridinidae) and *Heterorhabdus tanneri* (Giesbrecht) (Heterorhabdidae) are medium-sized oceanic copepods distributed in the subarctic Pacific, Bering Sea and Okhotsk Sea (cf. Brodsky, 1950). *P. scutullata* is abundant at 200-500 m depth in the subarctic Pacific (Furuhashi, 1966; Minoda, 1971; Morioka, 1972; Marlowe and Miller, 1975; Hattori, 1989; Tsuda and Sugisaki, 1994). *H. tanneri* occurs at 350-500 m depth off southwest Hokkaido (Morioka, 1972), 200-400 m depth in the Bering Sea and western subarctic Pacific (Minoda, 1971), and 200-1100 m depth in the Okhotsk Sea (Yamaguchi et al., 1998).

Pleuromamma species are known to undertake a diel vertical migration and graze on phytoplankton in the epipelagic zone at night (Hattori, 1989; Bennett and Hopkins, 1989; Morales et al., 1993; Landry et al., 1994; Tsuda and Sugisaki, 1994). *Pleuromamma* species have a specialized prey-predator link with mesopelagic fishes (Merrett and Roe, 1974; Lancraft et al., 1988; Hopkins and Sutton, 1998), and *P. scutullata* is an important prey of *Gonostomatidae* species in the western subarctic Pacific (Gordon et al., 1985). Information about the life cycle of *Pleuromamma* species is limited to the generation lengths of *P. gracilis* in the Adriatic Sea (Shmeleva and Kovalev, 1974) and of *P. robusta* in the Rockall Trough in the northeast Atlantic (Park, 1997). In contrast to *P. scutullata*, *Heterorhabdus* species are typically carnivores (Arashkevich, 1969; Minoda, 1971; Nishida and Ohtsuka, 1996). The only information available about the life cycle of a *Heterorhabdus* species is a report that isolated populations of *H. tanneri* in British Columbia reproduce continually throughout the year (Koeller, 1977).

In the present study, we evaluate the diel and seasonal vertical distribution patterns and life cycles of *P. scutullata* and *H. tanneri* in the Oyashio region of the western subarctic Pacific. Developmental characteristics of body allometry are also examined by measuring prosome length and wet, dry, and ash-free dry weights of each species.

Method

Field sampling

Samples were collected at nearly monthly intervals from 4 September 1996 through 5 October 1997 on board the T/S 'Oshoro-Marui' and T/S 'Hokusei-Marui' of the Faculty of Fisheries of Hokkaido University, R/V 'Tansei-Marui' of the Ocean Research Institute of Tokyo University, R/V 'Hokko-Marui' of the Hokkaido National Fisheries Research Institute, and R/V 'Hokushin-Marui' of the Kushiro Fisheries Experimental Station (Table I). All sampling was conducted between 41°30'-42°30'N and 145°00'-146°00'E in the Oyashio region off southeastern Hokkaido (hereafter referred as Site H) (Figure 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 and a TSK Depth Distance Recorder (Tsurumi Seiki, patent no. 552903) or RMD Depth meter (Rigosha) on the suspending line. The net was towed vertically at 1 m s⁻¹ through five discrete strata: 0-the bottom of thermocline (Th), Th-250, 250-500, 500-1000, and 1000-≤2000 m (Table I). When we failed to obtain this complete set of discrete depth samples, missing depth stratum data were interpolated using data from the most recent samplings before and after the sampling date (see Table I). Most sampling was conducted at night. To investigate the diel vertical migration patterns, day-night samplings were conducted on 8 December 1996, 11 April 1997, and 5 October 1997 (Table I). After collection, zooplankton samples were preserved immediately in a 5% formalin-seawater mixture buffered with borax. Temperature and salinity were measured with a CTD system (Neil Brown or Sea Bird) at each zooplankton sampling site. Chlorophyll a concentration data 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, *P. scutullata* and *H. tanneri* were sorted from the samples and counted under a dissecting microscope. Descriptions of development stages other than adults are not available for these species. To identify the pre-adult copepodite stages, we referred to descriptions of other species of the genera *Pleuromamma* (Ferrari, 1985) and *Heterorhabdus* (Mazza, 1965). Identification of males and female was made only

for adults, although the Metridinidae can be distinguished male/female from Copepodite stage 4 (C4) (Ferrari, 1985). Adult females of *H. tanneri* carrying spermatophores were recorded during the course of our observations.

The net mesh size used (0.10 mm) allowed us to collect C1 through adult stages of *P. scutullata*, and C3 through adult stages of *H. tanneri* (diagonal distance of the mesh is 0.14 mm, compared with the prosome width of 0.29 mm for C1 of *P. scutullata* and 0.28 mm for C3 of *H. tanneri*).

Depth where population resided

To make quantitative comparison possible, the depth where the 50% of population resided (D50%) was calculated (cf. Pennak, 1943).

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) and ash-free dry weight (AFDW) 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.

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). Site H of this study is located just south of the southwestward core 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) (Figure 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 30°C occurred from February to April 1997, when the top 150 m water column was vertically well mixed. 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 (Figure 2b). Oyashio Water, characterized by salinity between 33.0 and 33.5‰ and temperature lower than 30°C (Hanawa and Mitsudera, 1986), 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 (T. Kono, personal communication). Salinity below 500 m depth changed only slightly through the year (range: 34.0-34.5).

Phytoplankton biomass, estimated based on chlorophyll a concentrations, showed a marked seasonality (Figure 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, when 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 at the end of 1997. Chlorophyll a concentrations below 100 m depth were <0.2 mg m⁻³ throughout the year.

Diel and seasonal vertical distribution patterns

Both *P. scutullata* and *H. tanneri* exhibited a diel vertical migration characterized by nocturnal ascent (Figure 3). The distance of this vertical migration varied seasonally and ranged 20-249 m for *P. scutullata* and 37-363 m for *H. tanneri* (calculation based on D50% values). In both species, the smallest change in depth occurred in October, when surface temperatures were near the annual maximum at Site H.

Because of the diel vertical migration, only nighttime sampling data were used to analyze between-stage differences and seasonal changes in D50% within the same stage of both species. Comparisons within pooled stages (C1-C5 and adults for *P. scutullata*, and C3-C5 and adults for *H. tanneri*) revealed no appreciable seasonal variations in D50% values at night for either species (one-way ANOVA, $p>0.05$) (Figure 4). Between-stage differences in mean D50% values at night were significant

in both species (one-way ANOVA at $p=0.05$ level): C2-C5 were distributed much shallower (282-290 m) than C1 and C6 (371-480 m) in *P. scutullata*, and C5 and C6 females were significantly shallower and deeper, respectively, than other stages in *H. tanneri* (Figure 5). Based on the mean nighttime D50%, the vertical distribution range of *P. scutullata* (282-480 m) was much shallower than that of *H. tanneri* (600-819 m).

Population structure/life cycle

The abundance of each copepodite stage of *P. scutullata* showed a clear seasonal pattern (Figure 6). C1 was abundant in September, but few were collected in December-June. C2 was numerous in October. The abundance peak seen in C1 shifted consecutively with development; C3 and C4 peaked in October-December, and C5 and adults peaked in April (Figure 6). These patterns suggest that the life cycle of *P. scutullata* is annual. Annual mean abundance (integrated over $0\leq 2000$ m) ranged 48-140 individuals m^{-2} for C1-C5 and was 435 individuals m^{-2} for adults. For adults, the female:male ratio ranged from 0.52:1 to 4.35:1, with an annual mean of 1.19:1.

In *H. tanneri*, C3 and C4 were abundant in June-July (Figure 7). C5 was numerous in September-October, and adults were numerous in December. Annual mean abundance of each copepodite stage ranged 72-262 individuals m^{-2} . The female:male ratio of adults ranged 0.43:1 to 1.92:1, with an annual mean of 0.83:1. Adult females carrying spermatophores occurred throughout the year and were most abundant in January-June (16-45% of adult females) (Figure 7). These results suggest that the life cycle of *H. tanneri* is annual.

Abundance data were used to estimate biomass (DW), by multiplying the individual number and DW of each copepodite stage mentioned below. Biomass thus calculated ranged 50-255 mg DW m^{-2} (annual mean= 111) for *P. scutullata* (bottom panel of Figure 6) and 40-169 mg DW m^{-2} (annual mean= 82) for *H. tanneri* (bottom panel of Figure 7).

Body allometry

A power regression model was used to analyze the body allometry; $Y=aX^b$ (or $\log_{10}Y=b\cdot\log_{10}X+\log_{10}a$), where Y is WW, DW or AFDW (all in μg), X is PL (mm), and a and b are fitted constants. The data for *P. scutullata* closely fit the regression model ($r^2=0.989-0.995$, Table II), resulting in constant b (power) values of

2.72-3.02. In *P. scutullata*, water content ranged from 66.6% (C3) to 84.8% of WW (C6 females), and ash ranged from 22.4% (C6 females) to 39.7% (C3) of DW. There were no significant differences in mean water or ash contents among developmental stages (one-way ANOVA, $p>0.05$).

