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# Life cycle, population structure and vertical distribution of *Metridia* spp. (Copepoda: Calanoida) in the Oyashio region (NW Pacific Ocean)

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ABSTRACT: Vertical distribution and population structure of *Metridia pacifica* and *M. okhotensis* were investigated at Site H in the Oyashio region (western subarctic Pacific) to evaluate their life cycle modes. Although recruitment of *M. pacifica* continued throughout the year in the top 250 m of the water column, 2 pronounced generations were recognized. The first generation was characterized by rapid development during the spring phytoplankton bloom (generation length: 2–3 mo), and the second by slow development (generation length: 9–10 mo) with overwintering at Stage 5 in deeper-layers (up to 1000–2000 m). In contrast, *M. okhotensis* was consistently found at depth (250–1000 m) throughout the year, except for excursions to the subsurface layer for spawning during the phytoplankton bloom. Developmental sequences of *M. okhotensis* could not be resolved very clearly, largely because of extremely low abundance of Copepodite Stages 2 and 3 (C2–C3). As a tentative life cycle scenario, the C1 produced during one year was considered to overwinter and develop to C5 through the phytoplankton bloom of the next year. These C5 overwinter and molt to C6 and reproduce during the phytoplankton bloom of the following year. Thus, the generation length of *M. okhotensis* is estimated as 2 yr. For both species, active spawning and subsequent growth are closely associated with phytoplankton bloom. For overwintering stages of both species, a large deposition of lipid in the body and its gradual decrease toward the onset of phytoplankton bloom of the next year was seen. While no comparable life cycle data is presently available for *M. okhotensis*, the present results of *M. pacifica* are compared with the results from other regions, showing a large between-region variation in the life cycle patterns of this species. Further, the present results are discussed in the context of broad overwintering mechanisms of pelagic copepods living in high-latitude seas.

KEY WORDS: *Metridia pacifica* · *Metridia okhotensis* · Vertical distribution · Life cycle · Oyashio · Western North Pacific

## INTRODUCTION

Throughout the subarctic Pacific, the zooplankton fauna is characterized by the predominance of a few large grazing copepods, such as *Neocalanus cristatus*, *N. plumchrus*, *N. flemingeri* and *Eucalanus bungii* (Mackas & Tsuda 1999). These copepods often account for 80 to 95% of zooplankton biomass in the surface zone (Vinogradov 1970) and are important prey for pelagic fishes, whales and seabirds (Nemoto 1963, Takeuchi 1972, Odate 1994, Hunt et al. 1998, Mackas & Tsuda 1999). Because of their apparent trophic importance, intensive studies on life history patterns have been made on these large grazing copepods (Miller et al. 1984, Miller & Clemons 1988, Kobari & Ikeda 1999, 2000, 2001a,b, Tsuda et al. 1999). According to Vinogradov & Arashkevich (1969), in the western subarctic Pacific the most dominant copepod in terms of biomass is *N. cristatus*, followed by *E. bungii*, *N. plumchrus* (including *N. flemingeri*), *Metridia okhotensis* and *M.*

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*pacifica*, but almost nothing is known about the life history patterns of the 2 *Metridia* species in this region.

The calanoid copepods *Metridia pacifica* Brodsky (formally *M. lucens* or *M. lucens* var. *pacifica*, cf. Brodsky 1948) and *M. okhotensis* Brodsky are medium- or large-sized species; the former is distributed throughout the entire subarctic Pacific and the adjacent Japan, Bering and Okhotsk Seas and off the coast of California (Brodsky 1967), and the latter in the Okhotsk Sea, Bering Sea and possibly over the entire subarctic Pacific (Brodsky 1967, Minoda 1971, Coyle et al. 1990, Cooney et al. 2001, Ozaki et al. 2001). While Brodsky (1948) established *M. pacifica* as a new species, diagnostic features between *M. pacifica* and *M. lucens* have long been questioned among copepod taxonomists, and these 2 species were considered by some to be varieties of the same species. Bucklin et al. (1995), using mtDNA sequence data, confirmed that *M. lucens* and *M. pacifica* are distinct species.

*Metridia pacifica* has been known as a potential prey for pelagic chaetognaths in the western Subarctic Gyre (Terazaki 1998), and both *M. pacifica* and *M. okhotensis* are prey for the mesopelagic myctophid and gonostomatid fishes in the western subarctic Pacific (Gordon et al. 1985, Moku et al. 2000, Uchikawa et al. 2001). Nauplii of *Metridia* spp. have been reported as one of the most important prey items for the first-feeding larvae of walleye pollock *Theragra chalcogramma* in the coastal waters of southwestern Hokkaido, western subarctic Pacific (Nakatani 1995) and the Bering Sea (Hillgruber et al. 1995, Pinchuk & Paul 1998). In the epipelagic zone of the eastern subarctic Pacific *M. pacifica* contributes substantially to the zooplankton biomass, especially during the fall–winter season when the large grazing copepods reside in the deep layers (Batchelder 1986a). The late-copepodites of *M. pacifica* (excluding adult males) are known to undergo an extensive diel vertical migration (Batchelder 1985, Hattori 1989, Hirakawa 1991, Hirakawa & Imamura 1993). Integrated information about seasonal abundance, vertical migration and the life history of *M. pacifica* is presently available for the populations in the eastern subarctic Pacific (Batchelder 1985,1986a) and the Japan Sea (Hirakawa 1991, Hirakawa & Imamura 1993). However, comparable information is currently lacking for the population of *M. pacifica* in the Oyashio region of the western subarctic Pacific.

Until the present study, almost nothing was known about seasonal features of population structure, abundance and life cycles of *Metridia okhotensis*. This may be partly due to the fact that *M. okhotensis* is an abundant species in the Okhotsk Sea, but is less abundant in other waters of the subarctic Pacific. According to Vinogradov & Arashkevich (1969), most *M. okhotensis* in the Kurile–Kamchatka region live at less than 750 m depth. Coyle et al. (1990) recorded *M. okhotensis* in an Alaskan subarctic embayment during spring. Hattori (1989) documented the vertical distribution of *M. okhotensis* during day and night in the western subarctic Pacific.

As part of a research program to evaluate plankton dynamics in the Oyashio region, the present study aimed to document the vertical distribution, population structure, and life cycle of 2 dominant calanoid copepod species, *Metridia pacifica* and *M. okhotensis*, in this region by analyzing time-series samples. Overwintering stages have been identified, and the developmental pattern of the 2 species analyzed based on between-stage increments in body length and weight. The results are compared with *Metridia* spp. from other regions. Finally, differences in overwintering strategies between *Metridia* spp. and other large copepods (of the genera *Neocalanus* and *Eucalanus*) are discussed.

## MATERIALS AND METHODS

**Field sampling.** Zooplankton samples were collected at nearly monthly intervals from 4 September 1996 through 5 October 1997 (Table 1) in the Oyashio region rectangle defined by 41° 30′ to 42° 30′ N and 145° 00′ to 146° 00′ E, off southeastern Hokkaido (hereafter referred to as Site H, Fig. 1). Zooplankton were collected with a closing net (60 cm mouth diameter, 100 µm mesh size; Kawamura 1968, 1989) equipped with a Rigosha flow-meter in its mouth ring and a Tsurumi Seiki Kabushiki-Kaisha (TSK) depth-distance recorder or TSK RMD depth meter on its suspension cable to record sampling depth. The nets were towed vertically at a speed of 1 m $s^{-1}$ through 5 discrete depths: surface to bottom of the thermocline (BT), BT–250 m, 250–500 m, 500–1000 m and 1000–2000 m. During the winter season, when the thermocline was

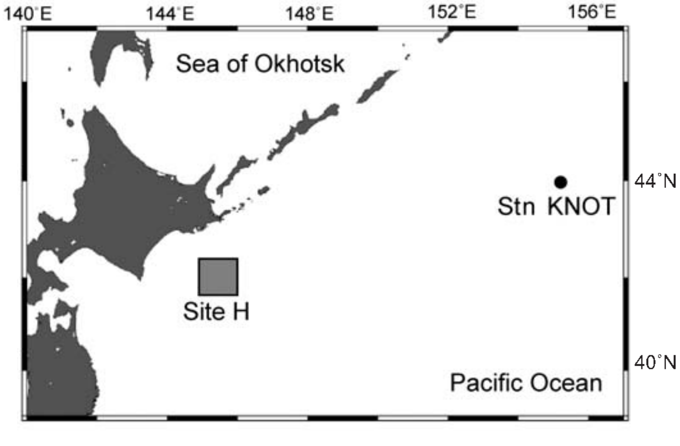

Fig. 1. Location of Site H and Stn KNOT in western subarctic Pacific

Table 1. Zooplankton sampling data

| Location/sampling date | Time (h local time) | Vessel | Discrete sampling depth (m) |
|---|---|---|---|
| Site H | | | |
| 4 September 1996 | 18:27–20:23, 07:28–09:26 | Oshoro-Maru | 0–30, 30–250, 250–500, 500–1000, 1000–1800 |
| 19 September 1996 | 17:37–19:44 | Hokusei-Maru | 0–30, 30–250, 250–500, 500–1000, 1000–1500 |
| 2 October 1996 | 23:25–02:05 | Hokusei-Maru | 0–30, 30–250, 250–500, 500–1000, 1000–1500 |
| 8 December 1996 | 01:10–02:48, 06:36–08:50 | Hokushin-Maru | 0–80, 80–250, 250–500, 500–1000, 1000–1700 |
| 13 January 1997 | 10:00–12:00 | Hokko-Maru | 0–50, 10–500, 300–1700 |
| 20 February 1997 | 02:30–05:10 | Hokushin-Maru | 0–100, 100–250, 250–500 |
| 17 March 1997 | 00:55–03:30 | Hokko-Maru | 0–100, 100–250, 250–500, 500–1000, 1000–2000 |
| 11 April 1997 | 02:40–04:40, 08:20–10:30 | Hokusei-Maru | 0–100, 100–250, 250–500, 500–1000, 1000–1500 |
| 7 May 1997 | 23:35–03:20 | Hokko-Maru | 0–100, 100–250, 500–1000, 1000–2000 |
| 4 June 1997 | 18:50–20:09 | Oshoro-Maru | 0–80, 80–250, 250–500, 500–1000 |
| 23 June 1997 | 21:23–23:26 | Hokusei-Maru | 0–20, 20–250, 250–500, 500–1000, 1000–2000 |
| 2 July 1997 | 19:53–22:08 | Hokusei-Maru | 0–40, 40–250, 250–500, 500–1000, 1000–2000 |
| 17 August 1997 | 19:45–21:39 | Oshoro-Maru | 0–80, 80–250, 250–500, 500–1000, 1000–2000 |
| 26 August 1997 | 10:10–12:01 | Tansei-Maru | 0–20, 20–250, 250–500, 500–1000, 1000–2000 |
| 5 October 1997 | 20:45–22:20, 15:05–17:15 | Hokusei-Maru | 0–75, 75–250, 250–500, 500–1000, 1000–2000 |
| Stn KNOT | | | |
| 19–21 August 1998 | 09:07–13:28, 22:06–05:02 | Hakurei–Maru No. 2 | 0–100, 100–200, 200–500, 500–1000, 1000–1500, 1500–2000, 2000–3000, 3000–4000 |

