



Title	Diel vertical migration, population structure and life cycle of the copepod <i>Scolecithricella minor</i> (Calanoida: Scolecitrichidae) in Toyama Bay, southern Japan Sea
Author(s)	Yamaguchi, Atsushi; Ikeda, Tsutomu; Hirakawa, Kazumasa
Citation	Plankton biology and ecology, 46(1), 54-61
Issue Date	1999-02
Doc URL	http://hdl.handle.net/2115/45763
Rights	© 1999 The Plankton Society of Japan
Type	article
File Information	vol46_1_054.pdf



[Instructions for use](#)

Diel vertical migration, population structure and life cycle of the copepod *Scolecithricella minor* (Calanoida: Scolecitrichidae) in Toyama Bay, southern Japan Sea

ATSUSHI YAMAGUCHI¹, TSUTOMU IKEDA¹ & KAZUMASA HIRAKAWA²

¹Biological Oceanography Laboratory, Faculty of Fisheries, Hokkaido University, 3-1-1, Minatomachi, Hakodate, Hokkaido 041-0821, Japan

²Japan Sea National Fisheries Research Institute, 1 Suido-cho, Niigata 951-8121, Japan

Received 23 July 1998; accepted 12 October 1998

Abstract: The seasonal population structure (copepodite-2 stage through adults) and diel vertical migration pattern of *Scolecithricella minor* in Toyama Bay, southern Japan Sea, were investigated. Eggs and nauplii were reared in the laboratory at three different temperatures (0.5, 5 and 10°C) as a basis to estimate generation length. Most copepodite stages occurred throughout the year; young copepodites (C2 to C5) were most abundant in May–October, while adults were most abundant in March–August. Reproduction continued throughout the year, with a peak in April–August. All copepodite stages were consistently distributed at 100–400 m depth. Limited nocturnal ascent was seen in adults, but not always for younger copepodites. Based on habitat temperature, development times of eggs and nauplii expressed as a function of temperature, and assumed proportion of these developmental times in one life cycle of calanoid copepods, the generation length of *S. minor* was estimated to be 44–76 d. Using this estimated generation length range as a guide, the sequential development of five cohorts was identified. An additional two extra cohorts, which were not clearly traceable, are considered to have occurred for a total of 7 cohorts per year for *S. minor* in Toyama Bay. The present data on the vertical distribution of *S. minor* are compared with those reported from other regions for the same species. Since *S. minor* is considered to be a typical detritus feeder, trophic-type-related sequences in major reproduction seasons are discussed by comparing the data of other calanoid copepods reported from Toyama Bay.

Key words: mesopelagic, omnivore, *Scolecithricella minor*, life cycle, Japan Sea

Introduction

Scolecithricella minor (Brady 1883) is a small calanoid copepod widely distributed throughout the high latitude seas of both the northern and southern hemispheres (Mori 1937; Jespersen 1940; Vervoort 1965). Zenkevitch (1963) listed *S. minor* as an important zooplankton species in the Far Eastern Seas and categorized it as a eurybathic species. *S. minor* occurs in the epi- and mesopelagic zones (Minoda 1971; Roe 1984). Diel changes in its vertical distribution (nocturnal ascent or non-migration) have been reported by previous workers (Marlowe & Miller 1975; Morioka 1976; Morioka et al. 1977; Longhurst 1985; Hirakawa et al.

1990). *S. minor* is considered to be omnivorous (Arashkevich 1969; Minoda 1971; Harding 1974). Recently, a close association with detrital particles, such as larvacean houses, has been reported for some scolecitrichid species (Steinberg et al. 1994; Steinberg 1995). Nishida & Ohtsuka (1997) consider that specialized setae on the maxillae and maxillipeds in scolecitrichid species function to detect the chemical signals of food particles. Despite the widespread distribution and possible importance of *S. minor* in the trophodynamics of pelagic systems, information on its life cycle is extremely scarce. The only information presently available is in Hansen (1960), who noted that after the phytoplankton spring bloom, *S. minor* in the southern part of the Norwegian Sea descends to deeper layers.

The present study aims to evaluate the diel vertical migration behavior and life cycle of *S. minor* in Toyama Bay,

southern Japan Sea, by combining data from their seasonal population structure data in the field with laboratory rearing data for their eggs and nauplii. Further, we compare the life cycle pattern of *S. minor* with that of the herbivorous copepods (*Pseudocalanus* spp. and *Metridia pacifica*) and the carnivorous copepod (*Paraeuchaeta elongata*) in Toyama Bay to determine if the different reproduction seasons of these species are related to trophic position.

Materials and Methods

Field Samplings

Field samplings were carried out at a station (37°00'N, 137°14'E; bottom depth about 1000 m) located in the center of Toyama Bay (Fig. 1). Day and night vertical distribution patterns of *Scolecithricella minor* were examined during three periods. Stratified vertical tows with a Palumbo-Chun-Petersen (PCP) type closing net (45-cm mouth diameter, 0.06-mm mesh) designed by Kawamura (1989) were made during 8–9 September 1990, 30 November–1 December 1991, and on 23 February 1997. Sampling depth strata were 0–100, 100–300, 300–500, 500–700 and 700–950 m in September 1990, 0–50, 50–100, 100–150, 150–250, 250–350, 350–500, 500–700 and 700–920 m in November–December 1991, and 0–10, 10–20, 20–30, 30–50, 50–75, 75–100, 100–150, 150–200, 200–300 and 300–500 m in February 1997. These discrete depth samples from different years were used to analyze seasonal changes in diel vertical distribution patterns of *S. minor* based on the premise that no interannual variations occurred.