As in *P. scutullata*, the WW-PL, DW-PL, and AFDW-PL relationships using data from *H. tanneri* closely fit the power regression model ($r^2=0.989-0.998$, Table III). The constant b (power) values of *H. tanneri* (3.46-3.91) were greater than those of *P. scutullata* (2.72-3.02). Water content of *H. tanneri* varied from 49.1% (C3) to 83.2% (C5) of WW, and differed significantly among copepodite stages (one-way ANOVA, $p=0.003$). Subsequent analysis revealed an anomalously low water-content value in C3 (multiple comparisons by Fisher's PLSD, $p<0.01$). Ash in *H. tanneri* ranged 8.4% (C3) to 32.1% (C5) of DW, and differed significantly among copepodite stages (one-way ANOVA, $p=0.0002$). Stages with higher ash amount (C4, C5) and stages with lower ash amount (C3, C6 females and males) were identified in subsequent analysis (Fisher's PLSD, $p<0.05$).

Discussion

Vertical distribution

The occurrence of *H. tanneri* deeper than *P. scutullata* (Figures 3 and 5) agrees with the previous observations of Furuhashi (1966), Minoda (1971), and Morioka (1972). *P. scutullata* was distributed chiefly at 250-500 m depth during daytime, and part of the population migrated 20-249 m (calculation based on D50% values) toward the surface at night (Figure 3a). The nocturnal ascent pattern and the magnitude of day-night vertical movement of *P. scutullata* observed in the present study confirm the previous results of Minoda (1971), Marlowe and Miller (1975), Hattori (1989), and Tsuda and Sugisaki (1994). Most of the population of *H. tanneri* was found at 400-1000 m depth during daytime, and part of the population migrated near the surface at night (Figure 3b). The magnitude of the day-night migration of *H. tanneri* was 37-363 m (calculated based on D50% values), which is consistent with the observation by Minoda (1971).

Thermal conditions in surface waters appear to be the prime cause of seasonal changes in the magnitude of day-night vertical movement of *P. scutullata* and *H. tanneri* (Figure 3). Among the three seasons in which day-night vertical distribution was examined, the night D50% of *P. scutullata* was the shallowest (121 m) in April (the

coldest month; mean temperature of upper thermocline=1.8°C), resulting in the largest diel vertical change (249 m: night D50%=121 m, day D50%=370 m). On the other hand, the night D50% of *P. scutullata* was the deepest (372 m) in October (the warmest month; mean temperature in thermocline=15.3°C), resulting in the smallest diel vertical change (20 m: night D50%=372 m, day D50%=392 m) (cf. Figure 3a). Similar lines of explanation are applicable to seasonal changes in day-night migration of *H. tanneri*; the migration distance was largest in April (363 m: night D50%=360 m, day D50%=723 m) and smallest in October (37 m: night D50%=983 m, day D50%=1020 m) (cf. Figure 3b). In both species, day-night vertical distances were intermediate in December, when thermal conditions in the upper layer were between those in April and October. Summer warming of surface waters appears to block the upward migration of some deep-living copepods (e.g. Moraitou-Apostolopoulou 1971). The extreme range of temperatures to which migrating *P. scutullata* encounter are 2.1-5.9°C (mean= 3.2°C), and that migrating *H. tanneri* encounter are 2.6-3.5°C (mean= 2.9°C).

Since season did not affect the vertical distribution patterns of C1-C5 and adults of *P. scutullata* and C3-C5 and adults of *H. tanneri* (Figure 4), between-stage comparisons were made for each species using pooled night D50% data (Figure 5). C2-C5 resided much shallower than C1 and C6 in *P. scutullata*, and C5 and C6 females were significantly shallower and deeper, respectively, than other stages of *H. tanneri* (Figure 5). Marlowe and Miller (1975) studied the vertical distribution and migration patterns of zooplankton at Station "P" in the eastern subarctic Pacific and categorized *P. scutullata* males, and *H. tanneri* copepodites and males as near bottom inhabitants of their sampling range (0-500 m), and *P. scutullata* females as vertical migrators that do not reach the surface. However, the present results (Figure 4) suggest that Marlowe and Miller's sampling range is too shallow to evaluate the vertical distribution of *P. scutullata* and *H. tanneri*. The deepest group for each species was adult females. This feature appears to be common for oceanic calanoid copepods (cf. Osgood and Frost, 1994; Falkenhaus et al., 1997).

Life cycle

Pleuromamma scutullata: For herbivorous copepods the abundance of phytoplankton is known to be the most important factor controlling the magnitude of their egg production (Runge, 1985; Hirche and Bohrer, 1987; Peterson, 1988). The diet of *P. scutullata*

includes diatoms, tintinnids, radiolarians and fecal pellet-like particles (Hattori, 1989; Toda et al., 1989), therefore the reproductive activity of *P. scutullata* may be related to phytoplankton blooms in the Oyashio region. Since neither eggs nor nauplii were collected in the present study, the only information available about the reproduction of *P. scutullata* is the abundance of adult females, which peaked in April when the phytoplankton bloom just started at the study site (Figures 2 and 6). Presumably, an abundant supply of phytoplankton would enter the mesopelagic zone later in the blooming season. Nevertheless, assuming that *P. scutullata* reproduces during the phytoplankton bloom, the development time of eggs and nauplii would be 5-6 months at most, since C1 peaked in October 1997 or September 1996 (Figure 6). The development time from C1 to adults was estimated to be 6-7 months by tracing the abundance peaks of each copepodite stage in Figure 6. The odd gap of about two months seen between the abundance peaks of C4 and C5 may be due to sampling errors. From this annual life scheme of *P. scutullata*, the copepodite development time is estimated to last 50-58% of the generation time (1yr), which falls within the general range of 45-68% established for various calanoid copepods reared in the laboratory (Landry, 1983; Webber and Roff, 1995).

The annual mean abundance of *P. scutullata* adults (435 individuals m⁻²) was much greater than those of other copepodite stages (48-140 individuals m⁻²) (Figure 6), indicating that adults live longest among the copepodite stages. A very large stock of adults relative to copepodites at all times of the year may be indicative of a sort of population reservoir, the equivalent of the C5 resting stages of *Neocalanus* copepods (Miller et al., 1984). The female:male ratio of adults (annual mean: 1.19: 1) suggests females live slightly longer than males. The longer adult stage implies *P. scutullata* may reproduce continuously throughout the year. However, the present results indicate that the phytoplankton bloom is the essential event for numerous successful life cycles of this copepod in the Oyashio region.

No comparable information is presently available regarding the life cycle of *P. scutullata* in the North Pacific. For the other *Pleuromamma* species, *P. gracilis* in the Adriatic Sea has three to four generations per year (Shmeleva and Kovalev, 1974). *P. robusta* in the Rockall Trough of the North Atlantic Ocean has three generations per year (Park, 1997). Thus, the 1 year life cycle considered for *P. scutullata* in the present study is much longer than for the other *Pleuromamma* species studied.

Heterorhabdus tanneri: The morphological characteristics of its feeding appendages suggest that *H. tanneri* is carnivorous (Arashkevich, 1969; Minoda, 1971). Other *Heterorhabdus* species consume copepods, polychaetes, and other zooplankters (Harding, 1974; Hopkins, 1985; Nishida and Ohtsuka, 1996). As a possible reflection of carnivorous feeding habit the major reproductive season of *H. tanneri*, as judged by the abundance of adults, is December (Figure 7), well before the onset of the spring phytoplankton bloom in the Oyashio region. The year-round occurrence of adults carrying spermatophores (Figure 7) suggests a possible continuous reproduction of *H. tanneri* throughout the year. Although high proportions of specimens carrying spermatophores in females were seen in January-June, the seasonal abundance of C3-C5 suggests strongly that those born in December form most of the population. An obvious advantage of this life cycle timing of *H. tanneri* is that the drastic increase in WW, DW or AFDW from C3 to adults is achieved during the season rich in animal-food, which is May-September in the Oyashio region (Odate, 1994; Saito et al., 1998).

In the only comparable work on the life cycle of *H. tanneri*, Koeller (1977) studied the isolated population of this species in the fjords of British Columbia. There, adults of *H. tanneri* are abundant throughout the year, but the juveniles are numerous only in summer (Koeller, 1977). While Koeller (1977) was unable to estimate the generation length of *H. tanneri* in British Columbia because of his long sampling interval (5 occasions in one year) and the large mesh size (0.33 mm) of the net he used, the general features of the occurrence of adult and juvenile copepodites are in good agreement with the present results (Figure 7).