not recognized, BT was assumed arbitrarily as 100 m depth. On 3 dates, 1 or more depth strata were not sampled. Data for missing samples were interpolated from the nearest samplings of that depth interval before and after the sampling dates (see Table 1). Samples to evaluate seasonal vertical distributions were collected during night hours except on 13 January 1997 and 26 August 1997. To investigate the diel vertical migration pattern, day–night samplings were conducted on 4 occasions, i.e. 9 September and 12 December 1996 and 11 April and 5 October 1997. After collection, zooplankton samples were immediately preserved in a 5% formalin-seawater solution buffered with borax. Temperature and salinity profiles were determined with a CTD system (Neil Brown, General Oceanics, or Sea Bird, Electronics) at each zooplankton sampling. Chlorophyll *a* profiles at Site H have been reported elsewhere (Kasai et al. 2001).

Additional day–night samplings were made on 19 to 21 August 1998 at Stn KNOT (44° N, 155° E) (Fig. 1), which is located in the southwestern part of the Western Subarctic Gyre (Fig. 1). Stn KNOT was chosen because effects of the discharge of water from the Okhotsk Sea, which would influence the interpretation of population dynamics of zooplankton, are considered unlikely here (cf. Kono 1997). Zooplankton was collected with a vertical multiple plankton sampler (VMPS) (100 × 100 cm mouth-opening, 90 µm mesh size; Terazaki & Tomatsu 1997) from 200–500, 500–1000, 1000–1500, 1500–2000, 2000–3000 and 3000–4000 m. The samples were taken from the surface–100 and 100–200 m depths using a modified NORPAC net (40 × 40 cm mouth-diameter, 90 µm mesh size; Motoda 1957). Details of the sampling program at Stn KNOT have been reported elsewhere (Yamaguchi et al. 2002).

**Identification and enumeration.** In the laboratory, *Metridia pacifica* and *M. okhotensis* were sorted from the entire or half aliquot of preserved zooplankton samples and counted under a dissecting microscope. The morphological features of adult males and females of both species have been given by Brodsky (1967, 1976). For identification of pre-adult copepodite stages of both species the description of *M. lucens* (= *M. pacifica*) by Morioka (1976) and our own data gained from laboratory rearing of *M. pacifica* from eggs to adults (Padmavati & Ikeda 2002) were used. Separation of males from females was possible from Copepodite Stage 4 (C4) for both species. Based on the condition of ovary development, C6 females were classified into 3 maturity stages adopting Batchelder's (1986b) system, except that 'immature' and 'partly mature' stages in his system were pooled as 'immature' stage in this study. In addition to 'immature' and 'mature' stages, a 'spent' stage was created in this study for specimens with empty ovaries and open genital pores.

**Lipid deposition.** In the course of our examination of specimens, we noticed a marked lipid deposition in C5 females of *Metridia pacifica* and C1, C5 and C6 females of *M. okhotensis*. To quantify this, specimens were classified into 3 types: rich, with having a large lipid globule exceeding half of the body length (Fig. 2a); medium, with a medium-sized lipid globule less than half of the body length); and poor, with no oil globule. Rich was not seen in C1 of *M. okhotensis*, so they were classified as 'medium' (Fig. 2b) and 'poor' only.

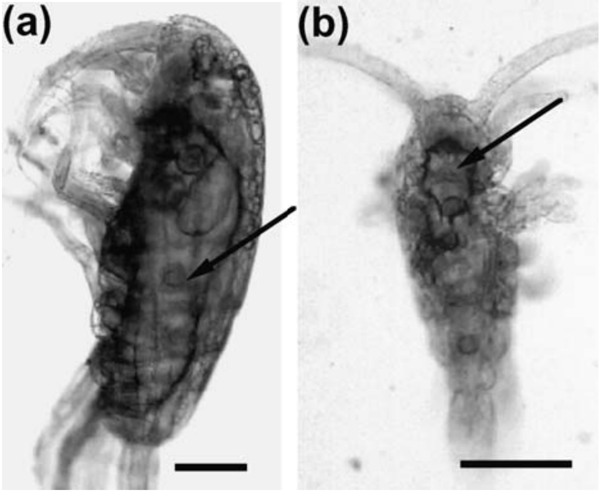

Fig. 2. *Metridia pacifica* and *M. okhotensis*. Lipid droplets (arrowed) of (a) 'rich' type Stage C5 of *M. pacifica* (lateral view), and (b) 'medium' type Stage C1 of *M. okhotensis* (dorsal view). Scale bars = 0.2 mm

## RESULTS

### Hydrography

The western boundary current of the subarctic circulation in the North Pacific is called the 'Oyashio Current'. It flows southwestward along the Kuril Islands to the east coast of the northern Honshu, Japan, and then turns east at about 40° N (Reid 1973). During its journey, the properties of Oyashio Current water are modified as a result of exchanges with Okhotsk Sea water and Kuroshio water (Kono 1997). Because of its meandering flow pattern, isolated loops of the Kuroshio extension are often entrapped between the downstream and return flows of the Oyashio Current and are called 'warm core rings'.

Site H of this study is near the southern end of the southwestward alongshore flow of the Oyashio Current. Over the study period, surface temperatures ranged from 2°C (March to April 1997) to 18°C (September to October 1996 and 1997) (Fig. 3a). Oyashio Current water, characterized by salinities from 33.0 to 33.3 psu and temperatures below 3°C (Ohtani 1971), occurred in the upper 150 m from February to April 1997. After April, less saline, seasonally warmed water (possibly originating from the Okhotsk Sea; T. Kono pers. comm.) occupied the upper 50 m of the water column. Surface temperatures above 10°C were observed in September to November 1996 and in June to October 1997, when the thermocline was well established at 20 to 50 m in the water column. Effects of warm-core rings originating from the Kuroshio extension were seen in September of both 1996 and 1997, and from December 1996 to January 1997, as judged by measurements of temperature at 200 m (>4°C) and salinity in the 0 to 200 m layer (>33.5 psu) (Fig. 3b). Temperature and salinity in the 200 to 1500 m layer were stable and nearly constant at 2 to 3°C and 33.5 to 34.5 psu, respectively, throughout the year.

Phytoplankton biomass, estimated in terms of chlorophyll *a* concentrations, showed a marked seasonality

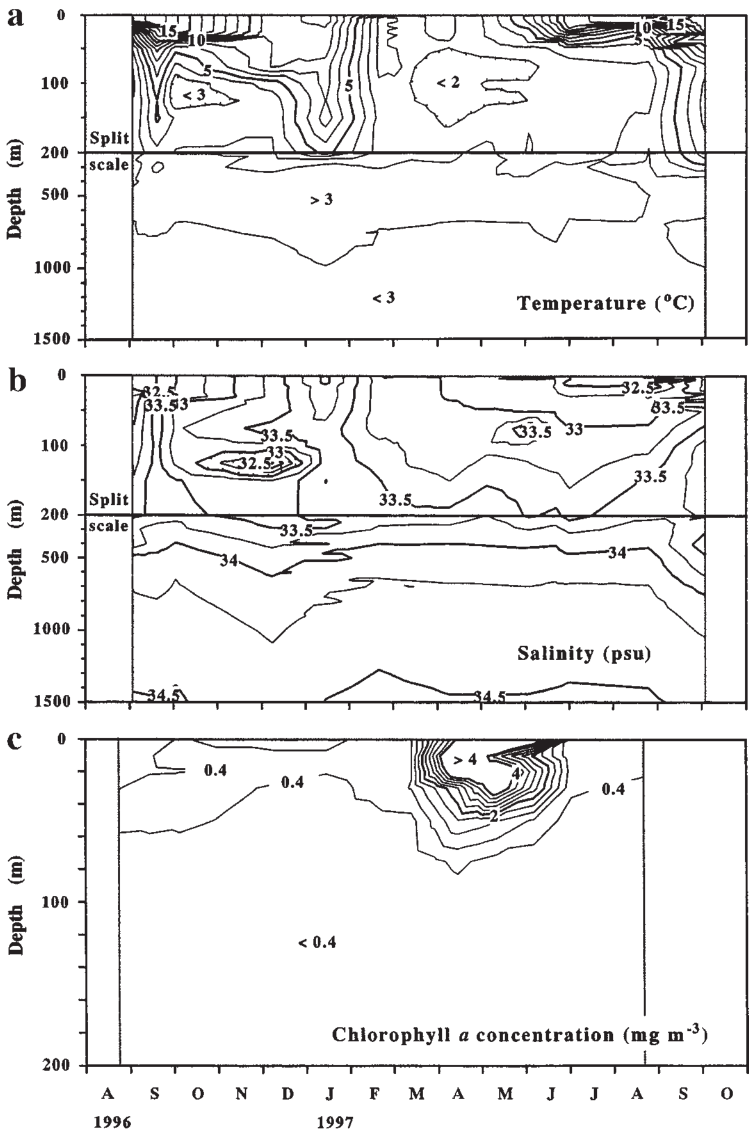

Fig. 3. Seasonal changes in (a) temperature, (b) salinity and (c) chlorophyll *a* at Site H. Note different depth scale in (c)

(Fig. 3c). Chlorophyll *a* at the surface was around 0.4 mg m$^{-3}$ from August 1996 to the end of February 1997, and then increased rapidly to >9 mg m$^{-3}$ in May 1997. During this period, concentrations above 2 mg m$^{-3}$ extended down to 50 m depth. The surface chlorophyll *a* concentrations had decreased to 2 mg m$^{-3}$ by the end of June and to 0.4 mg m$^{-3}$ toward the end of 1997. Chlorophyll *a* concentrations were <0.4 mg m$^{-3}$ below 100 m depth throughout the year.