Paired (twin-type) Norpac nets (45 cm mouth diameter, 0.33- and 0.10-mm mesh, Motoda 1957) were towed vertically from 500-m depth to the surface mostly during daylight hours at 2-week intervals from February 1990 through January 1991 (Hirakawa et al. 1992). Volumes of water filtered through the net were estimated from readings of a Rigosha flowmeter mounted in the mouth of each net. All Norpac and PCP net samples were immediately preserved in 10% buffered formalin-seawater solution. Temperature and salinity data were obtained by a CTD system (Neil Brown) at each zooplankton sampling.

Identification and enumeration of developmental stages

Based on the morphology of the fifth legs, Brodskii (1950) distinguished two forms of *S. minor*: *S. minor orientalis* from the Northern Pacific and *S. minor occidentalis* from the North Atlantic. The specimens found in the present study were similar to *S. minor orientalis*. Some diagnostic features of *S. minor* at copepodite stages 4 (C4) and 5 (C5) have been described by With (1915) and Morioka (1976). Recently, Ferrari & Steinberg (1993) described the C2 to C5 stages of *Scopalatum vorax* and the C4 and C5 stages of *Scolecithricella lobophora*. The developmental pattern of the copepodite stages of *S. minor* was similar to that for *S. vorax* described by Ferrari & Steinberg (1993)

(Yamaguchi, unpublished data). Details about the morphological characteristics of the developmental stages of *S. minor* will be published elsewhere.

At a land laboratory, copepodite stages of *S. minor* were sorted from a 7/8 aliquot (0.06-mm mesh PCP net), a 1/4 aliquot (0.10-mm mesh Norpac net), or entire samples (0.33-mm mesh Norpac net). The 0.10-mm mesh Norpac net retained C2 through to adult stages, but the 0.33-mm mesh Norpac net only retained adults. The 0.06-mm mesh PCP net caught naupliar and copepodite stages, but we made no attempt to count naupliar or C1 stages because of the difficulty in identifying them. Adult females carrying spermatophores were recorded. The prosome length of C5 stages and adults (both females and males) were measured to the nearest 0.01 mm using a digital micrometer (Mitutoyo Digi-Matic head and counter).

Laboratory experiments

Live females of *S. minor* were collected at a station (42°00'N, 141°30'E; bottom about 500 m deep) off Cape Esan, northwestern Pacific, on 15 July and 14 October 1997 with vertical hauls of an 80-cm ring net (0.33-mm mesh) from near the bottom to the surface. Concurrently, seawater was collected from 300-m depth with 20-liter Van-Dorn bottles and used for the following experiments. Upon retrieval of the net, the adult females were sorted and placed in 20-liter plastic containers filled with chilled seawater (about 5°C) and transported to the shore laboratory. At the laboratory, several batches of 10 to 20 females each were placed in a 500-ml polyethylene cylinder with a mesh (0.33 mm) bottom (to prevent eggs from being consumed by the females) and suspended in 1000-ml glass beakers filled with 800 ml of Whatman GF/F filtered seawater. The experiment was run at 0.5, 5 and 10°C in the dark. As food, a mixture of laboratory cultures of *Heterocapsa triquetra*, *Chaetoceros gracilis*, and *Pavlova* sp. were provided at a final concentration of $>2.0 \times 10^3$ cells ml⁻¹. The beakers were inspected daily for eggs. Upon release, eggs were transferred carefully into a 10-ml glass vial filled with the filtered seawater and incubated at 0.5, 5 or 10°C. After the nauplii hatched, their development up to the C1 stage was followed by collecting their molts.

Results

Hydrography

Toyama Bay is a deep canyon, the 1000-m isobath of which connects it to the deep basin of the central Japan Sea (Fig. 1). Seasonal changes in temperature and salinity in the top 250 m reflect local meteorological events and intrusions of the warm Tsushima Current (Hirakawa et al. 1992). During this study, temperatures and salinities recorded between 0 and 250-m depth ranged from 2°C (February, October and November) to $>26^\circ\text{C}$ (August), and from 33.0 PSU (August to November) to 34.4 PSU (August to September),

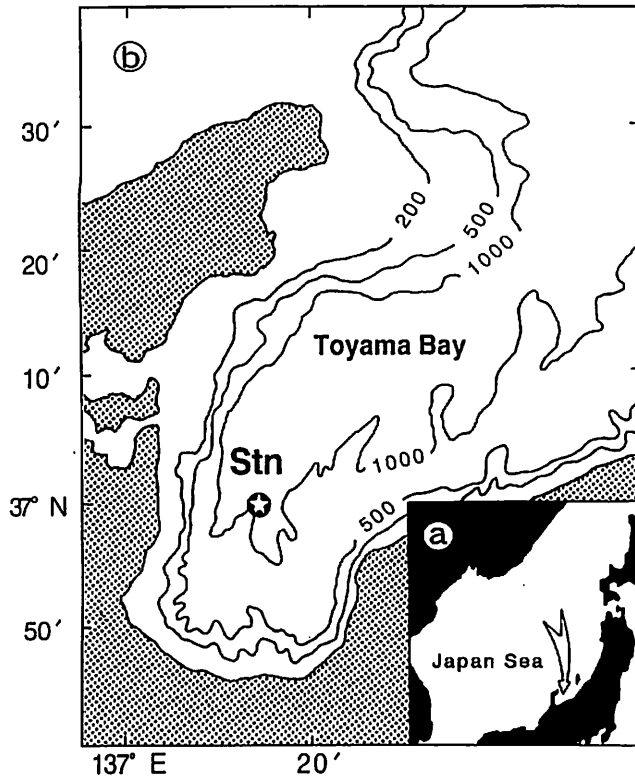


Fig. 1. a. Location of Toyama Bay in the southern Japan Sea. b. The sampling station (circled star) in Toyama Bay, in which depth contours (1,000, 500, and 200 m) are superimposed.

respectively (Fig. 2). Below 250-m depth, there was almost no seasonal variability in both temperature ($<4^{\circ}\text{C}$) and salinity (<34.1 PSU). Water characterized by temperatures lower than 1°C and salinities of 34.05–34.10 PSU is termed "Deep-Water" and is widespread over the entire Japan Sea (Nishimura 1969).

