富山湾の定点におけるMetridia pacifica (Copepoda: Calanoida) の季節的出現量及び生活史について

<table>
<thead>
<tr>
<th>項目</th>
<th>内容</th>
</tr>
</thead>
<tbody>
<tr>
<td>誌名</td>
<td>日本プランクトン学会報</td>
</tr>
<tr>
<td>ISSN</td>
<td>03878961</td>
</tr>
<tr>
<td>著者</td>
<td>平川, 和正 今村, 明</td>
</tr>
<tr>
<td>巻/号</td>
<td>40巻1号</td>
</tr>
<tr>
<td>掲載ページ</td>
<td>p. 41-54</td>
</tr>
<tr>
<td>発行年月</td>
<td>1993年7月</td>
</tr>
</tbody>
</table>
Seasonal Abundance and Life History of *Metridia pacifica* (Copepoda: Calanoida) in Toyama Bay, Southern Japan Sea\(^1\), \(^2\), \(^3\)

KAZUMASA HIRAKAWA\(^4\) AND AKIRA IMAMURA\(^5\)

Japan Sea National Fisheries Research Institute, 1 Suido-cho, Niigata 951\(^*\) and Toyama Prefectural Fisheries Experimental Station, 364 Takatsuka, Namerikawa, Toyama 936\(^*\)

**Abstract**

Seasonal abundance and generation cycle of *Metridia pacifica* in Toyama Bay, southern Japan Sea, were determined. The materials were obtained by a series of vertical hauls (0–500 m depth), with 0.10 mm and 0.33 mm mesh nets over one full year from February 1990 through January 1991. The annual maximum of the biomass was found in April, contributing 61.1 % (annual mean: 36.5 %) of the total copepod biomass. From the field data analyses and laboratory experiments, we concluded that *M. pacifica* completed one generation cycle in a year. Early nauplii in mid-January developed to copepodite stage V (CV) by the beginning of April, and the majority of CV molted to adults in November to December. This species in Toyama Bay was characterized by a distinct resting stage; it is either as CV with a remarkably prolonged development time (ca. 8 months) or as immature adult females with undeveloped ovaries. In the southern Japan Sea, “aestivation” of *M. pacifica* population by seasonal descent into deep water may be advantageous for synchronizing development of the young (nauplii to CV) with the winter-spring phytoplankton bloom.

**Keywords:** *Metridia pacifica*, life history, generation, vertical distribution, Japan Sea

As a subarctic copepod, the number of generations per year in *Metridia pacifica* BRODSKY has been known to show 3 to 4 in the western Bering Sea (HEINRICH 1962a), eastern North Pacific (BATCHELDER 1985) and off southwestern Sakhalin, northern Japan Sea (FEKTOTOVA 1975). On the other hand, the northern Bering Sea population had only one generation in a year, reproducing in early summer due to possible overwintering of CV until the following spring (HEINRICH 1962a). The autumn generation at St. P in the northeast Pacific showed a hiatus in female reproduction from November to January, and a marked reduction in the frequency of diel migration of CIII during winter that may be somewhat analogous to the diapause phase (BATCHELDER 1985). Generation numbers in cold water copepods are well known to reduce by delayed development or diapause of a stage. In contrast, there is few knowledge about the life history of *M. pacifica* in the southern Japan Sea where the surface warming (> 16–22 °C) during summer gives an impact on the diel vertical distribution of primarily cold-adapted copepods (MORIOKA et al. 1977).

1) Accepted 30 April 1993
2) 富山湾の定点における *Metridia pacifica* (Copepoda: Calanoida) の季節的出現量及び生活史について
3) 本報告の一部は1992年度プランクトンシンポジウムにおいて口頭発表した。
4) 平川和正, 日本海区水産研究所
5) 今村 明, 富山県水産試験場
The present study aims to elucidate the generation cycle of *M. pacifica* in Toyama Bay, southern Japan Sea, using field data based on the seasonal changes in both abundance and composition of the developmental stages over one full year. Laboratory experiments were conducted to examine egg production, and to observe molting sequences of CV to adults during the period from autumn to winter. Emphasis is placed on the relationships between diel vertical migration and spawning of *M. pacifica* together with environmental factors of especially temperature.