## Seasonal vertical distribution

Among the seasonal sampling data in Table 1, only nighttime data were used for this analysis. The C1, C2 and C3 stages of *Metridia pacifica* were distributed almost exclusively in the top 250 m of the water column throughout all seasons of the year (Fig. 4a). C4 individuals exhibited a much broader vertical distribution through the top 500 m of the water column) than the C1–C3 stages (Fig. 4b). The distribution pattern of C5 changed markedly with season; they were abundant in the top 500 m during spring–early summer (March–August), and below 500 m or even 1000 m depth during September–February (Figs. 4c & 5). Both C5 males and females showed a marked bimodal vertical distribution pattern in October through December 1996. The C6 females resided in the top 250 m of the water column while C6 males concentrated largely in the 250–500 m stratum throughout the year (Fig. 4d).

Of the copepodite stages of *Metridia okhotensis*, only C1, C5 and C6 females occurred throughout the year. C2, C3, C4 and C6 males were observed only seasonally. The C1, C5 and C6 females were distributed largely in the 250–1000 m depth strata (Fig. 6a,c,d). As exceptions, some fraction of the young stages (C1–C3) occurred in the surface layer (June, July and October 1997) and at 1000–2000 m depth (October 1996, and February–April, June, July, August and October 1997) (Fig. 6a). The vertical distribution pattern of C4 populations was similar to that of younger copepodites (Fig. 6b).

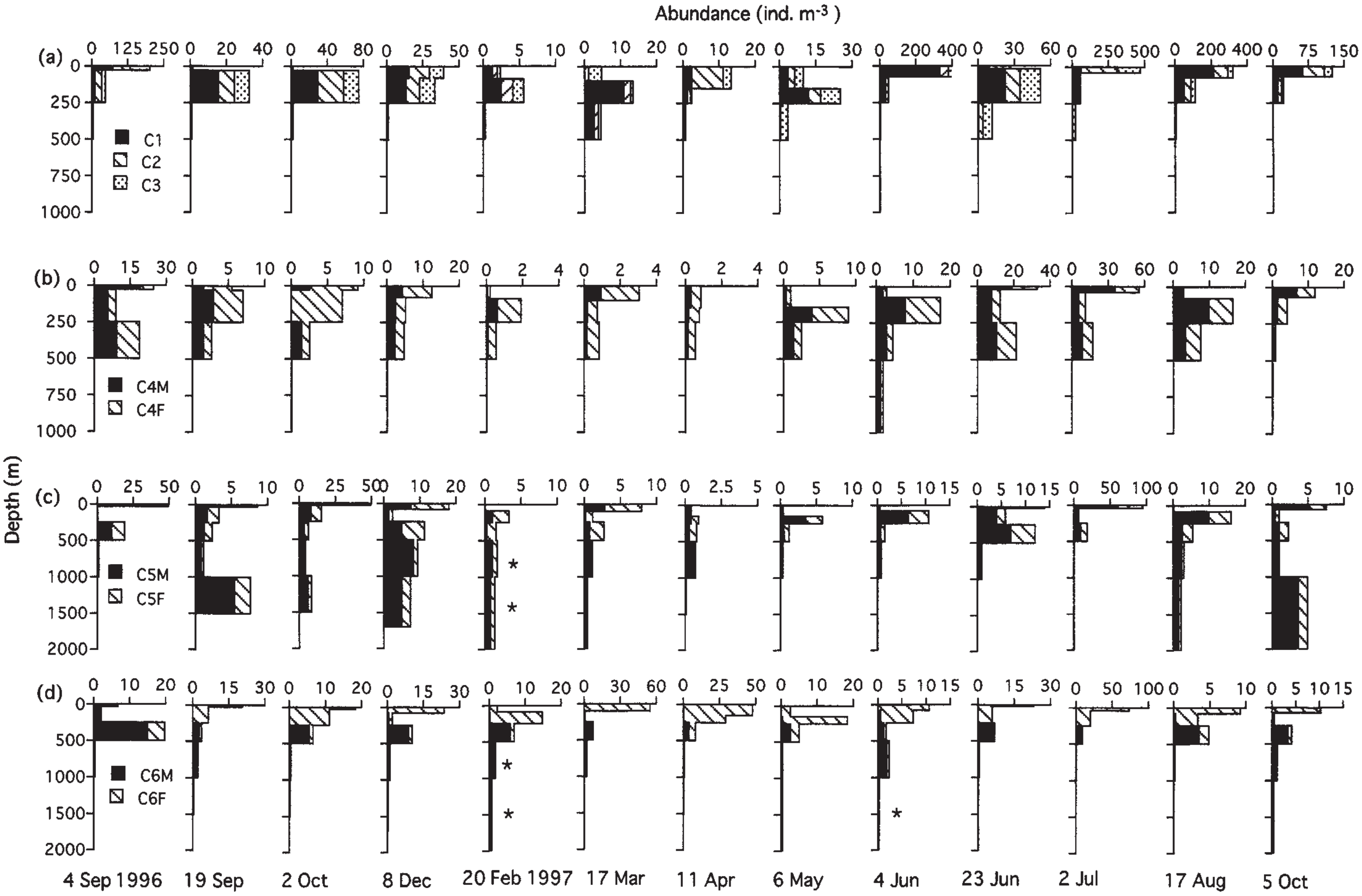

Fig. 4. *Metridia pacifica*. Seasonal changes in vertical distribution of (a) Stages C1–C3, (b) C4 males (M) and females (F), (c) C5 males and females, and (d) C6 males and females at Site H from September 1996–October 1997. Note that depth scale of (a) and (b) differ from that of (c) and (d). Asterisks denote interpolated values. Date of sampling is shown on bottom abscissa

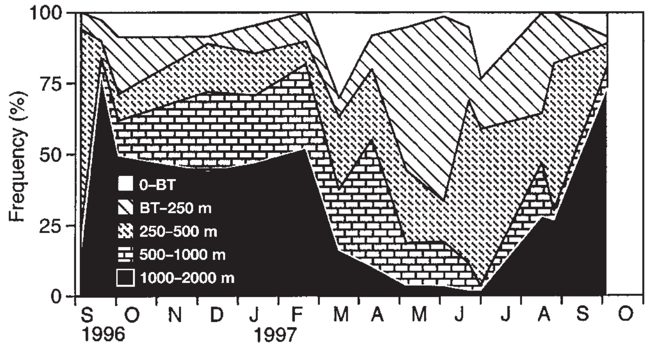

Fig. 5. *Metridia pacifica*. Seasonal changes in relative frequency of Stage C5 individuals in each stratum sampled at Site H from September 1996 to October 1997. BT: bottom of thermocline

### Day/night vertical distribution

The young copepodites (C1–C3) of *Metridia pacifica* occurred mainly in the top 250 m of the water column both day and night throughout the 4 seasons, with no diel vertical migration (DVM) patterns (Fig. 7a). Only a small fraction of the C4 (<14 % of the total population) and C5 (<21 %) populations migrated to the surface layer at night in September and December 1996. In April and October 1997, C4 and C5 occurred at the surface layer during both day and night (Fig. 7b,c). Most of the C5 population in December 1996 (44 and 88 % of the total population during daytime and nighttime, respectively) and in October 1997 (74 and 71 % of the total population during daytime and nighttime, respectively) were at 1000–2000 m, showing limited DVM. While part of the C6 female population migrated to the surface layer at night in September 1996 (15 % of the total population), December 1996 (59 %), April 1997 (44 %) and October 1997 (57 %), no DVM was seen in C6 males (Fig. 7d) (Kolmogorov-Smirnov test, $p > 0.05$).

Young copepodites (C1–C3) of *Metridia okhotensis* were never found at the surface; instead, they were most abundant between 250 and 500 m depth