Diel vertical migration

Day and night vertical distribution patterns of *Scolecithricella minor* in Toyama Bay in September 1990, November–December 1991, and February 1997 are shown in Fig. 3. Over these three seasons, all copepodite stages (C2 to adults) were distributed largely or entirely between 100 and 400-m depth both day and night. Within this bathymetric range, part of the population ascended at night; including all stages in February 1997, C4 to adults in November–December 1991, and adults in September 1990 (Fig. 3). From the calculation of weighted mean depth (cf. Bollens & Frost 1989), the magnitude of vertical migration distance was computed as 0–74 m for the C2 to C5 stages, and 28–158 m for adults.

Population structure

Sampling precision was examined by comparing the abundance of adults caught with the paired Norpac nets (the 0.10- and 0.33-mm mesh). There were no significant

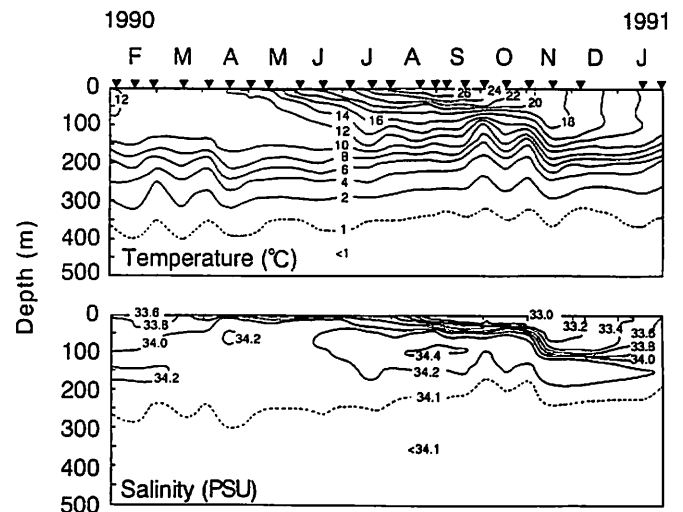


Fig. 2. Temperature and salinity profiles of the top 500-m water column at the station in Toyama Bay during the sampling period from February 1990 to January 1991. Sampling dates indicated by triangles on top abscissa.

differences between the numerical abundance estimated from these two nets (*t*-test; $t=1.24$, $df=23$, $p>0.2$). Hence, the data for adults from the 0.10- and 0.33-mm mesh Norpac nets were combined for the following analysis.

Numerical abundances of C2 through the C6 stages (adults) of *S. minor* over one full year are shown in Fig. 4. All of these stages occurred throughout the year, except for C2, which was absent on 14 February, 28 February and 3 April 1990. The C2 stage was most abundant from May to October 1990, with four irregular peaks ($448 \text{ indiv. m}^{-2}$ on 14 May, $643 \text{ indiv. m}^{-2}$ on 2 July, $444 \text{ indiv. m}^{-2}$ on 30 August, $353 \text{ indiv. m}^{-2}$ on 15 October 1990). The development sequence of these four peaks was traceable up to the C5 stage. Adults were most abundant from March to August 1990. There were three distinct peaks (1 May, 15 June, and 1 August 1990) and three indistinct ones (1 February, 2 October 1990, and 30 January 1991). Adult females with attached spermatophores occurred from February to mid-September 1990, with a pronounced peak in mid-June (27%), but they were absent from October to mid-January. After the C4 stage, females and males could be distinguished. Seasonal patterns in abundance of females and males were similar, and males were consistently less abundant than females (mean male : female ratio = 0.61 : 1 for the C4, 0.74 : 1 for the C5, and 0.25 : 1 for the adults).

Seasonal changes in body size

For both males and females, the body size of the C5 stage was larger in April–June and smaller in November–January (Fig. 5). The annual mean of the C5 prosome length was 0.96 mm for females and 0.98 mm for males. As for the C5 stage, both adult males and females showed a similar seasonal variation pattern; larger specimens oc-