**Materials and Methods**

*Field Samplings*

Samplings were made aboard the R/V “Tateyama-Maru” of the Toyama Prefectural Fisheries Experimental Station at a station in the central part of Toyama Bay from February 1990 through January 1991 (Figure 1). The sampling station is in the main route of the representative oceanic waters inflowing into the bay (IMAMURA et al. 1985, KITANI et al. unpubl.). Zooplankton was collected at intervals of approximately 2–4 weeks, using a twin-type Norpac nets (45 cm mouth diameter, 0.33 mm and 0.10 mm mesh apertures). The 0.10 mm mesh net was used to catch specimens of both naupliar and early copepodite stages (CI to CIII), and the 0.33 mm mesh net for specimens older than these. The nets were towed vertically from 500 m to the surface, mostly during daylight hours (04:00–15:00). Each net was equipped with a Rigosha flow-meter on the mouth ring to register the water volume passing through the net. In addition, stratified vertical tows with a Palumbo-Chun-Petersen (PCP) type closing net (45 cm mouth

![Fig. 1. Maps showing location of Toyama Bay (left) and position (37° 00' N, 137° 14' E) of the sampling station in the central part of Toyama Bay (right). Bathymetric contours (1200, 1000, 500 and 200 m) in Toyama Bay are also shown.](image-url)
diameter, 0.33 mm mesh apertures) designed by KAWAMURA (1989) were conducted at intervals of 6–8 h to cover an one-day cycle of vertical migration on the R/V “Mizuho-Maru” of the Japan Sea National Fisheries Research Institute. Sampling water columns were divided into the following depth intervals: 0–100 m, 100–300 m, 300–500 m, 500–700 m and 700–950 m on 8–9 September 1990 and 0–50 m, 50–100 m, 100–150 m, 150–250 m, 250–350 m, 350–500 m, 500–700 m and 700–920 m on 30 November-1 December 1991. All the collected samples were preserved in 10 % buffered formalin-seawater solution. Temperature and salinity profiles of 0–500 m layer (NORPAC net samplings) or of 0–900 m layer (PCP net samplings) were recorded using a CTD system (Neil Brown).

**Identification and Enumeration of Developmental Stages**
All six copepodite stages were distinguished from their diagnostic features reported by MORIOKA (1976). As the naupliar stages have not been described for *M. pacifica*, they were indentified on descriptions for NI to NVI of the closely related copepod *Metridia lucens* from the North Atlantic (GIBBONS 1938, cited from OGILVIE 1953). Due to difficulty, early naupliar stages (NI to NIII) of *M. pacifica* were not separated but lumped together in the present study.

The abundances of CIV to adults were estimated from 1/2 or 1/4 subsamples, and those of nauplii and CI to CIII were form 1/400 to 1/40 of the entire sample using a Folsom splitter and 1 ml pipette.

**Measurement of Volume of Oil Sac in CV**
The shape of oil sac of *M. pacifica* is elliptical. The volume of the oil sac (Ov) can be approximated by the formula for an ellipsoid:

\[ Ov = \frac{4}{3} \pi abc \]

where \(a\), \(b\) and \(c\) are semiaxes. Semiaxes were measured under a compound microscope with 0.025 mm accuracy.