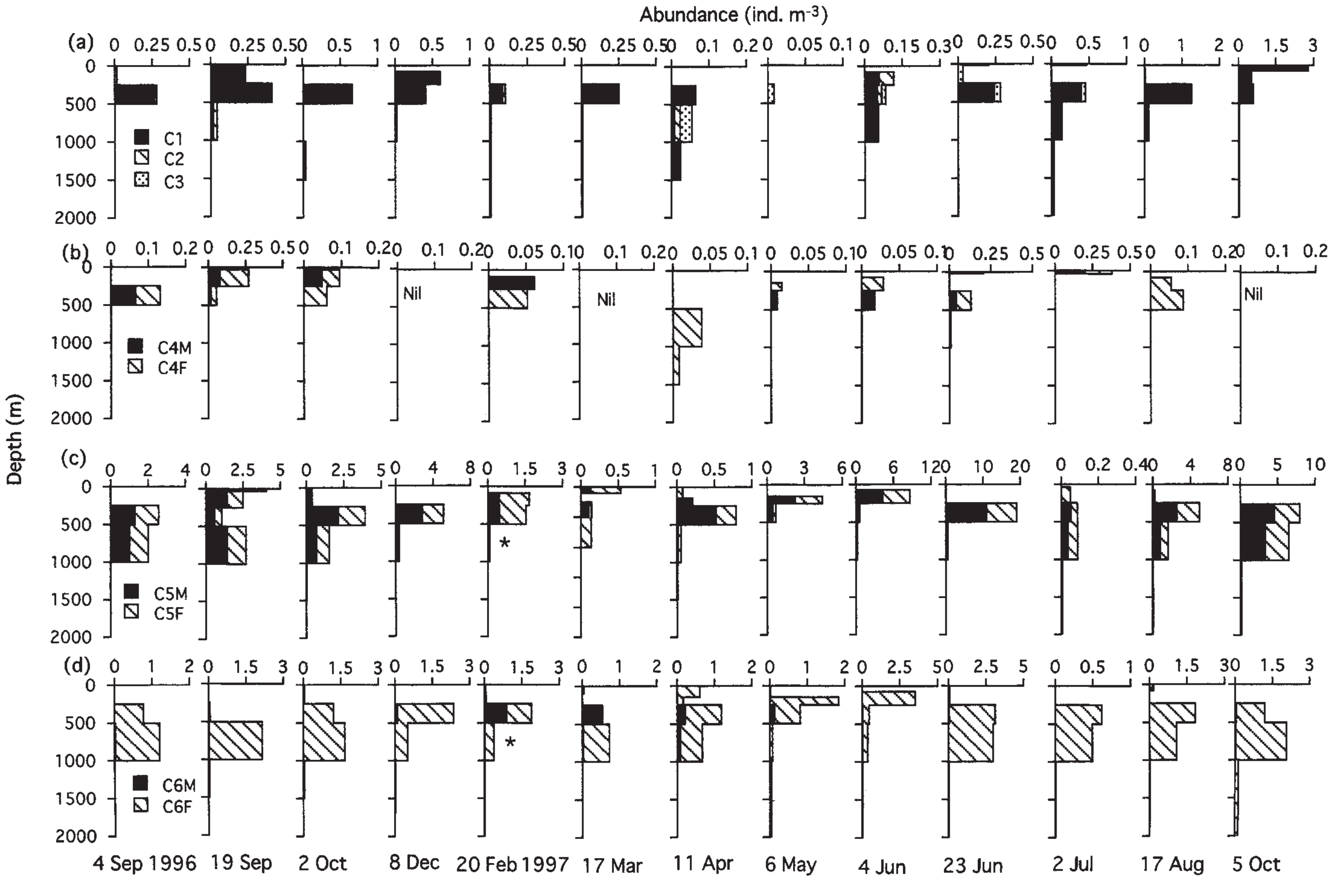

Fig. 6. *Metridia okhotensis*. Seasonal changes in vertical distribution of (a) Stages C1–C3, (b) C4 males and females, (c) C5 males and females, and (d) C6 males and females at Site H from September 1996–October 1997. Asterisks denote interpolated values. Date of sampling is shown on bottom abscissa

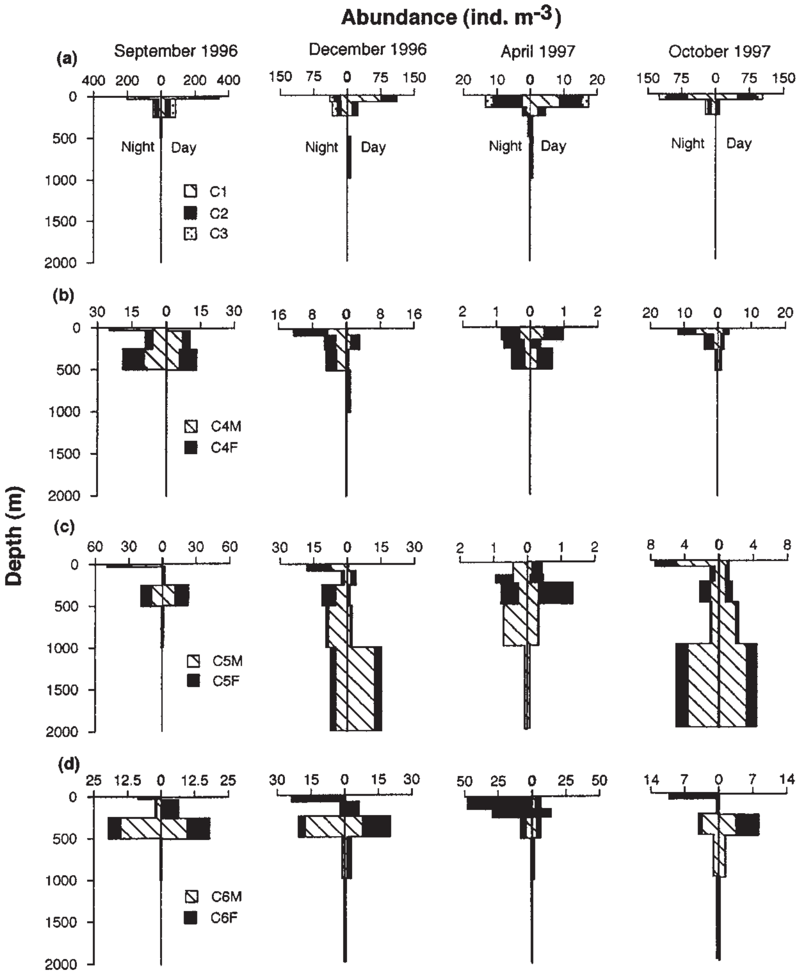

Fig. 7. *Metridia pacifica*. Day/night changes in vertical distribution of (a) Stages C1 to C3, (b) C4 males and females, (c) C5 males and females, and (d) C6 males and females at Site H. Date of sampling is shown on top abscissa

both day and night over the year with no DVM pattern (Fig. 8a). Both C4 males and females were few in number and their vertical distribution patterns were somewhat similar to those of the C1–C3 stages. C4 was not found in daytime samples in December 1996 and April 1997; and in nighttime samples in October 1997; therefore seasonal changes in their DVM pattern could not be analyzed (Fig. 8b). However, during the September 1996 sampling, when C4 were collected both day and night, there was evidence of possible nighttime migration to the surface (Fig. 8b). Most C5 and C6 populations were found in 250–1000 m depth and showed no DVM pattern (Fig. 8c,d) (Kolmogorov-Smirnov test, $p > 0.30$). During April 1997, a part of the C6 population (33% during daytime, 16% at night) was seen in the surface layer during both day and night.

## Seasonal variations in abundance and population structure

### *Metridia pacifica*

All copepodite stages occurred throughout the year, although the abundance of each stage varied greatly with season (Fig. 9). C1 formed 2 abundance peaks, one in June (during the phytoplankton bloom) and the other in August 1997 (after the phytoplankton bloom). The maximum abundance of the C2–C4 was seen between the periods of the 2 C1 peaks. C5 were most abundant in October to December 1996: 2 successive abundance peaks of C6 females were seen, the first prior to the first C1 peak (early April 1997), and the last between the 2 C1 peaks (early July 1997). The abundance of C6 males was less marked seasonally.

The female:male ratios ranged from 0.8:1–4.7:1 (annual mean = 1.2:1) for C4, 0.34:1–1.1:1 (0.62:1) for C5, and from 0.47:1–8.1:1 (1.5:1) for C6. Immature C6 females with undeveloped ovaries comprised a large fraction (52–88%) of the total adult female population throughout the year (Fig. 9b). Both mature and spent C6 females were found almost throughout the year, but the proportion they comprised of total females was low (0–24 and 7–43%, respectively). Over the year, the proportion of mature females became higher in June to August, corresponding in time with the seasonal peak in female C6 abundance (July).

In terms of stage composition of copepodites (grouped as C1–C3, C4, C5, C6 male and C6 female Fig. 10a) the copepodite population consisted mainly of younger copepodite stages (C1–C3) from May to September (45–78% of the total population), especially in June (78%) and August (73%). From September to February, C5 was the most dominant stage, comprising 37–45% of the population. During the winter, the proportion of C5 decreased gradually toward spring of the next year and reached less than 20% of the total population by March. At the same time, the proportion of C6 males increased from December to February, and that of C6 females from January to April. These seasonal sequences in copepodite stage composition, together with the incidence of mature females throughout the year (Fig. 9b), sug-

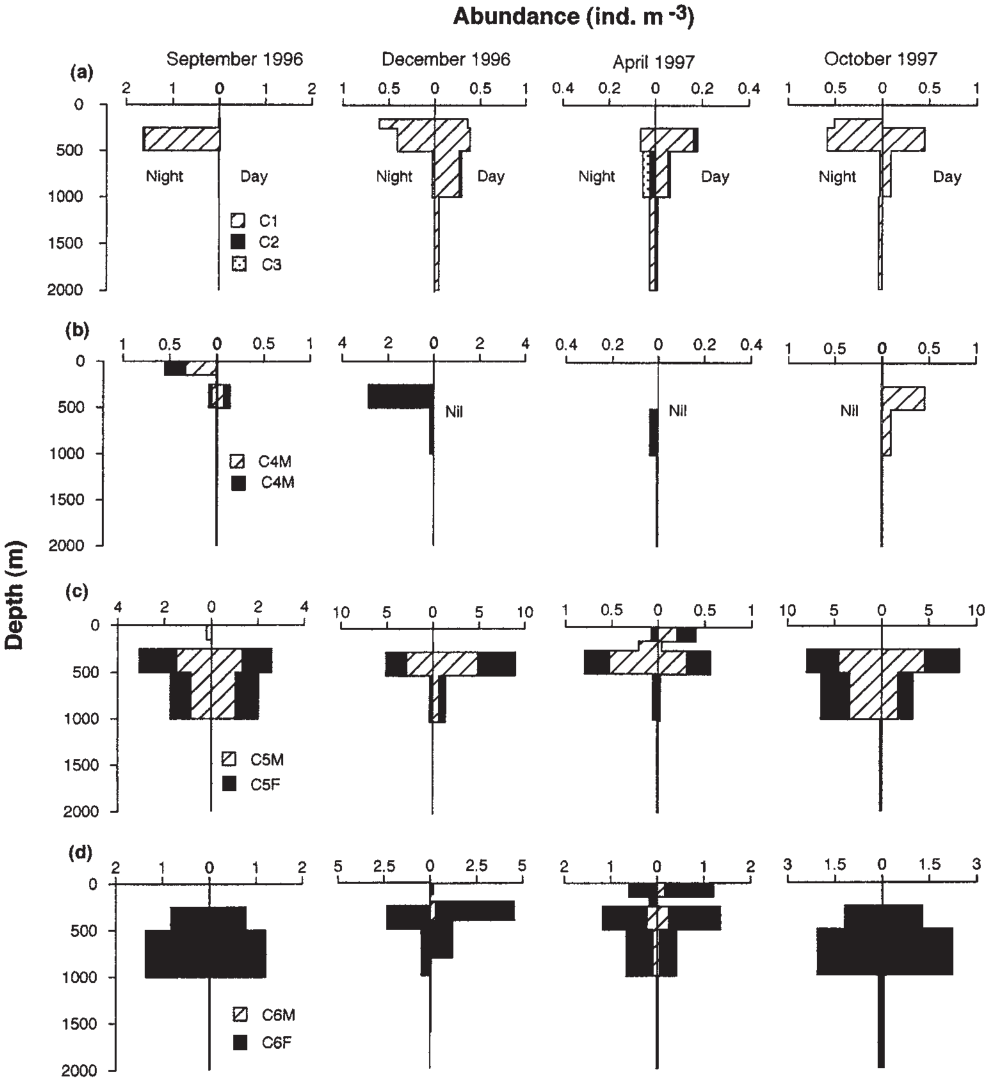

Fig. 8. *Metridia okhotensis*. Day/night changes in vertical distribution of (a) Stages C1 to C3, (b) C4 males and females, (c) C5 males and females, and (d) C6 males and females at Site H. Date of sampling is shown on top abscissa