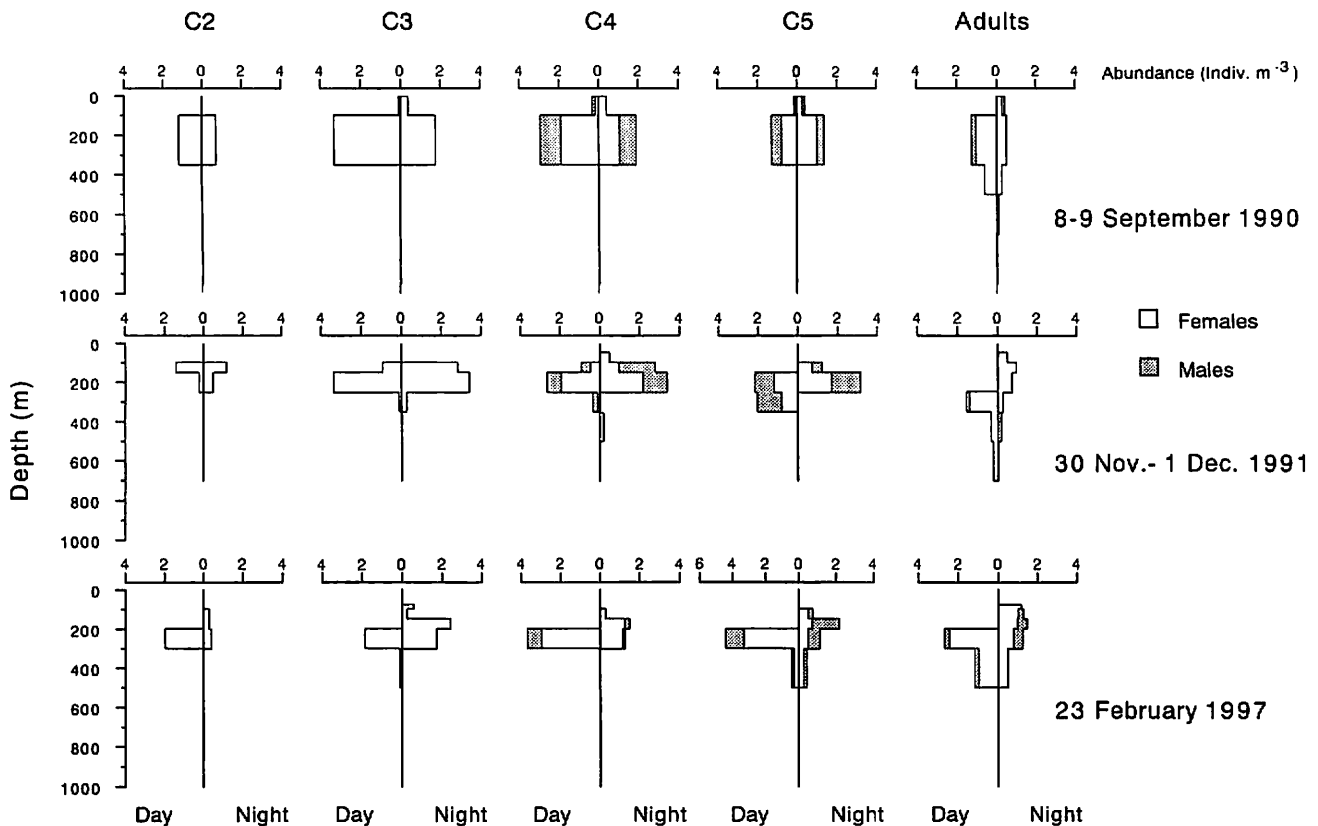


Fig. 3. Day (left) and night (right) vertical distribution of each developmental stage (C2 to adults) of *Scolecithricella minor* on 8–9 September 1990 (upper panels), 30 November–1 December 1991 (middle panels), and 23 February 1997 (lower panels). Male and female data were separated for C4, C5 and adults.

curred in May–July, and smaller ones occurred in January–March (Fig. 5). The annual mean of adult prosome length was 1.17 mm for females and 1.00 mm for males. The increase in prosome length from C5 to adults was larger in females (C5 : adults = 1 : 1.22, annual mean) than in males (C5 : adults = 1 : 1.02, annual mean).

Laboratory experiment

Table 1 summarizes the results of rearing experiments on the development time of eggs (egg hatching time) and from N1 to C1 (naupliar development time). Adult females of *S. minor* laid 2 to 6 spherical eggs (mean diameter = 174 μm , SD = 10 μm , $n = 15$) at each spawning. The development time of eggs was 1.75 d at 10°C, and 4.59 d at 0.5°C. Hatchability of eggs was 85% to 90%. Development time from N1 to C1 stage was 22.16 d and 17.92 d at 5°C and 10°C, respectively (no data at 0.5°C). Successful survival from the N1 to C1 stage was 50% at 5°C, and 82% at 10°C. The relationship between development time (D , days) and temperature (T , °C) can be expressed by the Bělehrádek equation: $D = a(T - \alpha)^b$, where a , b ($= -2.05$), and α are fitted constants (cf. Corkett & McLaren 1970). Fitting the data to the equation yielded $D = 1674(T + 17.173)^{-2.05}$ for egg development and $D = 13595(T + 17.173)^{-2.05}$ for nau-

pliar development (Fig. 6).

Discussion

Diel vertical migration

Diel vertical migration of *Scolecithricella minor* has been observed by Morioka (1976), Morioka et al. (1977), and Hirakawa et al. (1990) in the Japan Sea. All reported that *S. minor* is distributed below the thermocline in daytime and ascends at night. In areas where the surface layer is covered by the warm Tsushima Current, upward migration of *S. minor* is significantly reduced (Morioka 1976). Morioka (1976) suggested that high temperatures in the upper layer may act as a barrier preventing upward migration at night, and that 16–22°C is the maximum temperature range that *S. minor* can tolerate. The diel vertical migration behavior of *S. minor* has also been reported in the Bering Sea and the North Pacific (Minoda 1971), and in the northeast Atlantic (Roe 1984), where the nighttime distribution often reaches the surface. In contrast to these observations, Longhurst (1985) found that *S. minor* is distributed at 66 m both day and night in the eastern tropical Pacific Ocean (09°45'N, 93°45'W). At Ocean Station "P" in summer, *S. minor* exhibited a bimodal distribution: one peak