**Egg Production Experiments**
Egg production by adult female *M. pacifica* was observed for eight night occasions on the R/V “Mizuho-Maru”; in May, August, September 1990, October, December 1991, March, April and July 1992. These experiments were designed for determining the spawning season. Females were collected from the epipelagic zone (<100 m or 100–200 m depth) of Toyama Bay, using the PCP net at night (19:00–03:00 h). Adult females were sorted in groups of 50 to 120 individuals immediately after collection and kept in 500 ml polyethylene bottles with mesh (300 \(\mu\)m) bottoms to prevent eggs from predation by the females. The bottles were suspended in 1000 ml Styrol beakers containing 800 ml of Whatman GF/F filtered surface water and placed in an incubator in the dark. Natural phytoplankton assemblages dominated by *Skeletonema costatum*, *Chaetoceros sociale*, or *Protoperidinium* spp. or the laboratory cultured pennate diatoms, *Phaeodactylum tricornutum*, were added at concentration of > 0.5–3.4 \(\times\) 10^3 cells·ml^(-1). Temperature was adjusted to those of the surface water (March to May and December) and 50 m depth (July to October) of each sampling time. The number of eggs laid by the females was counted after 24 hours incubation.
Molting Observation
Molting frequency of CV (females and males) was measured during the period from October to December 1991 in the land laboratory, using CV specimens collected from 500–700 m depth with the PCP net in Toyama Bay on 7–8 October 1991. These copepods were placed in groups of 5–9 individuals in 100 ml glass bottles filled with Whatman GF/F filtered seawater of 500 m depth. Experiments were run under starved condition at 1, 5 and 10 °C in the dark. Seawater in each container was changed once a week when the containers were examined for molts and survival.

Results

Field Data
1. Temperature and salinity structures
The depth profiles of temperature and salinity by season at the sampling station are shown in Figure 2. The surface temperature varied from approximately 10 °C (February to April) to more than 26 °C (August to September). The thermal stratification of the water column was most pronounced in August and

Fig. 2. Seasonal variation in temperature (upper, °C) and salinity (lower) in the upper 500 m depth at the sampling station in the central part of Toyama Bay during the period from February 1990 to January 1991 (after Hirakawa et al. 1992). Sampling dates are indicated by solid triangles on the top abscissa.
September, and was weak in February to March. However, the seasonal changes of the temperature became obscure as the increase of depth and almost diminished below 350 m depth where the temperature was consistently lower than 1 °C throughout the year.

Salinity in the surface water also changed seasonally (<33.0 to 33.6). Salinity higher than 34.2 was observed consistently in 50–150 m depth during the period from June to February. The salinity maximum over 34.4 found during August and September is considered to indicate the intrusion of the warm Tsushima Current Core water. Salinity below 300 m depth was nearly homogeneous and remained unchanged throughout the year. Waters characterized by salinity of 34.05–34.10 and temperature lower than 1 °C are termed as the “Deep-Water” which widely spreads over the entire Japan Sea (NISHIMURA 1969). This deep water seen below 350 m depth in Toyama Bay showed an anticlockwise circulation extending to outside the bay (KITANI et al. unpubl.).

2. Seasonal variation in the biomass

Wet weight biomass of *M. pacifica* increased rapidly in early spring, reaching its annual maximum (13.8 mg·m$^{-3}$) on 3 April (Figure 3). *M. pacifica* contributed 61.1 % of the total copepod biomass. Then, it decreased sharply toward an annual minimum (1.9 mg·m$^{-3}$) in early July, and recovered to 9.2–9.4 mg·m$^{-3}$ in November and December. *M. pacifica* biomass accounted for 16.9–61.1 % (annual mean: 36.5 %) of total copepod biomass. The seasonal pattern seen in the biomass of *M. pacifica* is parallel to that of total copepods, so that *M. pacifica* was an important determinant of the seasonal variation pattern of copepod biomass in Toyama Bay.