Developmental characteristics

The present use of preserved specimens in formalin for WW, DW, and AFDW determinations may not be valid since loss of organic matter could occur during storage (Hopkins, 1968; Fudge, 1968). Nevertheless, the magnitude of error caused by formalin preservation is relatively small and unimportant for broad comparisons between stages of dissimilar species (cf. Gruzov and Alekseyeva, 1970). The constant *b* values of the regression lines of WW, DW, and AFDW on PL of *H. tanneri* were consistently greater (3.46-3.91, cf. Table III) than those of *P. scutullata* (2.72-3.02, cf. Table II), indicating that *H. tanneri* accumulates body mass more greatly per unit

increase in PL. This is more evident in between-stage increases in PL, WW, DW, and AFDW of these two species (Figure 8), i.e. 39-72% in PL, 168-965% in WW, 266-498% in DW, 359-422% in AFDW for *H. tanneri* and 10-34% in PL, 41-201% in WW, 37-198% in DW, 19-219% in AFDW for *P. scutullata*. This difference in development pattern between these two species explains why the present use of the 0.10-mm mesh nets retained all copepodite stages of the smaller *P. scutullata* (adults: 2.2-2.6 mm, Table II), but only C3-adults of the larger *H. tanneri* (adults: 2.7-2.9 mm, Table III). Extrapolation of between-stage growth in PL of *H. tanneri* suggests that their C1 and C2 are too small to be retained by 0.10-mm nets.

Ikeda and Hirakawa (1996) calculated the between-stage growth of all naupliar and copepodite stages of the mesopelagic copepod *Paraeuchaeta elongata* and noted a pronounced growth between C3 and C4 (52-53% in PL, 376-391% in WW, 541-550% in DW, 525-531% in AFDW). Except for WW, which showed a maximum at the C3/C4, between-stage increments in DW and AFDW of *H. tanneri* showed no appreciable differences between C3 and C6 (Figure 8). Water content and ash amount were nearly constant for C1-adults in *P. scutullata*, but varied in *H. tanneri* (Tables II and III). Extremely low water and ash content in C3 of *H. tanneri* strongly suggest that large amounts of lipid are deposited during this stage, as was noted for the larvae of the mesopelagic mysid *Meterythrops microphthalma* (Ikeda, 1992). Compared with adult females of *P. scutullata*, the lower ash of females of *H. tanneri* may be indicative of production of lipid-rich eggs by the latter. The present results for *P. scutullata* and *H. tanneri*, combined with those of *P. elongata* (Ikeda and Hirakawa, 1996), show clearly that material accumulation patterns in the course of development are quite species-specific among mesopelagic copepods. Presently available information about this accumulation pattern is too limited to make strong generalizations about the life of copepods living in mesopelagic realm of the ocean.

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References

- Arashkevich, Ye.G. (1969) The food and feeding of copepods in the northwestern Pacific. *Oceanology*, **9**, 695-705.
- Batchelder, H.P. (1985) Seasonal abundance, vertical distribution, and life history of *Metridia pacifica* (Copepoda: Calanoida) in the oceanic subarctic Pacific. *Deep-Sea Res.*, **32A**, 949-964.
- Bennett, J.L. and Hopkins, T.L. (1989) Aspects of the ecology of the calanoid copepod genus *Pleuromamma* in the eastern Gulf of Mexico. *Contrib. Mar. Sci.*, **31**, 119-136.
- Brodsky, K.A. (1950) Copepoda Calanoida of the far-eastern seas of the USSR and Arctic Seas. *Akad. Nauk SSSR Zool. Inst. Opred. Faune SSSR*, **35**, 1-442 (in Russian). (Israel Program for Scientific Translations, 1967, Jerusalem, 440 pp.)
- Falkenhaus, T., Tande, K.S. and Semenova, T. (1997) Diel, seasonal and ontogenetic variations in the vertical distributions of four marine copepods. *Mar. Ecol. Prog. Ser.*, **149**, 105-119.
- Ferrari, F.D. (1985) Postnaupliar development of a looking-glass copepod *Pleuromamma xiphias* (Giesbrecht, 1889), with analyses of distributions of sex and asymmetry. *Smithsonian Cont. Zool.*, **7**, 458-480.
- Fudge, H. (1968) Biochemical analysis of preserved zooplankton. *Nature*, **219**, 380-381.
- Furuhashi, K. (1966) Studies on the vertical distribution of copepods in the Oyashio region east of Japan and in the Kuroshio region south of Japan. *Publ. Seto Mar. Biol. Lab.*, **14**, 295-322.
- Gordon, J.D.M., Nishida, S. and Nemoto, T. (1985) The diet of mesopelagic fish from the Pacific coast of Hokkaido, Japan. *J. Oceanogr. Soc. Japan*, **41**, 89-97.
- Gruzov, L.N. and Alekseyeva, L.G. (1970) Weight characteristics of copepods from the equatorial Atlantic. *Oceanology*, **10**, 871-879.
- Hanawa, K. and Mitsudera, H. (1986) Variation of water system distribution in the Sanriku coastal area. *J. Oceanogr. Soc. Japan*, **42**, 435-446.
- Harding, G.C.H. (1974) The food of deep-sea copepods. *J. mar. biol. Ass. U.K.*, **54**, 141-155.
- Hattori, H. (1989) Bimodal vertical distribution and diel migration of the copepods

- Metridia pacifica*, *M. okhotensis* and *Pleuromamma scutullata* in the western North Pacific Ocean. *Mar. Biol.*, **103**, 39-50.
- Hirche, H.-J. and Bohrer, R.N. (1987) Reproduction of the Arctic copepod *Calanus glacialis* in Fram Strait. *Mar. Biol.*, **94**, 11-17.
- Hopkins, T.L. (1968) Carbon and nitrogen content of fresh and preserved *Nematoscelis difficilis*, a euphausiid crustacean. *J. Cons. Perm. Int. Explor. Mer.*, **31**, 300-304.
- Hopkins, T.L. (1985) Food web of an Antarctic midwater ecosystem. *Mar. Biol.*, **89**, 197-212.
- Hopkins, T.L. and Sutton, T.T. (1998) Midwater fishes and shrimps as competitors and resource partitioning in low latitude oligotrophic ecosystems. *Mar. Ecol. Prog. Ser.*, **164**, 37-45.
- Ikeda, T. (1992) Growth and life history of the mesopelagic mysid *Meterythropeus microphthalmus* in the southern Japan Sea. *J. Plankton Res.*, **14**, 1767-1779.
- Ikeda, T. and Hirakawa, K. (1996) Early development and estimated life cycle of the mesopelagic copepod *Pareuchaeta elongata* in the southern Japan Sea. *Mar. Biol.*, **126**, 261-270.
- Kawamura, A. (1989) Fast sinking mouth ring for closing Norpac net. *Nippon Suisan Gakkaishi*, **55**, 1121.
- Koeller, P.A. (1977) Observations on some bathypelagic copepods living in the British Columbia Mainland Inlets. *J. Oceanogr. Soc. Japan*, **33**, 219-226.
- Kono, T. (1997) Modification of the Oyashio water in the Hokkaido and Tohoku areas. *Deep-Sea Res. I.*, **44**, 669-688.
- Lancraft, T.M., Hopkins, T.L. and Torres, J.J. (1988) Aspects of the ecology of the mesopelagic fish *Gonostoma elongatum* (Gonostomatidae, Stomiiformes) in the eastern Gulf of Mexico. *Mar. Ecol. Prog. Ser.*, **49**, 27-40.
- Landry, M.R. (1983) The development of marine calanoid copepods with comment on isochronal rule. *Limnol. Oceanogr.*, **28**, 614-624.
- Landry, M.R., Peterson, W.K. and Fagerness, V.L. (1994) Mesozooplankton grazing in the southern California Bight. I. Population abundance and gut pigment contents. *Mar. Ecol. Prog. Ser.*, **115**, 55-71.
- Marlowe, C.J. and Miller, C.B. (1975) Patterns of vertical distribution and migration of zooplankton at Ocean Station "P". *Limnol. Oceanogr.*, **20**, 824-844.