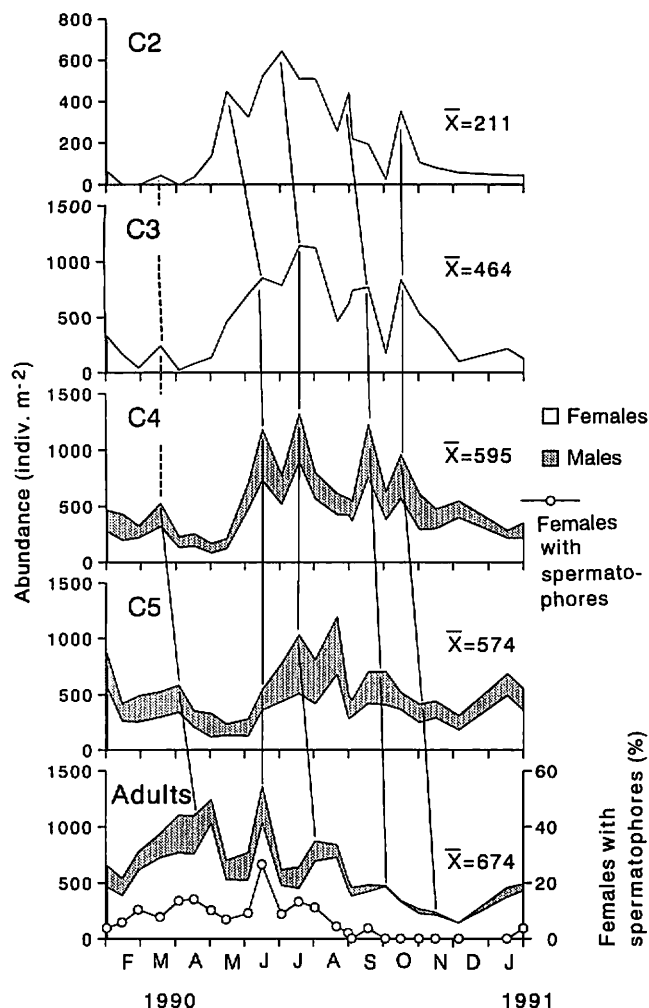


Fig. 4. Seasonal variation in abundance (indiv. m^{-2}) of each developmental stage (C2 to adults) of *Scolecithricella minor* collected at the station in Toyama Bay during the period from February 1990 to January 1991. The relative abundance (%) of females with spermatophores to total females are shown in the bottom panel. Clear and non-clear sequences of cohorts are indicated by solid and dotted lines, respectively. \bar{X} =annual mean abundance.

above 100 m and one below 200 m; this pattern did not change between the day and night (Marlowe & Miller 1975). The present results obtained over three seasons (Fig. 3) reconcile these contradictory views. That is, the magnitude of diel vertical migration of *S. minor* varies depending

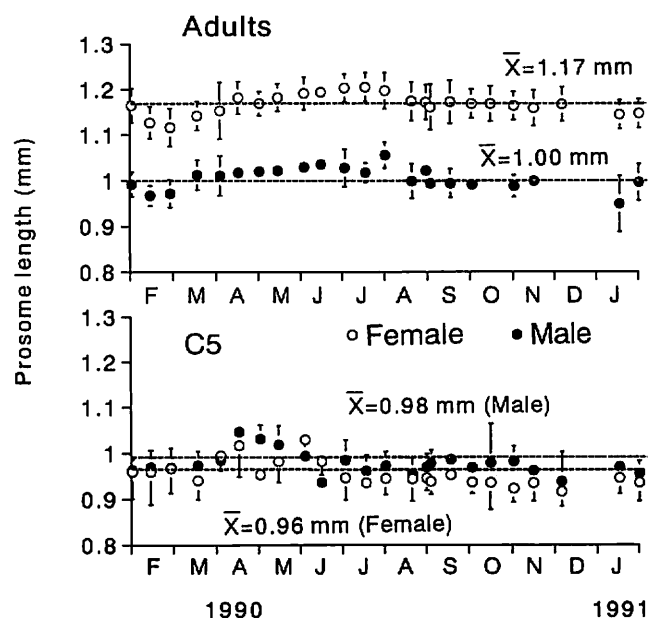


Fig. 5. Seasonal variation in the mean prosome lengths of males and females of C5 (lower panel) and adults (upper panel) of *Scolecithricella minor* in Toyama Bay. Vertical bar denotes 95% confidence intervals (only one side is shown for the C5s).

on the developmental stages and seasonal thermal structure of the upper water column. Among the copepodite stages, adults are the most active diel vertical migrators, and the migration of younger copepodites ceases upon warming of the surface layer. While there is no information on the ontogenetic vertical distribution for *S. minor*, the present results indicate that they descend as they develop (Fig. 3).

Life cycle

Two life cycle scenarios may be considered for *S. minor* in Toyama Bay. One scenario is that *S. minor* has an annual life cycle characterized by active reproduction during the early half of the year and rapid copepodite development during the middle of the year. The other scenario is that the regular peaks seen in the seasonal abundances of each copepodite stage represent discrete cohorts, suggesting that *S. minor* undergoes multiple generations during the course of one year. The first scenario implies a long residential time for the C5 or other stages and a large accumulation in

Table 1. Development time and survival success from eggs to N1 and from N1 to C1 of *Scolecithricella minor*. Values are Means \pm 1SD. Number of replicates is in parentheses. —: no data.