gest that while reproduction of this species may occur continuously year-round, 2 generations are completed in a year, the first generation yielding the abundance peak of C1 in early June and the C6 female peak in July. The second generation produced the peak of C1 in August, which did not develop to C6 until the following January–April.

### *Metridia okhotensis*

C1 individuals occurred throughout the year, but their abundance was high from August to December and low from January to July (Fig. 11a). C2 and C3 occurred part of the year, the former in October 1996 and from February–August 1997, and the latter in September 1996 and from April–September 1997. C4 were found in all seasons but their seasonal abundance showed an irregular pattern. The overall abundance of C2, C3 and C4 was considerably less than that of C1. C5 occurred throughout the year and formed marked abundance peaks in late June and October 1997. C6 males did not occur in early October 1996 and July–August 1997. In contrast, C6 females were found throughout the year and their abundance peak was in late June 1997.

The occurrence of both C4 females and males was not continuous, and a female:male ratio based on annual mean abundance of each was 2.9:1. Female: male ratios varied with season from 0.8:1–2.5:1 (annual mean = 1.1:1) for C5 and from 1.2:1–211:1 (13.1:1) for C6. Because of a large deposition of lipid in C6 females, observation of their gonads is often difficult, and therefore the classification of the maturity stage of this species may be less accurate than for females *Metridia pacifica*. Over the entire study period, matu-

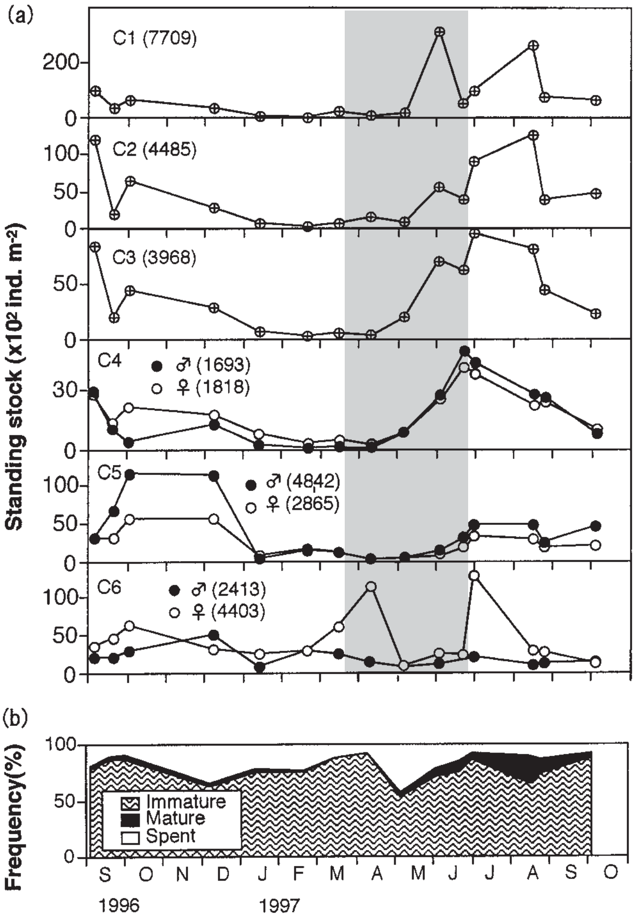

Fig. 9. *Metridia pacifica*. Seasonal changes in (a) standing stock of each developmental stage (C1–C6) and (b) composition of maturity stages (immature, mature, spent) at Site H from September 1996–October 1997. In (a) values in parentheses = annual means, shaded area = phytoplankton bloom period

rity stage composition of C6 females was characterized by the almost exclusive predominance of immature individuals, fewer mature individuals (observed only in May and June 1997) and no spent individuals (Fig. 11b).

Copepodite population structure was characterized by the extreme predominance of older stages (C5 and C6) throughout the year (Fig. 10b). The greatest proportion of younger stages (C1–C3) was 31% in early July 1997. As mentioned above, the C4 population was very small, comprising only 2–3% at most of the total population during late September to January. Within older stages, the proportion of C5 exceeded 50% (52–76%) of the total in September–December 1996 and April–June and August–October 1997, while that of C6 exceeded 50% of the total in January–March (67–68%) and in June 1997 (57%). These results would seem to suggest reproduction of *Metridia okhotensis* in late winter and recruitment of the resultant early copepodites in early summer (July), but the entire development sequence of the copepodites cannot be traced if one assumes the generation length of this species to be 1 yr or less (see 'Discussion').

## Lipid-deposition pattern

For *Metridia pacifica*, C5 individuals classified as rich type increased gradually from July, reaching a peak in September–October and decreasing toward March–May (Fig. 12a). Medium-type individuals showed a similar pattern. Poor-type individuals comprised less than 50% of the C5 population from August to October and more than 50% from December to June. The annual mean composition of rich, medium and poor types was 8.9, 32.7 and 58.4%, respectively.

In contrast to the C1 stage of *Metridia pacifica*, which contained no lipid droplets, many C1 specimens of *M. okhotensis* contained a small lipid droplet in the head part of the prosome. The C1 individuals classified as medium type comprised more than 60% of the C1 population throughout most seasons (Fig. 12b). The proportion of rich-type C5 individuals decreased from October 1996–March 1997, and then increased from April–September 1997 (Fig. 12c). Medium-type specimens showed a similar trend. Poor-type individuals were abundant from December to April. The annual mean composition of the 3 types of C5 was 24.4% for rich, 44.2% for medium and 31.4% for poor types. For C6 females, seasonal patterns of the 3 types were similar to those of C5 in general (Fig. 12d), but the proportion of rich type was greater (annual mean = 52.8%) and the proportion of poor type was less in C6 (15.5%) than the respective types in C5.

## Stn KNOT

During zooplankton sampling in August 1998, surface temperature, salinity and chlorophyll *a* were 13.5°C, 32.7 psu, and 0.8 mg $m^{-3}$, respectively, and depth profiles of these environmental parameters were similar to those observed at Site H in the same month of 1997 (August 1997, cf. Fig. 3). For details of hydrographic data for this sampling program, see Yamaguchi et al. (2002).

All copepodite stages of *Metridia pacifica* were found in the 0–500 m depth stratum during day and night (Fig. 13a). They were most numerous at 0–100 m depth during both day and night. Day–night differences in vertical distribution of the entire population

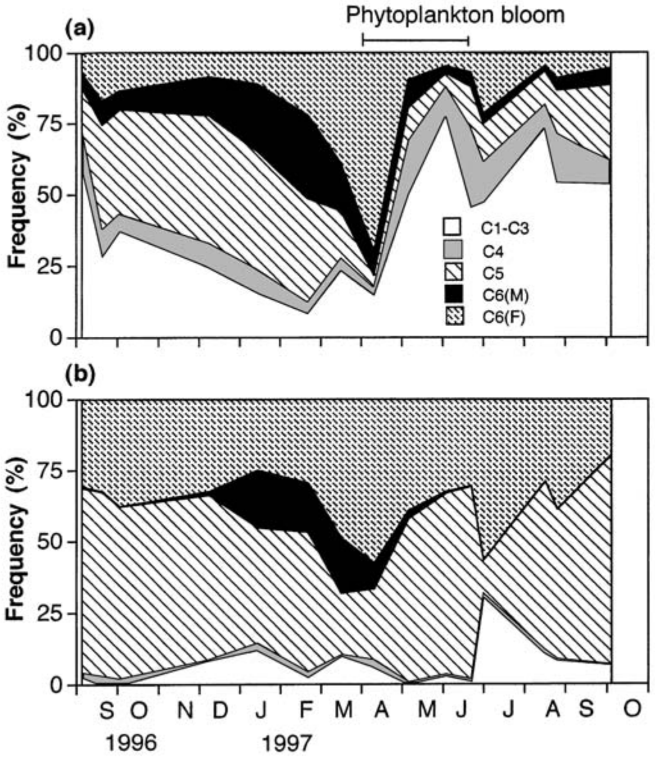

Fig. 10. (a) *Metridia pacifica* and (b) *M. okhotensis*. Seasonal changes in relative frequency of Stages C1–C3, C4, C5 and C6 males and females at Site H from September 1996 to October 1997

were not significant (Kolmogrov-Smirnov test, $p > 0.3$). However, DVM behavior was evident for older copepodite stages; e.g. most C4–C6 stages resided at 100–500 m depth during the daytime and ascended to 0–100 m depth at night (Fig. 13). The population structure was characterized by the predominance of C1 (24 % of the total) and adult females (24 %), suggesting August to be well within their active reproduction seasons.