- Mazza, J. (1965) Le développement de quelques copépodes en Méditerranée II. - Les stades jeunes de *Gaetanus kruppi* Giesb., *Euchirella messinensis* Cl., *Chiridius poppei* Giesb., et *Heterorhabdus spinifrons* Cl. Rev. Trav. Inst. Pêches marit., **29**, 285-320.
- Merrett, N.R. and Roe, H.S.J. (1974) Patterns and selectivity in the feeding of certain mesopelagic fishes. Mar. Biol., **28**, 115-126.
- Miller, C.B. and Clemons, M.J. (1988) Revised life history analysis for large grazing copepods in the subarctic Pacific Ocean. Prog. Oceanogr., **20**, 293-313.
- Miller, C.B., Frost, B.W., Batchelder, H.P., Clemons, M.J. and Conway, R.E. (1984) Life histories of large, grazing copepods in the subarctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the Northeast Pacific. Prog. Oceanogr., **13**, 201-243.
- Minoda, T. (1971) Pelagic copepoda in the Bering Sea and the northwestern North Pacific with special reference to their vertical distribution. Mem. Fac. Fish. Hokkaido Univ., **18**, 1-74.
- Moraitou-Apostolopoulou, M. (1971) Vertical distribution, diurnal and seasonal migration of the copepods in Saronic Bay, Greece. Mar. Biol., **9**, 92-98.
- Morales, C.E., Harris, R.P., Head, R.N. and Tranter, P.R.G. (1993) Copepod grazing in the oceanic northeast Atlantic during a 6 week drifting station: the contribution of size classes and vertical migrants. J. Plankton Res., **15**, 185-211.
- Morioka, Y. (1972) Vertical distribution of calanoid copepods off the southeast coast of Hokkaido. In Takenouchi, A.Y. et al. (eds), Biological oceanography of the northern North Pacific Ocean. Idemitsu Shoten, Tokyo, pp. 309-321.
- Nishida, S. and Ohtsuka, S. (1996) Specialized feeding mechanism in the pelagic copepod genus *Heterorhabdus* (Calanoida: Heterorhabdidae) with special reference to the mandibular tooth and labral glands. Mar. Biol., **126**, 619-632.
- Odate, K. (1994) Zooplankton biomass and its long-term variation in the Western North Pacific Ocean, Tohoku Sea Area, Japan. Bull. Tohoku Natl. Fish. Res. Inst., **56**, 115-173 (in Japanese with English abstract).
- Omori, M. and Ikeda, T. (1984) Methods in marine zooplankton ecology. John Wiley & Sons, New York.
- Osgood, K.E. and Frost, B.W. (1994) Ontogenetic diel vertical migration behaviors of

- the marine planktonic copepods *Calanus pacificus* and *Metridia lucens*. Mar. Ecol. Prog. Ser., **104**, 13-25.
- Park, J.S. (1997) Population dynamics of the oceanic calanoid copepod *Pleuromamma robusta* (Crustacea) with respect to the intermoult cycle for interpreting some population parameters. In PICES Abstracts., Pusan, pp. 34.
- Pennak, R.W. (1943) An effective method of diagramming diurnal movements of zooplankton organisms. Ecology, **24**, 405-407.
- Peterson, W.T. (1988) Rates of egg production by the copepod *Calanus marshallae* in the laboratory and in the sea off Oregon, USA. Mar. Ecol. Prog. Ser., **47**, 229-237.
- Runge, J.A. (1985) Relationship of egg production of *Calanus pacificus* to seasonal changes in phytoplankton availability in Puget Sound, Washington. Limnol. Oceanogr., **30**, 382-396.
- Saito, H., Kasai, H., Kashiwai, M., Kawasaki, Y., Kono, T., Taguchi, S. and Tsuda, A. (1998) General description of seasonal variations in nutrients, chlorophyll a, and netplankton biomass along the A-line transect, western subarctic Pacific, from 1990 to 1994. Bull. Hokkaido Natl. Fish. Res. Inst., **62**, 1-62.
- Shmeleva, A.A. and Kovalev, A.V. (1974) Cycles biologique des copepodes (Crustacea) de la mer Adriatique. Boll. Pesca, Piscic., Idrobiol., **29**, 49-70.
- Toda, T., Suh, H.-L. and Nemoto, T. (1989) Dry fracturing: A simple technique for scanning electron microscopy of small crustaceans and its application to internal observations of copepods. J. Crustacean Biol., **9**, 409-413.
- Tsuda, A. and Sugisaki, H. (1994) In situ grazing rate of the copepod population in the western subarctic North Pacific during spring. Mar. Biol., **120**, 203-210.
- Yamaguchi, A., Kobari, T. and Ikeda, T. (1998) Vertical distribution (0-2,000 m) of some planktonic calanoid copepod species in the south of Kuril Chain and the Okhotsk Sea. In Report on the 1996 R/V Kaiyo-maru Juvenile Salmon Reserch, Salmon Report Series No. 40, Nat. Res. Inst. Far Seas Fish., Shimizu, pp. 26-40 (in Japanese with English abstract).
- Webber, M.K. and Roff, J.C. (1995) Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. Mar. Biol., **123**, 481-495.

Figure Legends

- Fig. 1.** Location of the Oyashio region in the western North Pacific Ocean (**a**). The sampling area (Site H, shaded box) in the Oyashio region, where depth contours (200, 1000, 3000, 5000, and 7000 m) are superimposed (**b**).
- Fig. 2.** Seasonal changes in temperature (°C) (**a**), salinity (‰) (**b**), and chlorophyll a (mg m⁻³) (**c**) at Site H. Note the differences in depth scales of each panel. Solid triangles in the upper panel indicate each sampling date.
- Fig. 3.** Day-night vertical distribution of *Pleuromamma scutullata* C1-adults (**a**) and *Heterorhabdus tanneri* C3-adults (**b**) in 8 December 1996, 11 April 1997, and 5 October 1997 at Site H. Temperature profiles are superimposed in daytime sampling panels.
- Fig. 4.** Seasonal vertical distribution of *Pleuromamma scutullata* (**a**) and *Heterorhabdus tanneri* (**b**) in nighttime at Site H. Open histograms denote copepodite stages 1-5 (*P. scutullata*) or 3-5 (*H. tanneri*) and shaded histograms adults (C6).
- Fig. 5.** Annual mean of the depths where the 50% population of each developmental stage was distributed in nighttime. Open and solid symbols indicate *Pleuromamma scutullata* and *Heterorhabdus tanneri*, respectively. Vertical bars show standard deviations.
- Fig. 6.** Seasonal abundance of each copepodite stage and biomass of *Pleuromamma scutullata* at Site H (integrated over 0–2000 m). Open symbols mean no occurrence. Horizontal broken lines and figures in parentheses denote annual mean abundance (individuals m⁻² for copepodite stages, mg DW m⁻² for biomass).
- Fig. 7.** Seasonal abundance of each copepodite stage and biomass of *Heterorhabdus tanneri* at Site H (integrated over 0–2000 m). Open symbols show no occurrence. Horizontal broken lines and figures in parentheses denote annual mean abundance (individuals m⁻² for copepodite stages, mg DW m⁻² for biomass).
- Fig. 8.** *Pleuromamma scutullata* (**left**) and *Heterorhabdus tanneri* (**right**). Changes (%) between consecutive copepodite stages in prosome length (PL), wet weight (WW), dry weight (DW), and ash-free dry weight (AFDW) (F: female, M: male).

Table I. Zooplankton 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 II. *Pleuromamma scutullata* . Summary data of prosome length (PL), wet weight (WW), dry weight (DW), ash-free dry weight (AFDW), water content (%WW) and ash (%DW). Values are mean $\pm$ 1SD. Number of replicates is in parenthesis. Power regression model $Y = a X^b$ was used, where Y is WW, DW, or AFDW (μ g) and X is PL (mm). Water (%WW) and Ash (%DW) were calculated and difference between stage were tested by ANOVA.

Developmental stage	PL (mm)	WW (μ g)	DW (μ g)	AFDW (μ g)	Water (%WW)	Ash (%DW)
C1	0.66 $\pm$ 0.02 (40)	25.38 $\pm$ 10.59 (4)	6.59 $\pm$ 1.00 (4)	4.35 $\pm$ 0.39 (4)	68.5 $\pm$ 19.5 (4)	33.0 $\pm$ 10.3 (4)
C2	0.90 $\pm$ 0.04 (39)	53.39 $\pm$ 19.97 (4)	12.63 $\pm$ 4.89 (4)	8.72 $\pm$ 2.73 (4)	76.1 $\pm$ 4.0 (4)	29.0 $\pm$ 9.0 (4)
C3	1.15 $\pm$ 0.02 (30)	82.26 $\pm$ 20.03 (4)	26.68 $\pm$ 3.41 (4)	15.98 $\pm$ 1.47 (4)	66.6 $\pm$ 5.5 (4)	39.7 $\pm$ 6.0 (4)
C4	1.54 $\pm$ 0.03 (23)	253.2 $\pm$ 40.5 (4)	65.81 $\pm$ 22.29 (4)	39.68 $\pm$ 6.15 (4)	74.3 $\pm$ 6.1 (4)	36.9 $\pm$ 11.4 (4)
C5	2.03 $\pm$ 0.02 (20)	607.2 $\pm$ 164.9 (4)	121.7 $\pm$ 32.6 (4)	77.70 $\pm$ 15.19 (4)	79.6 $\pm$ 3.7 (4)	34.9 $\pm$ 9.2 (4)
Adult females (C6F)	2.64 $\pm$ 0.06 (20)	1604 $\pm$ 70.2 (4)	243.8 $\pm$ 35.8 (4)	190.1 $\pm$ 35.8 (4)	84.8 $\pm$ 2.1 (4)	22.4 $\pm$ 3.4 (4)
Adult males (C6M)	2.22 $\pm$ 0.03 (20)	808.1 $\pm$ 87.2 (4)	193.8 $\pm$ 48.2 (4)	145.2 $\pm$ 32.1 (4)	76.0 $\pm$ 5.5 (4)	24.5 $\pm$ 4.7 (4)
Regression statistics						
	Constant (a)	72.84	18.91	12.29	df	6
	Power (b)	3.016	2.723	2.812	F	2.044
	r^2	0.989	0.995	0.991	p	0.1046 (ns)
						0.067 (ns)