Temperature ($^{\circ}C$)	Development time (day)		Survival success (%)	
	Eggs to N1	N1 to C1	Eggs to N1	N1 to C1
0.5	4.59 \pm 1.18 (6)	—	86	—
5	3.11 \pm 1.32 (10)	22.16 \pm 2.06 (5)	90	50
10	1.75 \pm 0.24 (22)	17.92 \pm 1.35 (18)	85	82

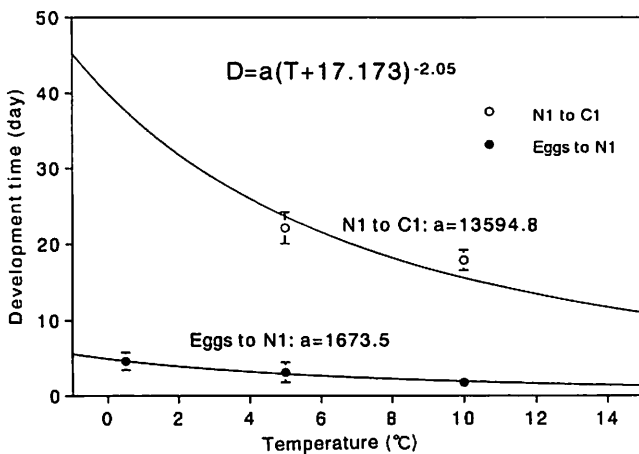


Fig. 6. The relationship between mean development time (D) of *Scolecithricella minor* and temperature (T) fitted to the Bělehrádek equation. Development time from eggs to N1 is indicated by the solid circles and that from N1 to C1 by the open circles. Vertical bars represent 95% confidence intervals. See text for details.

these stages toward the end of the year, but this is not the case. Thus, we abandon the first scenario.

The estimation of the generation length of *S. minor* is of central importance in order to justify the multi-generation scenario. For marine calanoid copepods, the partition of generation time between the development of eggs, nauplii, and copepodites is known to be 4–22, 22–44, and 45–68%, respectively (Landry 1983; Webber & Roff 1995). From these general proportions for the developmental time of eggs, nauplii, and copepodites over one generation, coupled with the laboratory data for egg and naupliar development time obtained in the present study, we attempted to estimate the generation length of *S. minor*. Designating a habitat temperature of 6°C (which corresponds to about 200 m depth in Toyama Bay where most of the population resided throughout the year, cf. Fig. 3), the Bělehrádek equations (Fig. 6) predict the development time to be 2.7 d for eggs and 21.6 d for naupliar stages (total development from eggs to the C1 is 2.7+21.6=24.3 d). As the percentage of one generation time composed of the eggs to C1 period is 32–55% for calanoid copepods in general as mentioned above, the generation length of *S. minor* can be calculated to be 44–76 d ($24.3/[0.32 \text{ or } 0.55]$). As an independent estimate, the relationship between generation length and habitat temperature of a similar sized calanoid copepod (*Pseudocalanus minutus*) established by McLaren et al. (1989) may be used. Application of the relationship found by McLaren et al. (1989) for an in situ temperature of 6°C yielded a generation length of 62.3 d, which falls well within the 44–76 d range estimated above.

With this measure of generation length, a possible sequence of multi-cohorts of *S. minor* was traced (Fig. 4). Among the five cohorts distinguished during March to November, a clear sequence is not always seen. This is partly

because of the longer sampling interval (2 weeks) in the present study relative to the estimated generation length of *S. minor* (44–76 d). There were one or two moderate abundance peaks during December to February, but their sequences were not traceable. Thus, the present results suggest that between 5 and 7 (if two untraceable extra cohorts in mid winter are taken into account) generations occur per year in Toyama Bay, with a reproduction peak in April to August (inferred from peak abundances of the C2 in May–September and a development time of 24.3 d from eggs to the C1). Females with attached spermatophores were relatively numerous in March–July, but disappeared from October to the end of January. Increased sampling effort may find some females with attached spermatophores during October to January since the C2 stage was still found in this winter period.

Larger specimens were seen in April–June for the C5 stage and April–August for the adults (Fig. 5). Seasonal variations in body size have been well documented in shallow-living calanoid copepods and the variation is usually well synchronized between copepodite stages (Marshall & Orr 1955; McLaren 1969; Batchelder 1986). Compared with the C5 stage, the longer duration for the occurrence of large adults may reflect a longer residence time of the latter, as the mean annual abundance of adults was greater than that of the C5 stage (cf. Fig. 4).

In tracing the development sequence of each cohort in Fig. 4, it is evident that a higher abundance of young copepodites does not necessarily yield a high abundance of adults, or vice versa. While the lack of information about the development time of each copepodite stage prevents analysis of cohort-specific mortality, the firefly squid *Watasenia scintillans* (Hayashi & Hirakawa 1997) and the amphipod *Themisto japonica* (Ikeda et al. 1992) have been postulated to be predators on *S. minor* in Toyama Bay. In terms of vertical distribution patterns, both *W. scintillans* and *T. japonica* are diel vertical migrators and their bathymetric ranges at night overlap that of *S. minor*. The lower abundances of the C5 stage and adults than that expected from the abundances of C2–C4 stages in September–November in Fig. 4 may be due to predation, since the above predators are abundant in these seasons (Hayashi 1990; Ikeda et al. 1992). Other potential predators of *S. minor* in Toyama Bay include the chaetognath *Sagitta elegans*, the copepod *Paraeuchaeta elongata*, the euphausiid *Euphausia pacifica*, and the mesopelagic fish *Maurolicus muelleri*, but evidence to support these suppositions is currently lacking.

Reproduction season

In Toyama Bay, the reproduction cycles of calanoid copepods including *Metridia pacifica* (Hirakawa & Imamura 1993), *Paraeuchaeta elongata* (Ikeda & Hirakawa 1996), and *Pseudocalanus minutus* and *P. newmani* (Yamaguchi et al. 1998) have been evaluated. While all these species are cold-water species (Morioka 1973), they are at different

trophic levels: *M. pacifica* and *Pseudocalanus* spp. are herbivores, and *P. elongata* is a carnivore (Arashkevich 1969). *S. minor* from the present study is a typical detritus feeder (Minoda 1971). Comparing the present results with those of previous studies, it is interesting to note how these dissimilar trophic features are reflected in their reproduction seasons in the same habitat.