*Metridia okhotensis* occurred at 200–1000 m depth, and showed no DVM pattern (Fig. 13b). While day–night differences in vertical distribution of the entire population were not significant (Kolmogrov-Smirnov test, $p > 0.1$), a small fraction (3 %) of the population was found at 0–100 m depth only at night. In contrast to *M. pacifica* (see above), the population structure of *M. okhotensis* was dominated by C5 (males and females) and C6 (females), which together accounted for 93 % of the total population. Young copepodites (C1–C4) and adult males were extremely scarce or absent (C3).

When the same season (August) is compared, the vertical distribution and population structure of *Metridia pacifica* and *M. okhotensis* at Stn KNOT are consistent with those observed at Site H.

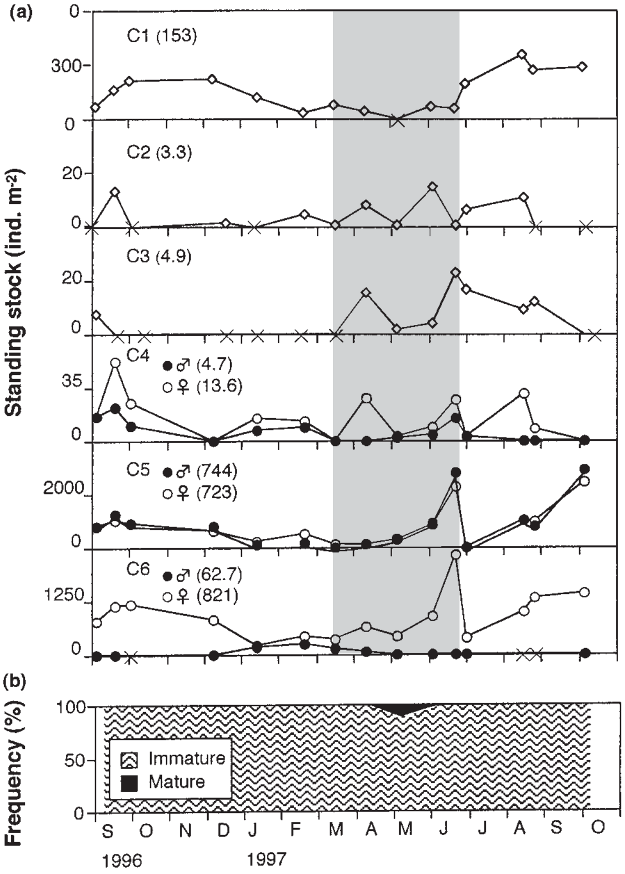

Fig. 11. *Metridia okhotensis*. Seasonal changes in (a) standing stock of each developmental stage (C1–C6) and (b) composition of maturity stages (immature, mature) at Site H from September 1996–October 1997. In (a) values in parentheses = annual means, shaded area = phytoplankton bloom period. ×: no occurrence. Note differing ordinate scales in (a)

## DISCUSSION

### Vertical distribution

Seasonal distribution patterns of *Metridia pacifica* at Site H in the Oyashio region were characterized by the shallow occurrence (<250 m) of young copepodites (C1–C3) and C6 females, a slightly deeper occurrence (250–500 m) of C6 males, and a great variation in C5 from the surface layer to 1000–2000 depth (Fig. 5). The only information comparable to the present results is that of Batchelder (1985) at Stn P in the eastern subarctic Pacific. As a habitat for *M. pacifica*, Stn P differs from Site H of this study in that phytoplankton biomass at Stn P does not show clear seasonality throughout the year (0.1–0.6 mg chlorophyll *a* m$^{-3}$) although primary production reaches its maximum in May–July (cf. Welshmeyer et al. 1993). In contrast, the occurrence of a phytoplankton bloom (2–9 mg chlorophyll *a* m$^{-3}$) between March and June is a regular annual event at

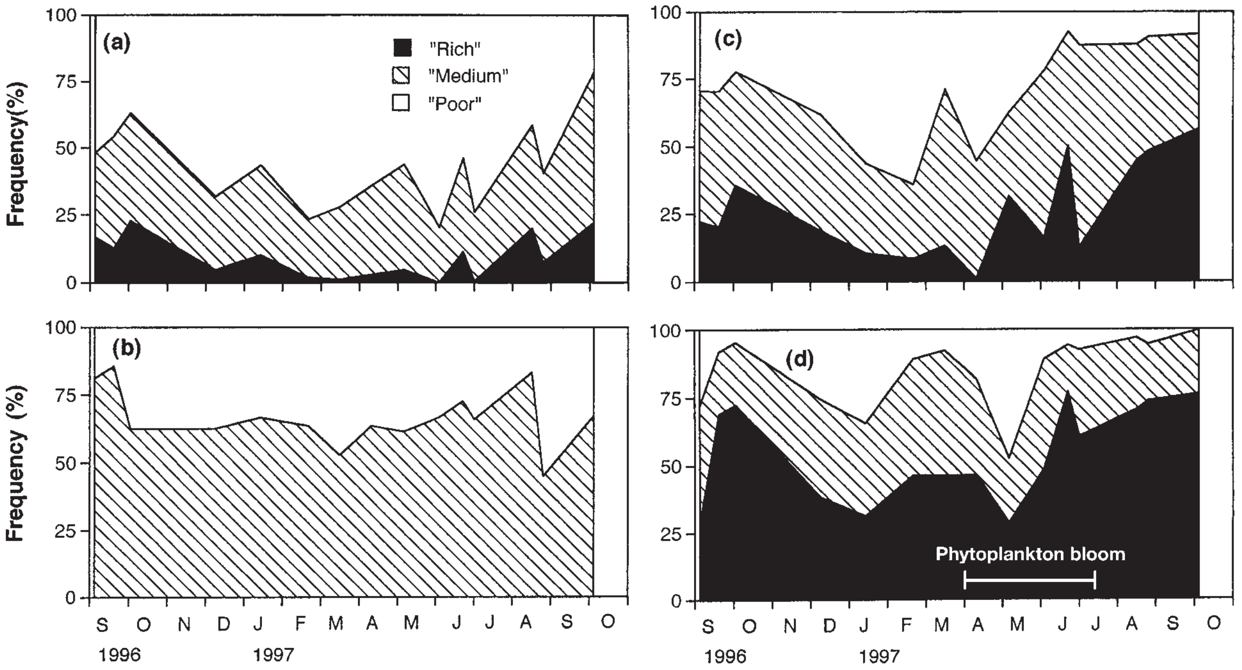

Fig. 12. *Metridia pacifica* and *M. okhotensis*. Seasonal changes in relative frequency of lipid deposition types (rich, medium, poor) of (a) Stage C5 *M. pacifica*, and (b) C1, (c) C5 and (d) C6 *M. okhotensis* at Site H from September 1996–October 1997. Note rich type did not occur for C1 *M. okhotensis*

Site H in the Oyashio region (Kasai et al. 2001). The annual range in surface temperatures at Stn P is narrower (6 to 14°C; see Fig. 1 in Batchelder [1985]) than at Site H (2 to 18°C, cf. present Fig. 2). Notwithstanding these different habitat conditions between Site H and Stn P, seasonal vertical distribution patterns of each copepodite stage of *M. pacifica* at these 2 sites were almost the same. Deeper excursions (>500 m depth) of C5 *M. pacifica* have also been reported in Toyama Bay, southern Japan Sea, where summer surface temperatures (>26°C) rise beyond the limit of this species (Hirakawa & Imamura 1993).

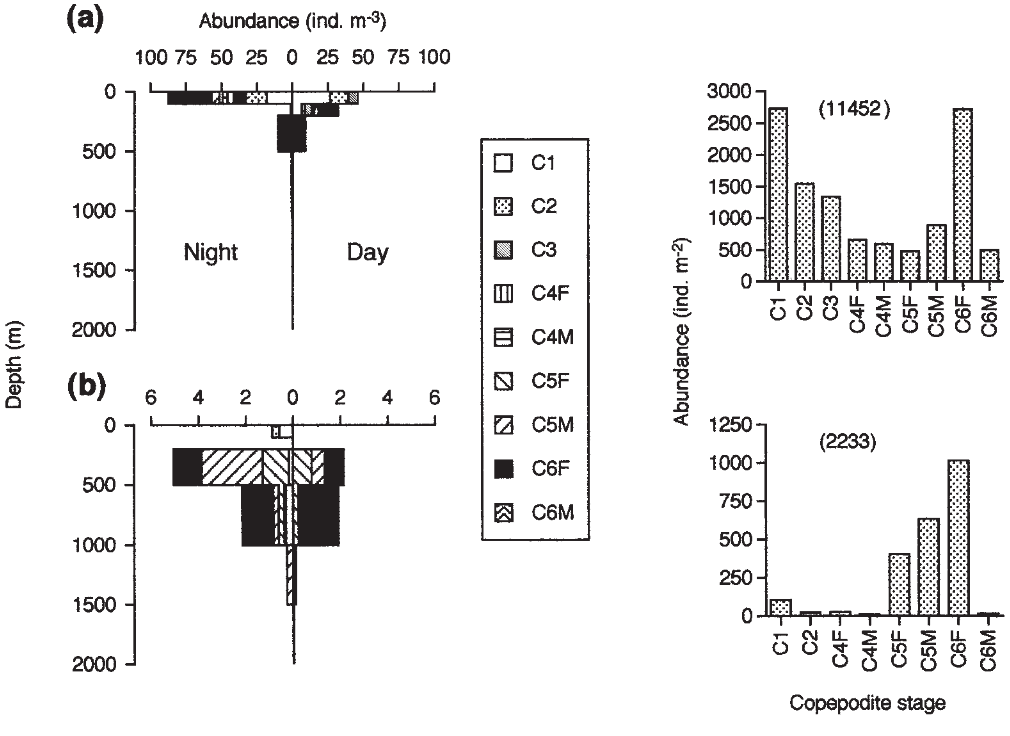

Fig. 13. (a) *Metridia pacifica* and (b) *M. okhotensis*. Day/night changes in vertical distributions (right) and their population structures (left) at Stn KNOT from 19–21 August 1998. Population structure represented by mean abundance of each developmental stage (no occurrence of C3 for *M. okhotensis*) in daytime and nighttime samplings (total in parentheses). (Note that despite sampling to 4000 m depth, neither species occurred beyond 2000 m depth)

*Metridia okhotensis* rarely occurred in the surface layer at Site H. Young stages (C1 to C4) occurred mostly from 250–500 m depth and older stages (C5, C6) from 250–1000 m depth (Fig. 6). Thus, these 2 sympatric species partition their distribution vertically for most of the year. Vertical separation of the habitat has already been noted for *Neocalanus* spp. in the subarctic Pacific (Mackas & Tsuda 1999). While no comparable seasonal study on the vertical distribution of *M. okhotensis* is presently available, incidental records from the northwestern subarctic Pacific (50–1000 m: Minoda [1971]; 250–500 m deep: Hattori [1989]) and from the Bering Sea (200–1000 m: Minoda [1971]) are consistent with our results. As an exception, *M. okhotensis* in the northern and central Okhotsk Sea occur at shallow depths (25–100 m deep) (Russian literature compiled by Pinchuk & Paul [2000]). Taking into account water temperatures in the depth stratum where *M. okhotensis* live in the northern and central Okhotsk Sea (near 0°C), the major reason for the deeper distribution in the subarctic Pacific (including Site H) and Bering Sea may be avoidance of warmer water near the surface. Submergence of cold-water zooplankton at lower latitudes or nearby areas where the surface is covered by warmer waters has been well documented (cf. Banse 1964 for review).