Table III. *Heterorhabdus tanneri* . Summary data of prosome length (PL), wet weight (WW), dry weight (DW), ash-free dry weight (AFDW), water content (%WW) and ash (%DW). Values are mean $\pm$ 1SD. Number of replicates is in parenthesis. Power regression model $Y = a \cdot X^b$ was used, where Y is WW, DW, or AFDW (μ g) and X is PL (mm). Water (%WW) and Ash (%DW) were calculated and difference between stage were tested by ANOVA and Fisher's PLSD. Any two stages not underscored by the same line are significantly different.

Developmental stage	PL (mm)	WW (μ g)	DW (μ g)	AFDW (μ g)		Water (%WW)	Ash (%DW)
C3	0.71 $\pm$ 0.04 (40)	8.64 $\pm$ 6.58 (4)	3.32 $\pm$ 0.39 (4)	3.23 $\pm$ 0.43 (4)		49.1 $\pm$ 22.2 (4)	8.4 $\pm$ 2.6 (4)
C4	1.22 $\pm$ 0.03 (40)	91.94 $\pm$ 26.06 (4)	18.12 $\pm$ 2.03 (4)	13.93 $\pm$ 1.02 (4)		78.8 $\pm$ 7.4 (4)	22.8 $\pm$ 5.0 (4)
C5	1.96 $\pm$ 0.03 (24)	648.2 $\pm$ 56.5 (4)	108.4 $\pm$ 13.5 (4)	72.72 $\pm$ 1.58 (4)		83.2 $\pm$ 2.2 (4)	32.1 $\pm$ 8.7 (4)
Adult females (C6F)	2.92 $\pm$ 0.05 (12)	2199 $\pm$ 111 (4)	431.2 $\pm$ 41.6 (4)	370.6 $\pm$ 35.8 (4)		80.4 $\pm$ 1.6 (4)	14.0 $\pm$ 2.3 (4)
Adult males (C6M)	2.73 $\pm$ 0.09 (12)	1738 $\pm$ 312 (4)	397.0 $\pm$ 60.2 (4)	352.3 $\pm$ 60.7 (4)		76.8 $\pm$ 4.4 (4)	13.5 $\pm$ 3.1 (4)
Regression statistics					ANOVA		
	Constant (a)	37.54	10.25	8.76	df	4	4
	Power (b)	3.908	3.530	3.463	F	6.764	12.763
	r^2	0.995	0.998	0.989	p	0.0026	0.0002
					Fisher's PLSD	<u>C3 C4 C5 F M</u>	<u>C3 M F C4 C5</u>

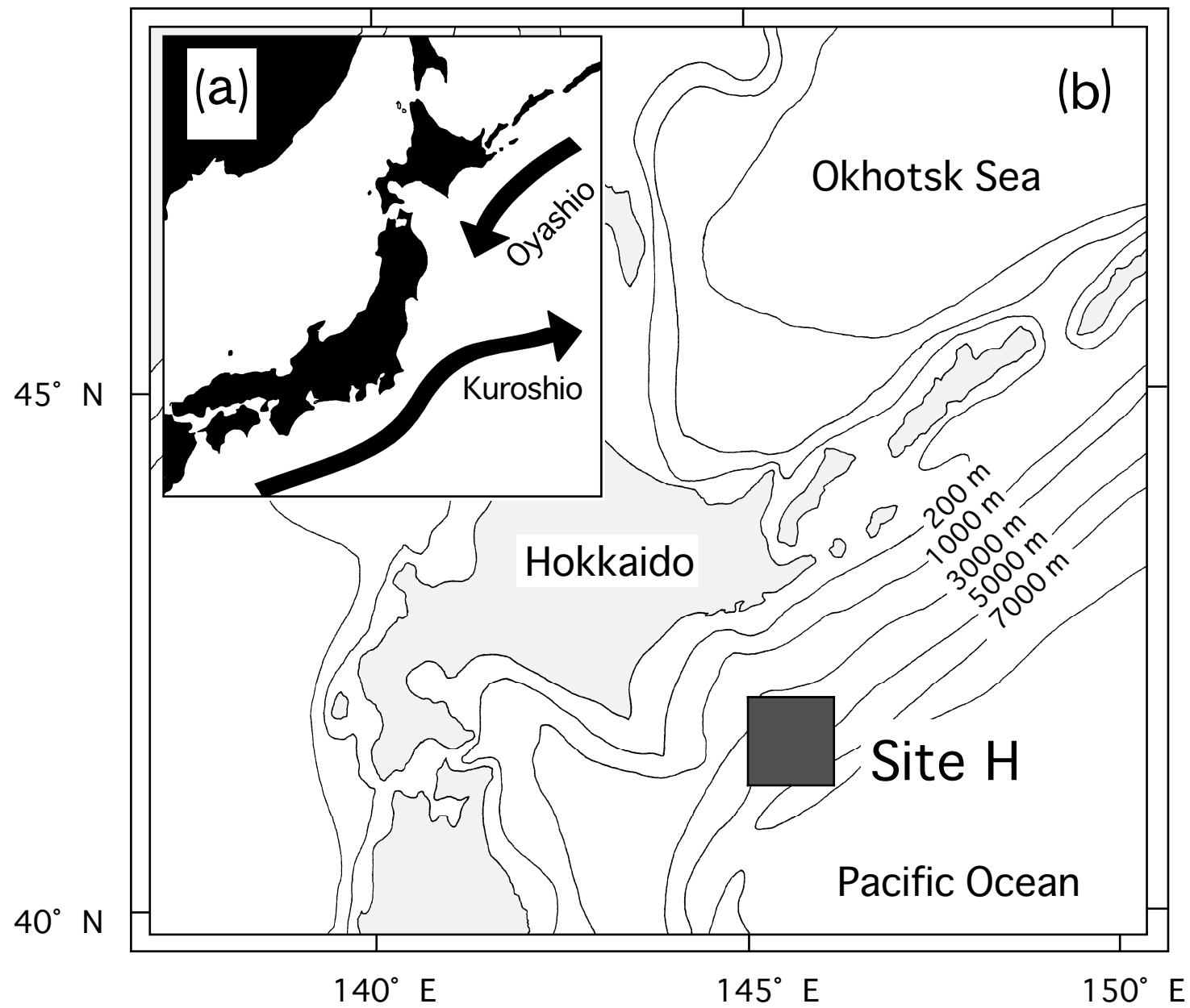


Fig. 1 (Yamaguchi and Ikeda 2000)