Although information is presently limited to herbivores, food supply is known to be important at the onset of reproduction in marine copepods (Runge 1985; Hirche & Bohrer 1987; Peterson 1988). In Toyama Bay, the phytoplankton bloom occurs from December to February (Taniguchi et al. 1997), and zooplankton biomass in the top 500 m reaches its annual maximum in August–September (Hirakawa et al. 1992). In response to the phytoplankton bloom, active reproduction and growth of herbivores (*Metridia pacifica* and *Pseudocalanus* spp.) occurs in January to April in *M. pacifica* (Hirakawa & Imamura 1993), and February to April in *Pseudocalanus* spp. (Yamaguchi et al. 1998). The carnivorous copepod *Paraeuchaeta elongata* living in the mesopelagic zone reproduces throughout the year, but its major spawning season is August to October (Ikeda & Hirakawa 1996), or the peak season for zooplankton biomass. The present study revealed that the major reproductive season for the detritivorous *S. minor* is April to August, which falls between that of the herbivores (January to April) and the carnivore (August to October). While no quantitative data on detrital abundance in Toyama Bay is available at present, the results of a seasonal survey of appendicularian (mostly *Oikopleura longicauda*) abundance indicate that their abundance peaks in June in Toyama Bay (M. Tomita, personal communication). High abundance of appendicularians implies a high production rate of discarded “houses” (a source of detritus), and the discarded houses have been observed to be an important dietary component for Scolecitrichidae copepods (Steinberg et al. 1994; Steinberg 1995). In addition to discarded appendicularian houses, the production of cast molts (another source of detritus) by the euphausiid (*Euphausia pacifica*) is greatest during April to August in Toyama Bay (Iguchi & Ikeda 1999). Thus, as with the herbivorous (*M. pacifica* and *Pseudocalanus* spp.) and the carnivore (*P. elongata*), the major reproductive season of the detritivore *S. minor* appears to be well matched to the likely maximum abundance of detritus in Toyama Bay.

Acknowledgments

We are grateful to the captain and crew members of R/V *Tateyama-Maru* of the Toyama Prefectural Fisheries Experimental Station for their help in field samplings. We also thank Dr John R. Bower for his technical help with the manuscript.

Literature Cited

- Arashkevich, Ye. G. 1969. The food and feeding of copepods in the north-western Pacific. *Oceanology* **9**: 695–709.
- Batchelder, H. P. 1986. Phytoplankton balance in the oceanic subarctic Pacific: grazing impact of *Metridia pacifica*. *Mar. Ecol. Prog. Ser.* **34**: 213–225.
- Bollens, S. M. & B. W. Frost 1989. Zooplanktivorous fish and variable diel vertical migration in the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.* **34**: 1072–1083.
- Brodskii, K. A. 1950. Calanoida of the far-eastern seas and polar basin of the USSR, p. 1–442. In *Keys to the Fauna of the USSR*, No. 35 (ed. Strelkov, A. A.). Moskva, Leningrad. (English translation, I.P.S.T., Jerusalem, 1967.)
- Corkett, C. J. & I. A. McLaren 1970. Relationships between development rate of eggs and older stages of copepods. *J. Mar. Biol. Ass. U.K.* **50**: 161–168.
- Ferrari, F. D. & D. K. Steinberg 1993. *Scopalatum vorax* (Esterly, 1911) and *Scolecitrichella lobophora* Park, 1970, calanoid copepods (Scolecitrichidae) associated with a pelagic tunicate in Monterey Bay. *Proc. Biol. Soc. Wash.* **106**: 467–489.
- Hansen, V. K. 1960. Investigations on the quantitative and qualitative distribution of zooplankton in the southern part of the Norwegian Sea. *Medd. fra Denmarks Fiskeri og Havundersøgelser Ny Serie* **2**: 1–53.
- Harding, G. C. H. 1974. The food of deep-sea copepods. *J. Mar. Biol. Ass. U.K.* **54**: 141–155.
- Hayashi, S. 1990. Seasonal abundance and vertical distribution of fish eggs and larvae in Toyama Bay, the Japan Sea. *Bull. Toyama Pref. Fish. Exp. Stn.* **2**: 1–17. (In Japanese with English abstract.)
- Hayashi, S. & K. Hirakawa 1997. Diet composition of the Firefly Squid, *Watasenia scintillans*, from Toyama Bay, southern Japan Sea. *Bull. Jpn Sea Natl Fish. Res. Inst.* **47**: 57–66.
- Hirakawa, K. & A. Imamura 1993. Seasonal abundance and life history of *Metridia pacifica* (Copepoda: Calanoida) in Toyama Bay, southern Japan Sea. *Bull. Plankton Soc. Jpn* **40**: 41–54.
- Hirakawa, K., T. Ikeda, & N. Kajihara 1990. Vertical distribution of zooplankton in Toyama Bay, southern Japan Sea, with special reference to Copepoda. *Bull. Plankton Soc. Jpn* **37**: 111–126.
- Hirakawa, K., A. Imamura & T. Ikeda 1992. Seasonal variability in abundance and composition of zooplankton in Toyama Bay, southern Japan Sea. *Bull. Jpn Sea Natl Fish. Res. Inst.* **42**: 1–15.
- Hirche, H.-J. & R. N. Bohrer 1987. Reproduction of the Arctic copepod *Calanus glacialis* in Fram Strait. *Mar. Biol.* **94**: 11–17.
- Iguchi, N. & T. Ikeda 1999. Production, metabolism and *P*:*B* ratio of *Euphausia pacifica* (Crustacea: Euphausiacea) in Toyama Bay, southern Japan Sea. *Plankton Biol. Ecol.* **46**: 68–74.
- Ikeda, T. & K. Hirakawa 1996. Early development and estimated life cycle of the mesopelagic copepod *Paraeuchaeta elongata* in the southern Japan Sea. *Mar. Biol.* **126**: 261–270.
- Ikeda, T., K. Hirakawa & A. Imamura 1992. Abundance, population structure and life cycle of a hyperiid amphipod *Themisto japonica* (Bovallius) in Toyama Bay, southern Japan Sea. *Bull. Plankton Soc. Jpn* **39**: 1–16.
- Jespersen, P. 1940. Non-parasitic Copepoda. *The Zoology of Iceland* **3**: 1–116.
- Kawamura, A. 1989. Fast sinking mouth ring for closing Norpac