Many species belonging to the genus *Metridia* are known to perform DVM (Raymont 1983). Batchelder (1985) studied DVM behavior of *M. pacifica* at Stn P during July, August and January. His results showed that C3, C4, C5 (males and females) and C6 (females only), all of which were absent or rare at the surface during daytime, increased abundance significantly in the same layer at night, thus demonstrating normal DVM behavior (no observations for C1 and C2). The present observation on *M. pacifica* in September, December, April and October confirmed DVM for a fraction of the populations of females and males of C4 and C5 in 2 out of the 4 seasonal samplings, and C6 females in all these seasons (Fig. 7). The present results differ from those of Batchelder's (1985) in that C3 did not perform DVM in the present study. C3 occurred in the surface layer during both day and night.

Except for 1 isolated observation on C4 in September 1996, *Metridia okhotensis* did not perform DVM at Site H (Fig. 8). Hattori (1989) also noted the lack of DVM behavior for *M. okhotensis* at 2 stations in the western subarctic Pacific. However, in the Okhotsk Sea, where this species is abundant, Vinogradov & Arashkevich (1969) reported extensive DVM (magnitude of 500–700 m) for *M. okhotensis*.

DVM of zooplankton is not a fixed behavior, but is flexible depending on environmental conditions such as light, temperature, oxygen, food availability, and presence or absence of predators (Lampert 1993, Hays et al. 1998, 2001 and references therein). According to a recent study, variations in the intensity of the turbulence of the upper layer (Incze et al. 2001) could also influence DVM behavior of zooplankton. The presence and absence of DVM within the same population, as was the case for *Metridia pacifica* in this study (Fig. 7) and in that of Hattori (1989), may have been due to individual variations in nutritional conditions (Hays et al. 1998, 2001). According to Hays et al. (2001), those individuals migrating to the surface layer to feed were characterized by lower lipid reserve. Unfortunately, we did not record lipid content in migrating and non-migrating individuals in this study, and therefore Hays et al.'s (2001) hypothesis could not be verified.

## Life cycle

Seasonal population structure data on a given zooplankton species at a fixed location may not be valid for analysis of its life cycle patterns because of possible transportation of the original population elsewhere by currents during the study period. In this respect, the present study site (Site H) in the Oyashio region is characterized by a complex flow field (see 'Results'). However, the vertical distribution and population structure of *Metridia pacifica* and *M. okhotensis* at Stn KNOT in August 1998 (Fig. 13) are almost consistent with those observed at Site H in the same month of a different year, suggesting that spatial variations in the life cycle patterns of these 2 *Metridia* species between Site H and Stn KNOT are insignificant. Kobari & Ikeda (1999, 2001a,b), comparing life history patterns of *Neocalanus cristatus*, *N. plumchrus* and *N. flemingeri* at Site H with those of individuals from various locations throughout the entire subarctic Pacific, noted the lack of any significant regional variation. Since these *Neocalanus* copepods are characterized by extensive ontogenetic migrations whose range covers the vertical distribution ranges of *M. pacifica* and *M. okhotensis*, and since the time-series samples used by Kobari & Ikeda (1999, 2001a, b) were the same as those in this study, there is no reason to assume that the present results on the life cycle of *Metridia* spp. at Site H are exceptional.

### *Metridia pacifica*

The occurrence of all copepodite stages including mature females throughout the year (Fig. 9a) is indicative of some reproduction of *M. pacifica* throughout the year at Site H in the Oyashio region. However, the stage composition data (Fig. 10a) suggests the occurrence of 2 major generations per year. Combining the seasonal vertical distribution patterns (Fig. 4), the schematic life cycle pattern of *M. pacifica* at Site H is presented in Fig. 14a. The first generation is represented by a peak in C1 abundance in early June, and the second generation by a C1 peak in mid-August. Based on the egg-hatching time and naupliar developmental time determined by laboratory-rearing experiments (Padmavati & Ikeda 2002), spawning precedes peak C1 abundance by 1.5–2 mo. The timing of the abundance peak of C6 females which created the first generation (early April) and the second generation (early July) is consistent with this scenario. Thus, the first major spawning coincides with the phytoplankton bloom, and the second spawning occurs at the end of the bloom. Taking into account the wide sampling interval of this study (ca. 1 mo between samples), the generation length of the first generation can be estimated as 2–3 mo, whereas the second generation exhibits interrupted development, with the C5 copepodites remaining at depth (>1000 m) throughout autumn and early winter (generation length = 9–10 mo). Our laboratory experiments (Padmavati & Ikeda 2002), in which eggs were successfully raised to C6 under saturated feeding conditions, suggested that 2–3 mo generation times are reasonable if conditions (food, temperature) remain suitable. Female:male ratios of C4, C5 and C6 stages varied greatly with season (Fig. 9a), as was observed for *M. longa* in Balsfjorden, northern Norway (Tande & Grønvik 1983). The variations have been interpreted by sexual differences in development rates and in longevity for C6 (Tande & Grønvik 1983).

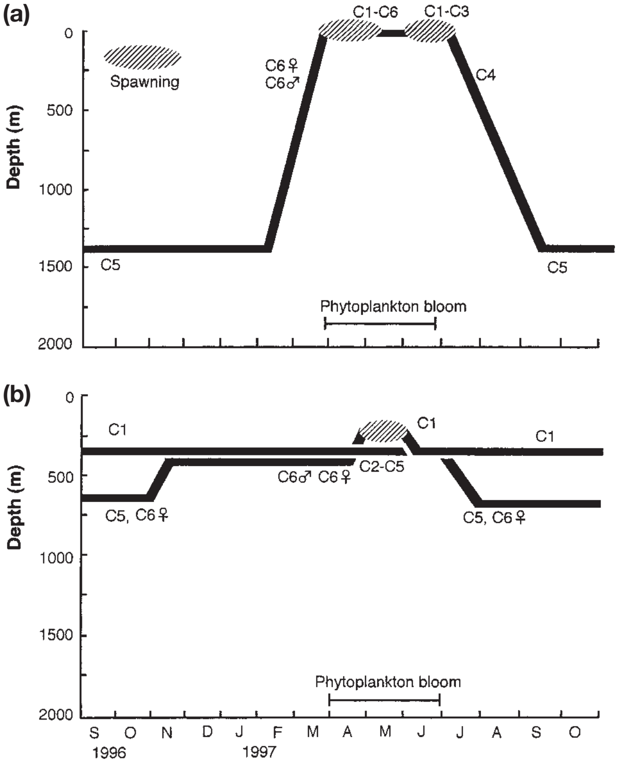

Fig. 14. (a) *Metridia pacifica* and (b) *M. okhotensis*. Schematic representation of life cycle trajectory combined with vertical migration patterns of major cohorts at Site H in Oyashio Current region

At Stn P in the eastern subarctic Pacific, Batchelder (1986b) observed 3 marked peaks in the proportion of mature females of *Metridia pacifica* (>80% of the total females) in mid-April, early July and late September, and concluded that there were 3 generations per year. Each generation took 3 mo to mature to C6 females, but egg production by the third generation was delayed by 'supposedly unfavorable environmental conditions' in November to early January (Batchelder 1986b). Comparing these results at Stn P with those at Site H, it is apparent that while the timing of initiation of the first (April) and second (July) generations is similar, a third generation is lacking at Site H. It is notable also that the proportion of mature specimens in C6 females over the year at Site H was considerably low (24% at most, cf. Fig. 9b) than that at Stn P. While no immediate explanation is presently available for the large differences in the proportion of mature females between our and Batchelder's (1986b) results, our wider sampling intervals (about 1 mo, compared with weekly intervals in Batchelder's study) may have missed peaks of maturation events of the females.

The study of Hirakawa & Imamura (1993) in Toyama Bay, southern Japan Sea, revealed another example of regional variation in the life cycle of *Metridia pacifica*. In Toyama Bay, numerous nauplii occur during a phytoplankton bloom in mid-winter (January–February) and develop to C5 in early April. C5 specimens descend to deeper layers in summer to fall to avoid high lethal temperature in the surface layer (>26°C), and molt to C6 end of the year. Thus, this species has only 1 generation per year in Toyama Bay.