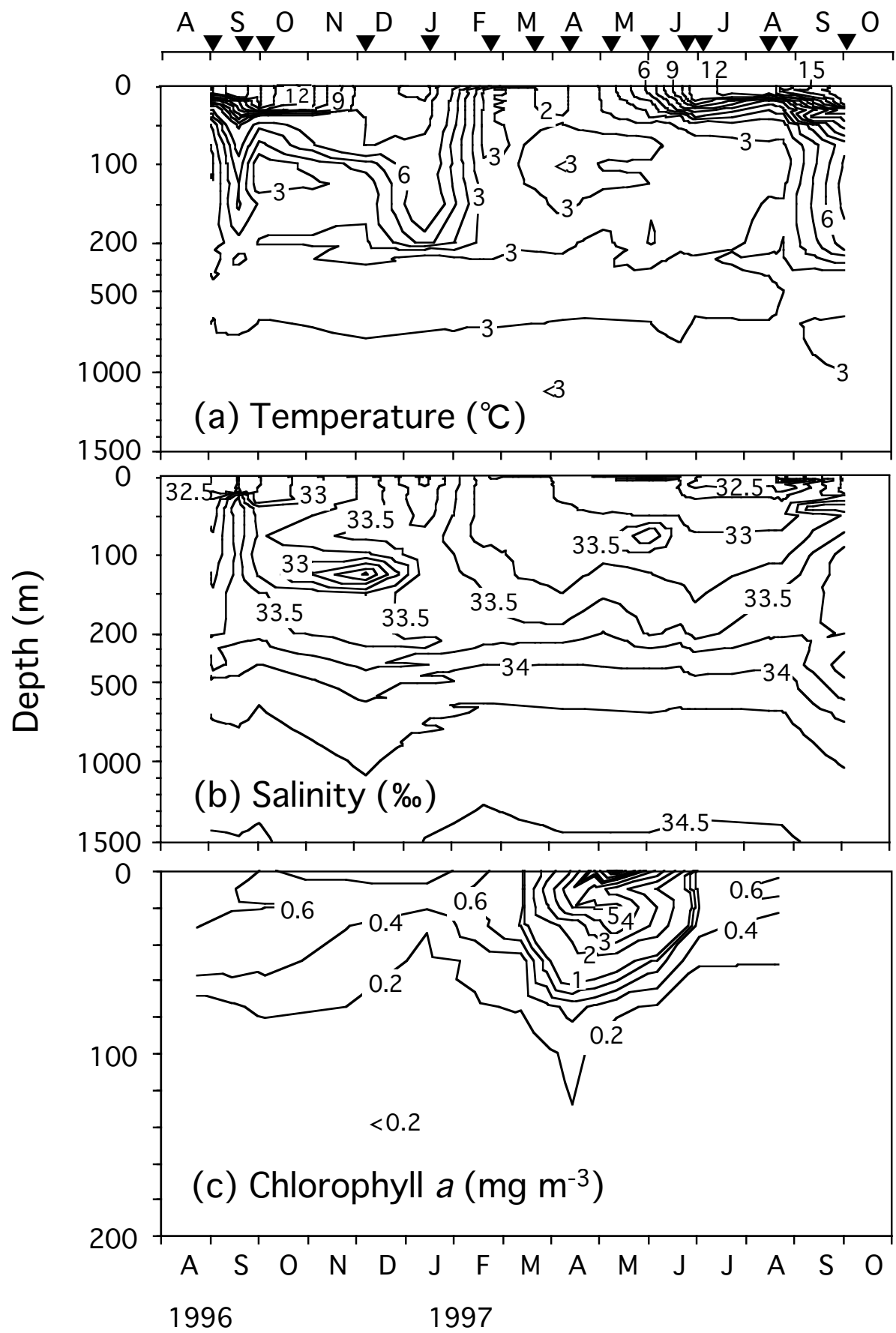
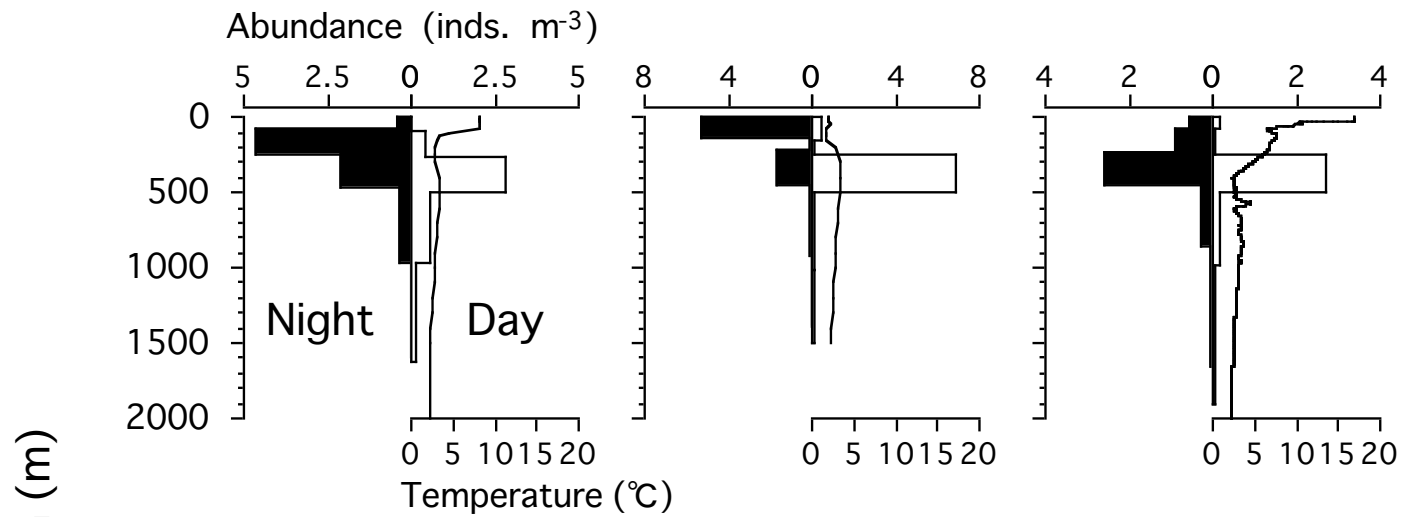


Fig. 2 (Yamaguchi and Ikeda 2000)