![Graph showing seasonal variation in wet weight biomass of *Metridia pacifica* and total copepods](image-url)

Fig. 3. Seasonal variation in wet weight (mg·m$^{-3}$) of *Metridia pacifica* and that of total copepods collected with a Norpac net (0.33 mm mesh apertures) at the station in the central part of Toyama Bay during the period from February 1990 to January 1991.
Fig. 4. Seasonal variation in abundance (number of individuals·m⁻³) of each developmental stage of *Metridia pacifica* collected with a twin-type NORPAC nets (0.33 mm and 0.10 mm mesh apertures) at the station in the central part of Toyama Bay during the period from February 1990 to January 1991.
3. Seasonal variation in the developmental stages

Numerical abundance of each developmental stage of *M. pacifica* over one full year is shown in Figure 4. Early naupliar stages (NI to NIII) occurred for ca. 8 months from December to the beginning of July. They were more abundant in winter and early spring, with the annual maximum (94 inds·m⁻³) on 16 January. NIV increased sharply in January and its peak abundance (144 inds·m⁻³) was found on 1 February. NV to CI and CII to CIV reached their annual maxima (21–45 and 15–30 inds·m⁻³) on 14 and 28 February, respectively. CV of both females and males began to increase in March and showed its annual maximum (31 inds·m⁻³) on 3 April. By tracing the peak abundances of these developmental stages from 16 January until 3 April, it is estimated that early nauplii took ca. 2.5 months to develop into CV. All the young stages (NI to CV) declined in early and mid-spring. While NI to CIV were absent during the period from late summer to autumn, CV persisted in lower abundance (1–7 inds·m⁻³) in the bay toward winter. From mid-November onward, however, they became very scarce, and were mostly females. The proportion of male CV decreased between 1 November (female: male = 1:2.5) and 15 November (1:0.5), indicating faster development of males than females. As CV diminished, both adult females and males increased gradually and reached their annual maxima (female: 10 inds·m⁻³, male: 8 inds·m⁻³) on 5 December. Approximately 8 months were required for the development from CV to adults (from 3 April until 5 December). Adult females maintained a higher abundance relative to adult males until mid-January. The change in the sex ratio during early winter (female: male = 1:0.8 on 5 December and 1:0.4 on 16

![Fig. 5. Diel vertical distribution of *Metridia pacifica* (CV and adults) and their cores (females: shaded area, males: dotted area) at the station in the central part of Toyama Bay on 8–9 September 1990. The position of the cores is enclosed between the 25 % and 75 % levels of abundance. Water temperatures (1 and 0.5 °C) are superimposed (hatched line).](image-url)
January) may reflect shorter lives of males than females after mating. Adults occurred throughout the entire year, as did CV. Their abundances showed no definable seasonal trend from February to October, ranging from 3 to 7 inds·m⁻³.

4. Vertical distribution

Diel vertical distributions of CV and adults of *M. pacifica* are shown in Figures 5 and 6. In September (Figure 5), CV and adults were most abundant below 500 m depth during both day and night. Their core populations were consistently confined to 500–900 m layer, where the temperature was lower than 0.5 °C.

In November–December (Figure 6), CV females were distributed almost homogeneously from 200 m depth to near the bottom during both day and night; their core populations were restricted to the water column from 300 to 800 m depth (< 1 °C). CV males were rare throughout the whole water column. On the other hand, adult females and males were numerous in the same water column (250–700 m depth) during both day and night. These patterns were essentially similar to that found in September, i.e. the core population depths were not variable throughout the day. However, the core population depths of adult females tended to shift into the warmer upper layers (1–0.5 °C, 250–500 m depth) from September to December. Their relative abundance in 0–100 m layer at night (20:00–01:35) was higher (3.2 %) in December than in September (1.7 %). Thus, diel vertical migration by adult females was relatively intensified in December, as compared with that in September.