- net. *Nippon Suisan Gakkaishi* **55**: 1121.
- Landry, M. R. 1983. The development of marine calanoid copepods with comment on isochronal rule. *Limnol. Oceanogr.* **28**: 614–624.
- Longhurst, A. R. 1985. Relationship between diversity and the vertical structure of the upper ocean. *Deep-Sea Res.* **32**: 1535–1570.
- Marlowe, C. J. & C. B. Miller 1975. Patterns of vertical distribution and migration of zooplankton at Ocean Station "P". *Limnol. Oceanogr.* **20**: 824–844.
- Marshall, S. M. & A. P. Orr 1955. *The Biology of a Marine Copepod*. Oliver and Boyd., Edinburgh, 188pp.
- McLaren, I. A. 1969. Population and production ecology of zooplankton in Ogac Lake, a landlocked fjord on Baffin Island. *J. Fish. Res. Bd. Can.* **26**: 1485–1559.
- McLaren, I. A., J.-M. Sévigny & C. J. Corkett 1989. Temperature-dependent development in *Pseudocalanus* species. *Can. J. Zool.* **67**: 559–564.
- 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.
- Mori, T. 1937. *The Pelagic Copepoda from the Neighboring Waters of Japan*. Published by the author, Tokyo, 150 pp. (Reprinted 1964, Soyo Co., Tokyo.)
- Morioka, Y. 1973. The occurrence of cold-water calanoid copepods in the coastal waters of the San'in district, Japan Sea. *Bull. Jpn Sea Reg. Fish. Res. Lab.* **24**: 77–84.
- Morioka, Y. 1976. Vertical invasion of boreal calanoid copepods into the shallow warm stratum. *Bull. Jpn Sea Reg. Fish. Res. Lab.* **27**: 91–101.
- Morioka, Y., M. Nagahara & Y. Komaki 1977. Calanoid copepods as indicators of the cold water mass in the Japan Sea. *Bull. Jpn Sea Reg. Fish. Res. Lab.* **28**: 51–58.
- Motoda, S. 1957. North Pacific standard plankton net. *Inf. Bull. Planktol. Jpn* **4**: 13–15.
- Nishida, S. & S. Ohtsuka 1997. Ultrastructure of the mouthpart sensory setae in mesopelagic copepods of the family Scolecithricidae. *Plankton Biol. Ecol.* **44**: 81–90.
- Nishimura, S. 1969. The zoogeographical aspects of the Japan Sea. Part V. *Publ. Seto Mar. Biol. Lab.* **17**: 67–142.
- 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.
- Roe, H. S. J. 1984. The diel migrations and distributions within a mesopelagic community in the north east Atlantic. 4. The copepods. *Prog. Oceanogr.* **13**: 353–388.
- 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.
- Steinberg, D. K. 1995. Diet of copepods (*Scopelatum vorax*) associated with mesopelagic detritus (giant larvacean house) in Monterey Bay, California. *Mar. Biol.* **122**: 571–584.
- Steinberg, D. K., M. W. Silver, C. H. Pilskaln, S. L. Coale & J. B. Paduan 1994. Midwater zooplankton communities on pelagic detritus (giant larvacean houses) in Monterey Bay, California. *Limnol. Oceanogr.* **39**: 1606–1620.
- Taniguchi, A., Y. Nakamura, T. Suzuki, K. Hirakawa, A. Imamura & T. Ikeda 1997. Seasonal variations in the phytoplankton assembly in Toyama Bay, southern Japan Sea. *Bull. Jpn Sea Natl. Fish. Res. Inst.* **47**: 33–55. (In Japanese with English abstract.)
- Vervoort, W. 1965. Pelagic copepoda, II, Copepoda calanoida of the families Phaennidae up to and including Acartiidae, containing the description of a new species of Aetideidae. *Atlantide Rep.* **8**: 9–216.
- Webber, M. K. & J. C. Roff 1995. Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. *Mar. Biol.* **123**: 481–495.
- With, C. 1915. Copepoda, I, Calanoida Amphascandria. *Danish Ingolf Exped.* **3**: 1–260.
- Yamaguchi, A., T. Ikeda & N. Shiga 1998. Population structure and life cycle of *Pseudocalanus minutus* and *Pseudocalanus newmani* (Copepoda: Calanoida) in Toyama Bay, southern Japan Sea. *Plankton Biol. Ecol.* **45**: 183–193.
- Zenkevitch, L. 1963. *Biology of the Seas of the U.S.S.R.* (English translation by S. Botcharkaya). George Allen and Unwin Ltd., London, 955pp.