(a) *Pleuromamma scutellata*



(b) *Heterorhabdus tanneri*

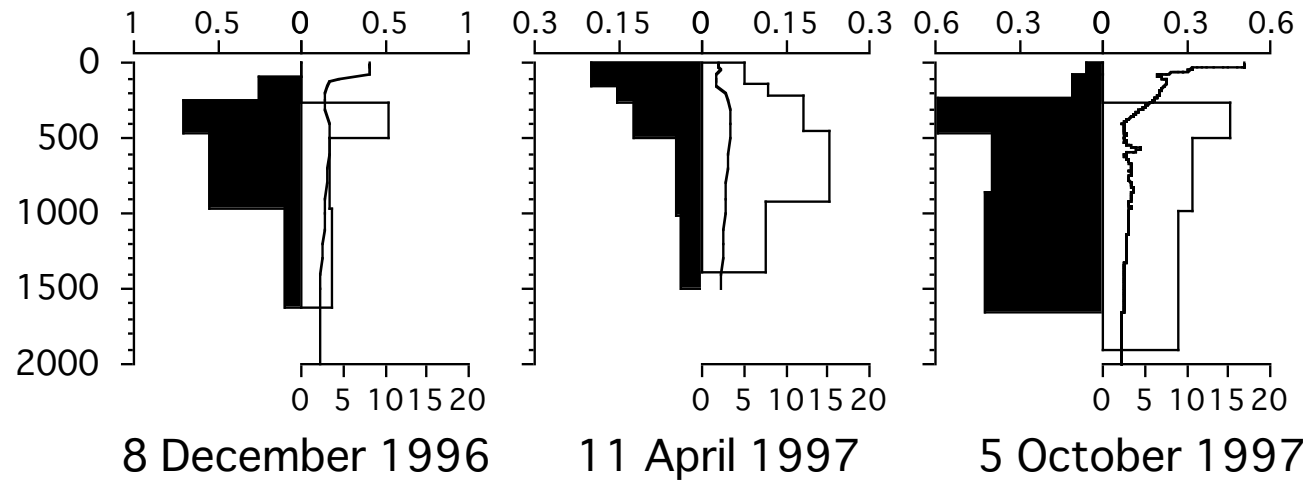


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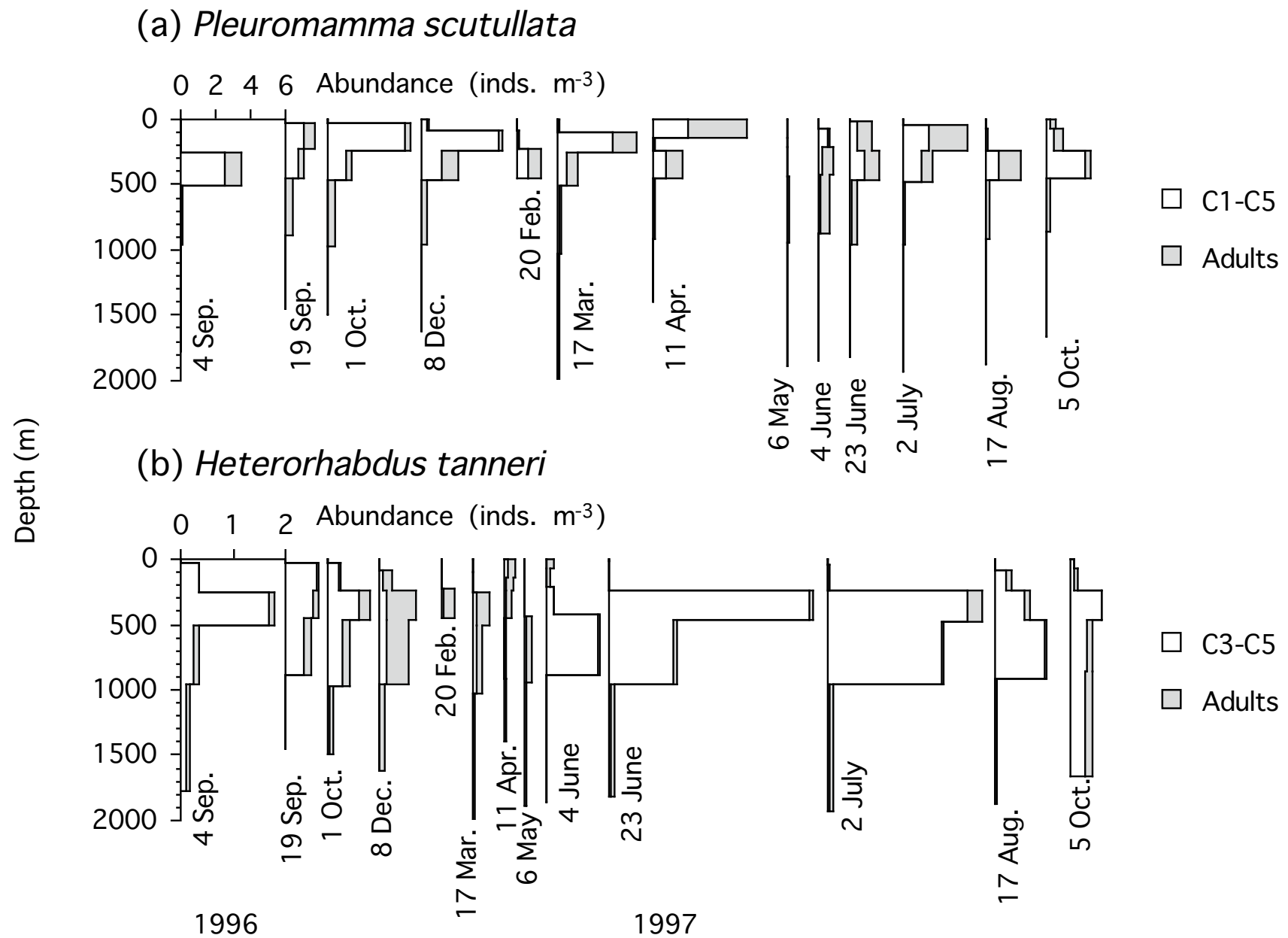


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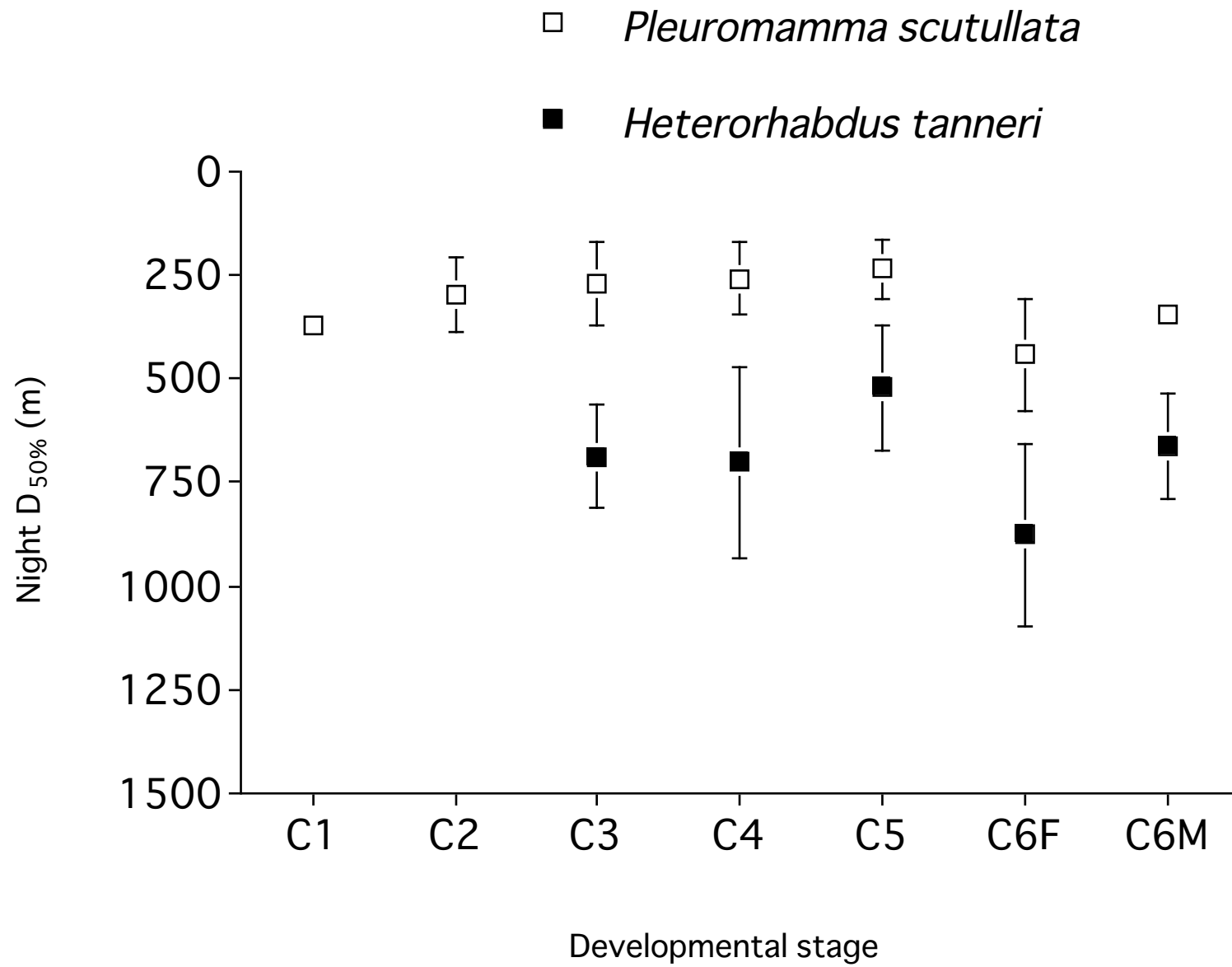


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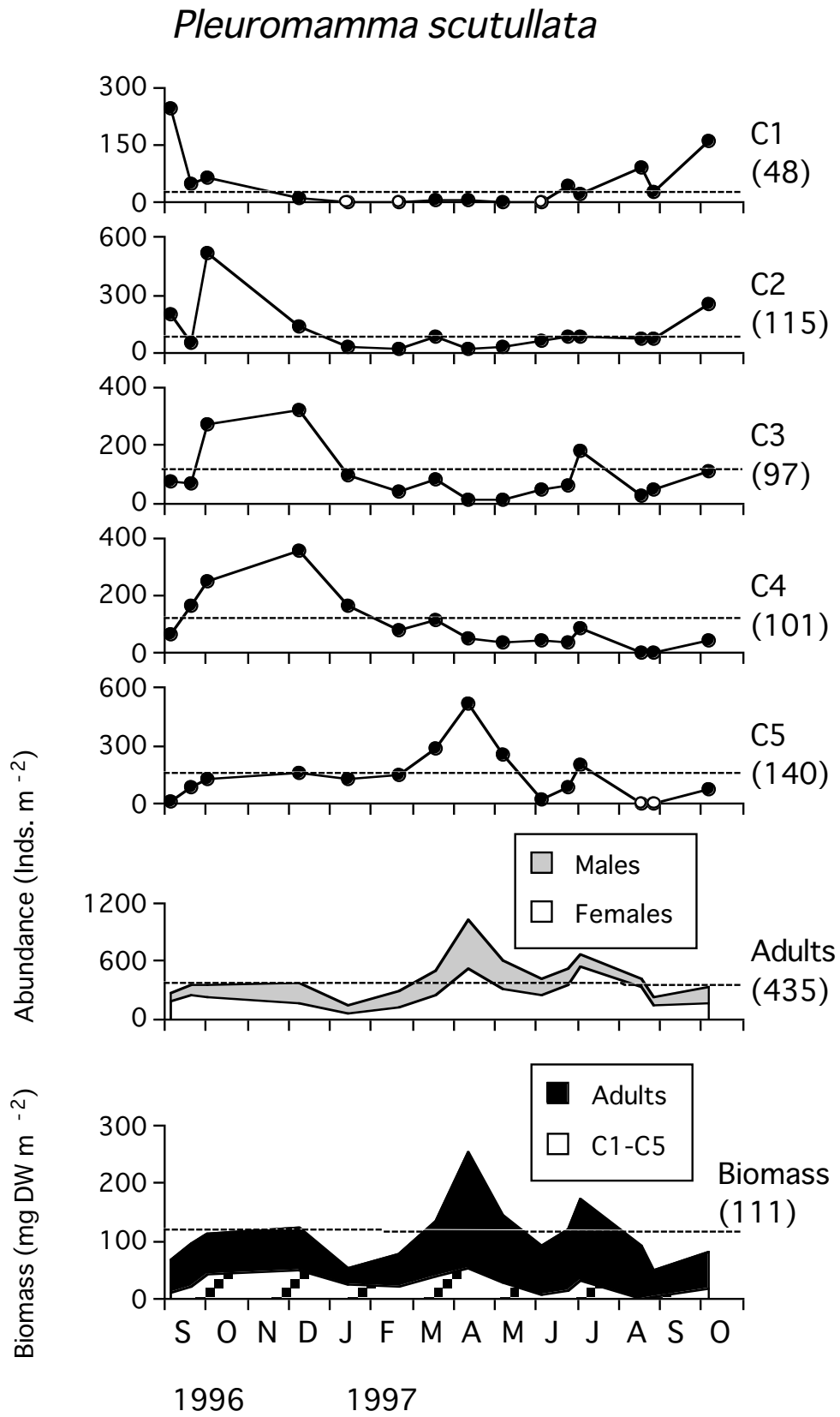