Fig. 6. Diel vertical distribution of *Metridia pacifica* (CV and adults) and their cores (females: shaded area, males: dotted area) at the station in the central part of Toyama Bay on 30 November–1 December 1991. The position of the cores is enclosed between the 25 % and 75 % levels of abundance. Water temperatures (1 and 0.5 °C) are superimposed (hatched line).
TABLE 1. PROSOME LENGTH (PL, mm) AND VOLUME OF OIL SAC (Ov × 10^-3 mm^3) IN Metridia pacifica CV COLLECTED AT THE STATION IN THE CENTRAL PART OF TOYAMA BAY IN SEPTEMBER 1990 AND NOVEMBER–DECEMBER 1991. DIFFERENCES BETWEEN MEANS OF PL AND Ov WERE EXAMINED BY t-TEST. MEAN±1SD. NS: NOT SIGNIFICANT.

(N) September 1990*  (B) November–December 1991** Ho: (A) ≠ (B)

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>PL</th>
<th>Ov</th>
<th>N</th>
<th>PL</th>
<th>Ov</th>
<th>p</th>
<th>NS</th>
</tr>
</thead>
<tbody>
<tr>
<td>♀</td>
<td>78</td>
<td>1.57±0.06</td>
<td>51.19±16.55</td>
<td>78</td>
<td>1.58±0.05</td>
<td>31.01±12.10</td>
<td>&lt;0.4</td>
<td>NS</td>
</tr>
<tr>
<td>♂</td>
<td>79</td>
<td>1.40±0.04</td>
<td>40.98±15.22</td>
<td>28</td>
<td>1.39±0.05</td>
<td>26.18±13.05</td>
<td>&lt;0.2</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

* collected from 660–997 m depth in daytime (12:00–13:35)
** collected from 486–700 m depth both day and night

5. Prosome length and oil sac volume in CV
The mean prosome length (PL) and mean volume of oil sac (Ov) in CV were compared between the September and November–December samples collected from meso-bathypelagic zone (Table 1). No significant difference in PL of females and males was detected between both samples (t-test, p > 0.4 for females, p > 0.2 for males). A decrease of their Ov was evident from September to November–December (t-test, p < 0.001 for both females and males). The losses (as % of September Ov) were 35–40 % of the initial Ov in both sexes.

TABLE 2. SUMMARY OF EGG-LAYING OBSERVATIONS IN Metridia pacifica.

<table>
<thead>
<tr>
<th>Date</th>
<th>Collection depth(m)</th>
<th>No. of female</th>
<th>Temp. (°C)</th>
<th>No. of eggs female^-1.d^-1</th>
<th>Foods* (Most dominant species)</th>
</tr>
</thead>
<tbody>
<tr>
<td>11–13 Mar. 1992</td>
<td>0–100</td>
<td>300</td>
<td>10.0</td>
<td>5.57(3.60–7.98)</td>
<td>N (Chaetoceros sociale)</td>
</tr>
<tr>
<td>27–30 Apr. 1992</td>
<td>0–100</td>
<td>256</td>
<td>10.0</td>
<td>1.24(0.85–1.63)</td>
<td>C (Phaeodactylum tricornutum)</td>
</tr>
<tr>
<td>15–18 May 1990</td>
<td>0–100</td>
<td>338</td>
<td>15.0</td>
<td>0.96(0.04–1.46)</td>
<td>N (Skeletonema costatum)</td>
</tr>
<tr>
<td>27–29 Jul. 1992</td>
<td>0–100</td>
<td>70</td>
<td>20.0</td>
<td>0</td>
<td>C (Phaeodactylum tricornutum)</td>
</tr>
<tr>
<td>4–5 Aug. 1991</td>
<td>100–200</td>
<td>54</td>
<td>20.0</td>
<td>0</td>
<td>N (Skeletonema costatum)</td>
</tr>
<tr>
<td>6–9 Sep. 1990</td>
<td>100–200</td>
<td>108</td>
<td>20.0</td>
<td>0</td>
<td>N (Protoperidinium spp.)</td>
</tr>
<tr>
<td>8–10 Oct. 1991</td>
<td>100–200</td>
<td>160</td>
<td>18.5</td>
<td>0</td>
<td>C (Phaeodactylum tricornutum)</td>
</tr>
<tr>
<td>1–4 Dec. 1991</td>
<td>0–75</td>
<td>78</td>
<td>16.5</td>
<td>0.02(0.00–0.03)</td>
<td>C (Phaeodactylum tricornutum)</td>
</tr>
<tr>
<td>0–75</td>
<td>88</td>
<td>16.5</td>
<td>0.05(0.02–0.07)</td>
<td>N (Skeletonema costatum)</td>
<td></td>
</tr>
</tbody>
</table>