These regional variations in the life cycle patterns of *Metridia pacifica* imply that the cue initiating the first generation of the year is the onset of the phytoplankton bloom for Site H and Toyama Bay populations. At Stn P, there is no appreciable phytoplankton bloom, but the annual maximum of primary production is around May–June (cf. Welschmeyer et al. 1993) with a possible sub-maximum in October (Harrison et al. 1999). The number of generations per year appears to be related to thermal regimes of each habitat; the single generation of Toyama Bay may be attributable to 'aestivation' at depth during summer to avoid high temperatures (Hirakawa & Imamura 1993). The annual range of surface temperatures at Stn P (6 to 14°C; Batchelder 1985) is much smaller than at Site H (2 to 18°C; Fig. 3), suggesting that thermal conditions at Stn P are more favorable for *M. pacifica*. *M. pacifica* has been reported as probably having 4 generations in the waters joining Comandor Isles and Providens Bay, western Bering Sea (Heinrich 1962), and 1 generation in Anadyr Bay, northern Bering Sea (Heinrich 1962), and in the Okhotsk Sea (Shebanova 1994), but the lack of temperature and phytoplankton biomass data does not allow our hypothesis to be tested. Regional variations in copepod life cycles have been documented in other copepods such as *Neocalanus flemingeri* (Miller & Terazaki 1989), *Pseudocalanus minutus* and *P. newmani* (Yamaguchi et al. 1998), *Calanoides acutus* (Atkinson et al. 1997), *Rhincalanus gigas* (Ward et al. 1997), *Calanus finmarchicus* (Planque et al. 1997) and *C. hyperboreus* (Hirche 1997).

### *Metridia okhotensis*

While seasonal sequences of population structures of *Metridia okhotensis* (Fig. 11) and *M. pacifica* (Fig. 9) at Site H are broadly similar to each other, the former is markedly different from the latter in that the abundance peaks of C1 preceding the peaks of the subsequent copepodite stages were absent during the phytoplankton bloom despite the occurrence of mature C6 females in April–May. In addition, the population structure of *M. okhotensis* is characterized by extremely low abundance of C2–C4 stages (Fig. 11). Possible transportation of part of the population from the Okhotsk Sea to Site H via the Oyashio Current may be the cause of this anomalous feature in the seasonal sequence of the population structure of *M. okotensis*. It is known that *M. okhotensis* is very abundant in the Okhotsk Sea (see below). However, the population structure data at Stn KNOT, where any effect of the Okhotsk Sea water is unlikely, do not support theory (Fig. 13b). Indeed, the Stn KNOT data collected in August show the same features seen at Site H in the same month of a different year, i.e. extremely low abundance of C2–C4 (C3 was not found). A plausible explanation is that spawning is seasonal (in contrast to year-round spawning of *M. pacifica*), and the development of C2–C4 stages is rapid. A 2 yr life cycle scenario is most consistent with the observed seasonal sequence of *M. okhotensis* population structure at Site H (Fig. 14b). Spawning of eggs and development through the naupliar stages occur during the spring phytoplankton bloom of Year 1. By the end of the productive season and time of high surface temperatures, *M. okhotensis* have progressed only to C1, a phenomenon never yet observed in any other species. The C 1 descend to 250–500 m until the phytoplankton bloom in the following year, at which time they mature, mate and spawn the next cohort. According to this life cycle scenario, *M. okhotensis* is characterized by a much slower development and a much longer life span than *M. pacifica*. Female:male ratios of C6 *M. okhotensis* were extremely biased towards females (annual mean = 16.5:1), suggesting that the males are short-lived. The absence of spent females (Fig. 11b) suggests also that the females die off quickly after spawning. The 2 yr life cycle scenario (Fig. 14b) does not explain why the abundance of C1 (annual mean = 153 ind. $m^{-2}$, cf. Fig. 12b) is less than that of C5 (1467 ind. $m^{-2}$). Possibly some significant peaks in C1 abundance were overlooked in this study because of low sampling frequencies (monthly) and/or some of the C5 individuals may live 1 more yr. To prove/disprove the tentative life cycle scheme proposed in this study, increased sampling effort is needed in the future.

There is no information available about the life cycle of the *Metridia okhotensis* population in the northern Okhotsk Sea except on their spawning season (July–October) (Pinchuk & Paul 2000). The spawning season of the Site H population in the life cycle scenario suggested above is much earlier (April–May) than that of the Okhotsk Sea population. Considering that the phytoplankton bloom is a major driving force in the life cycle of *M. okhotensis* (and *M. pacifica* also), regional differences in the spawning season of *M. okhotensis* may reflect differences in the timing of phytoplankton production in the 2 regions. Analyzing coastal zone color scanner (CZCS) data, Saitoh et al. (1996) noted 2 seasonal surface chlorophyll *a* maxima, one in April–June and the other in August–November in the entire Okhotsk Sea. Dissimilar life cycle patterns of the grazing copepod *Neocalanus cristatus* at Site H and in the Okhotsk Sea have already been reported by Kobari & Ikeda (1999).

In the central and northern Okhotsk Sea, *Metridia okhotensis* occur very abundantly, and their biomass is reported to be greater than that of *M. pacifica* (Pinchuk & Paul 2000). In contrast, *M. okhotensis* was less abundant than *M. pacifica* at Site H. Considering thermal conditions at the distribution depth of *M. okhotensis* in the northern and central Okhotsk Sea (as low as ~0°C), it is evident that *M. okhotensis* is adapted to colder temperatures than *M. pacifica*. For *Metridia* spp. copepods living in low water temperatures (near 0°C), generation lengths as long as 2 yr have been reported for *M. gerlachei* in the Weddell Sea, Antarctica, although this species is known to have 1 or more life cycles per year in waters near the Antarctic Convergence and Gerlache Strait, Antarctica (Huntley & Escritor 1992, Kurbjeweit 1993).

## Feeding conditions and overwintering strategies

Observations on feeding appendages (Arashkevich 1969, Romano et al. 1999), gut contents (Hattori 1989, Romano et al. 1999) and laboratory feeding experiments (Haq 1967) all suggest that *Metridia* spp. living in the epipelagic realm of the ocean are capable of feeding on phytoplankton, protozoans, copepods and even detritus. Nevertheless, the present results suggest strongly that the phytoplankton bloom (mostly diatoms) plays an integral role, directly or indirectly, in inducing spawning and facilitating rapid development of both *M. pacifica* and *M. okhotensis* in the Oyashio region. Diatoms sink at a speed of approximately 175 m $d^{-1}$ in the subarctic Pacific, regardless of taxa, size or morphology (Takahashi 1986); thus they may reach the habitat depth of *M. okhotensis* (250–1000 m) in 1.4–5.7 d (250 or 1000/175). According to a recent study (Shinada et al. 2001), microzooplankton (ciliates, flagellates, copepod nauplii) becomes abundant after the phytoplankton bloom in the Oyashio region. Considering the broad diet of *Metridia* spp. it is obvious that these microzooplankton, together with phytoplankton and mesozooplankton, could be important food sources for repeated generations of both *M. pacifica* and *M. okhotensis* in the Oyashio region. However this raises the question: How do these copepods survive during winter when all these food resources become depleted in the water column?

For grazing copepods living in high-latitude seas where phytoplankton abundance is highly seasonal, mechanisms for surviving the phytoplankton-poor winter season have been a long-standing issue. Atkinson (1998), working on copepods in the Southern Ocean, classified mechanisms into 3 types, i.e. (1) herbivory in summer, a short reproductive period and winter diapause at depth; (2) a predominantly omnivorous/detritivorous diet, an extended period of feeding, growth and reproduction, and less reliance on diapause at depth; (3) overwintering and feeding within sea ice as early nauplii or copepodites. While the third type is not applicable to oceanic copepods in the subarctic North Pacific since there is no ice-cover in winter, the first type has been postulated for such copepods as *Neocalanus cristatus*, *N. plumchrus*, *N. flemingeri* and *Eucalanus bungii* in this region (Miller et al. 1984, Kobari & Ikeda 1999, 2000, 2001a,b, Tsuda et al. 1999, Shoden 2000). Specimens in diapause at depth have large accumulations of body lipid (mostly in the form of wax ester, cf. Hagen & Schnack-Schiel 1996, Saito & Kotani 2000) in the body, cease feeding, are neutrally buoyant (= motionless) and have reduced metabolism. Lipid deposition in the body and its continuous reduction through winter, as observed for overwintering C5 *Metridia pacifica* (Fig. 12a) and C5 and C6 *M. okhotensis* (Fig. 12c, d) in this study, has also been noted for *M. longa* in Norwegian arctic fjords and the Barents Sea (Hopkins et al. 1985), and *M. gerlachei* in the Southern Ocean (Hagen & Schnack-Schiel 1996). For overwintering *Neocalanus* spp. and *E. bungii* that have ceased feeding at depth, the energy needed for metabolism and gonad development is fueled by stored lipid only. Conversely, the energy needs of overwintering *Metridia* spp. appear to be supplied by both feeding and stored lipid. Dependence on dual energy sources by *Metridia* spp. may be due to a higher energy requirement to sustain continuous glide-swimming at depth (in contrast to *Neocalanus* spp. and *E. bungii*, which largely remain notionless in the water column). Greater proportions of rich-type specimens of *M. okhotensis* than *M. pacifica* (Fig. 12a,c,d) may suggest that overwintering specimens of the former are less dependent on a year-round energy supply (continuous feeding) than those of the latter. For *M. okhotensis*, the seasonal pattern of lipid deposition was less marked in Stage C1 (Fig. 12b) than in Stages C5 or C6 (Fig. 12c,d). Perhaps the lipid droplets in C1 individuals are deposited in eggs (as has been postulated for *Paraeuchaeta elongata*, cf. Ikeda & Hirakawa 1996) and, because of their smaller size, food supply in the surface layer is sufficient for them throughout the year (food concentrations critical for the survival of copepods decrease with decreasing body size, cf. Vidal 1980).

Evidence suggests that overwintering *Metridia* spp. are not in diapause, e.g. (1) oxygen consumption data for *M. pacificus* in the southern Japan Sea (Ikeda & Hirakawa 1998), (2) lipid, metabolic enzyme and gut-fluorescence data for *M. pacificus* in the San Diego Trough, eastern subarctic Pacific (Ohman et al. 1998), (3) gut content, digestive enzyme activity and oxygen consumption data for *M. longa* in Norwegian fjords (Båmstedt et al. 1985), (4) ammonia excretion data for *M. gerlachei* in the Southern Ocean (Huntley & Nordhausen 1995). This evidence, combined with the broad feeding habits of *Metridia* spp., indicates that the overwintering mechanism of *M. pacifica* and *M. okhotensis* recorded in this study is consistent with Type 2 of Atkinson (1998).

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