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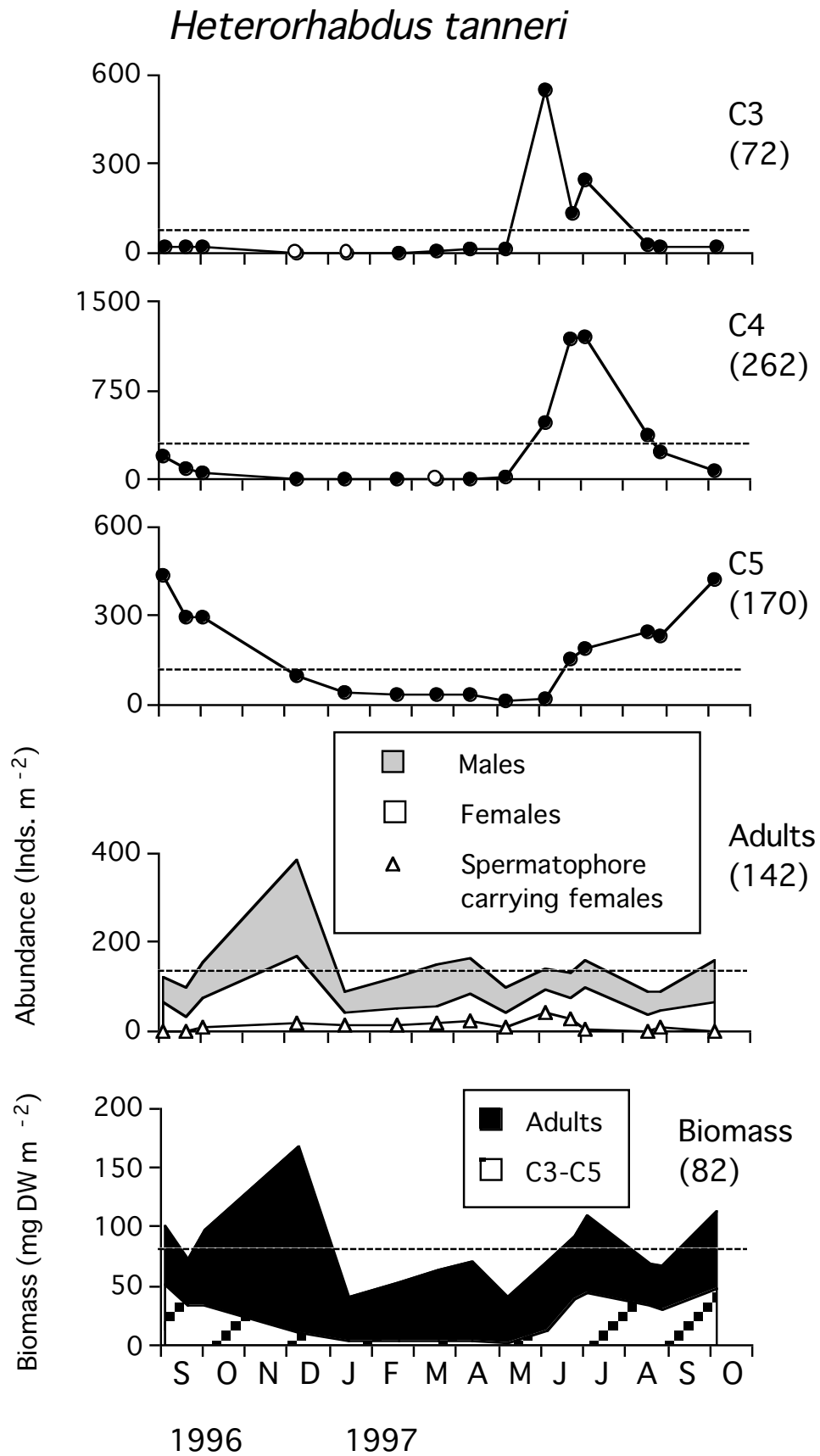


Fig. 7 (Yamaguchi and Ikeda 2000)

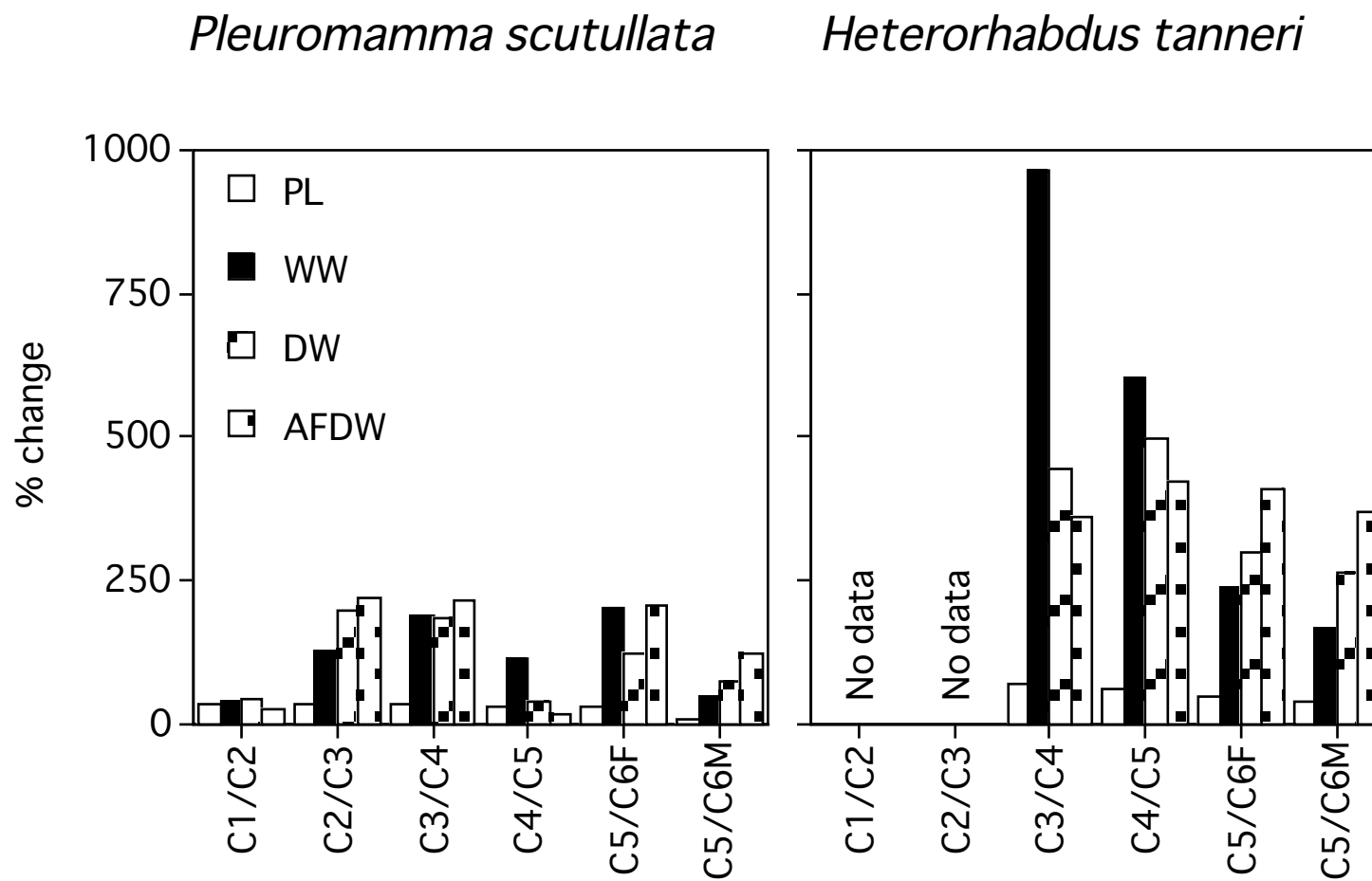


Fig. 8 (Yamaguchi and Ikeda 2000)