*N: natural phytoplankton assemblage, C: cultured phytoplankton

Laboratory Experiments
1. Egg production
Metridia pacifica females collected from the upper 100 m in March to May and in December laid eggs at 10–16.5 °C (Table 2). On the other hand, females, which fractionally migrated into the upper layer (0–200 m depth) at night in July to October never produced eggs at 18.5–20 °C. Egg production rate was maximal (5.57 eggs·female^-1·d^-1) in mid-March and minimal (0.02 eggs·female^-1·d^-1) in early December. These results were considered to be closely linked with the seasonal
Fig. 7. Molting of *Metridia pacifica* CV (females and males) to adults at three water temperatures (10, 5 and 1 °C) during the period from October to December 1991. Abundance of adult females (solid circle) and males (open circle) molted from CV (solid triangle) are shown by cumulative numbers of individuals.
variation in the number of early nauplii found from the field observations (Figure 4).

2. Molting of CV to adults
CV collected from the meso-bathypelagic zone in early October molted to adults at all three temperatures (Figure 7). Molting of adult males preceded that of females. Adult males appeared synchronously on 18 October, at all three temperatures. In contrast, the molting of adult females was delayed at lower temperatures; the first molt was observed on 30 October at 10 °C, 6 November at 5 °C and 20 November at 1 °C. As a result, the number of adult females living after molting increased from November to December at 1 °C, in contrast to October-November at 10 °C. The female number at 1 °C peaked in mid-December. The timing in abundance was similar to that of the annual maximum of adult females in the field (Figure 4). No spawning was observed in newly molted adult females, despite the presence of adult males and some successful mating. Some adult females had a single spermatophore attached to their genital openings.

Discussion
The present results from field survey and laboratory experiments suggest that *Metridia pacifica* in Toyama Bay had a one-year life cycle. Early nauplii in mid-January developed to CV by the beginning of April, and the majority of CV molted to the adult stages in November to December. Although their egg laying was not confirmed in our molting experiments, the results from egg production experiments imply that adult females matured and mated at lower temperatures than 5 °C in early winter. Spawning season continued from December to the beginning of July.

In September, a marked reduction was seen in the intensity of diel vertical migration of adult female *Metridia pacifica* (Figure 5), in contrast to active migration up to the surface at night in June (HIRAKAWA 1991). The previous laboratory experiments indicated that the summer and autumn non-migratory females laid no eggs, and exhibited low feeding activity, as judged by fecal pellet production (HIRAKAWA 1991). In November–December, however, a small fraction of these adult females migrated into the upper 100 m depth at night (Figure 6), and began to lay their eggs (Table 2), as they matured. Newly molted adult female *Metridia pacifica* persisted for long period (ca. 4–6 months) in an immature stage with quiescent ovaries, as in the case of *Neocalanus flemingeri* in the Japan Sea (MILLER & TERAZAKI 1989).

On the other hand, the development time of CV, which remained in deep layers (> 500 m depth) may be significantly lengthened due to the extremely low temperature (< 0.5 °C) and scarcity of phytoplankton food, as discussed by CLARKE (1983). According to MCLAREN (1963), the adaptive significance of the seasonal descent is minimization of metabolic expenditure in cold layers at depth. For example, water temperatures higher than 11 °C exclude *Neocalanus plumchrus* CV from the surface and induce a diapause phase in deep water (MILLER et al. 1984, MILLER & TERAZAKI 1989). *N. plumchrus* diapauses at depths greater than 200 m and subsists on lipids stored in their bodies (HEINRICH 1962b). For *Metridia pacifica* in Toyama Bay, therefore, a decrease of oil sac volume (Table 1) indicates that they rely upon stored lipids, especially wax ester, as an important energy source.
TABLE 3. GEOGRAPHIC COMPARISON OF THE LIFE CYCLES OF *Metridia pacifica* IN THE SUBARCTIC WATERS.

<table>
<thead>
<tr>
<th>Sea area</th>
<th>Surface water temperature(°C)</th>
<th>No. of generation per year</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bering Sea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern region (Anadyr Bay)</td>
<td>7.2–8.6</td>
<td>1</td>
<td>HEINRICH (1962a)</td>
</tr>
<tr>
<td></td>
<td>&lt; 7.2-8.6</td>
<td>1</td>
<td>FLEMING (1955)</td>
</tr>
<tr>
<td>Western region*</td>
<td>8.6–10.0</td>
<td>4</td>
<td>HEINRICH (1962a)</td>
</tr>
<tr>
<td></td>
<td>&lt; 8.6-10.0</td>
<td>4</td>
<td>FLEMING (1955)</td>
</tr>
<tr>
<td>Pacific Ocean</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eastern subarctic region (St. P)</td>
<td>5.6–13.9</td>
<td>3</td>
<td>BATECHLDER (1985)</td>
</tr>
<tr>
<td>Japan Sea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Off southwestern Sakhalin</td>
<td>0.0–18.0</td>
<td>4</td>
<td>FEDOTOVA (1975)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>ZENKEVITCH (1963)</td>
</tr>
<tr>
<td>Toyama Bay</td>
<td>10.5–27.9</td>
<td>1</td>
<td>Present study</td>
</tr>
</tbody>
</table>

*located northwest of the line which joins the Comandor Isles and Providens Bay (KOTANI 1992) during their aestivation.

According to DAVIS (1984), the number of generations of planktonic copepods is known to increase in lower latitudes, which is generally associated with higher water temperatures. From this view, Toyama Bay is located in the lowest latitude among the locations (Table 3) from which the number of generations of *M. pacifica* has been reported. Thus, 3–4 generations or more might have been anticipated for *M. pacifica* in Toyama Bay before the present study. However, the present results demonstrated a significant reduction of generation number, as in the northern Bering Sea (Anadyr Bay) population found by HEINRICH (1962a) (Table 3). The generation cycle of calanoid copepods is closely associated with their trophic position and environmental conditions; for herbivores, the spawning and development of young are scheduled to coincide with the season of high phytoplankton production (MARSHALL & ORR 1972). Similarly, synchronizing development of young *M. pacifica* with the winter-spring diatom bloom (January to March during the study period, TANIGUCHI & NAKAJIMA unpubl.) is part of the reproductive strategy of this species in the southern Japan Sea.

In conclusion, the life history pattern of *M. pacifica* in Toyama Bay is characterized by either a remarkably prolonged development of CV or a discontinuity of egg production during summer and autumn seasons. Major mechanism for this anomalous life history of *M. pacifica* is related to the limited reproduction success due to the warming of euphotic layer (> 18 °C, HIRAKAWA 1991) beyond the limit of thermal tolerance for this species.

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. Part of this research was supported by the project “Analysis and Prediction of the Impact of Global Environmental Changes on Agro-, Forest-and Marine
Ecosystem” from the Agriculture, Forestry and Fisheries Research Council Secretariat, Ministry of Agriculture, Forestry and Fisheries, Japan. We also acknowledge Prof. C. B. MILLER of the Oregon State University, Drs. T. IKEDA and Y. OGAWA of the Japan Sea National Fisheries Research Institute for their critical readings of the manuscript and valuable comments. This is Contribution No. B-9204 from the Japan Sea National Fisheries Research Institute.

**Literature Cited**


