Experimental Studies on Hatching Conditions of the Resting Eggs of Marine Cladocerans and Their Seasonal Variation in Onagawa Bay

Tohoku Journal of Agricultural Research
Vol. 52 No. 3-4, March 2002
Printed in Japan

Experimental Studies on Hatching Conditions of the Resting Eggs of Marine Cladocerans and Their Seasonal Variation in Onagawa Bay

Hiroyuki KOMAZAWA and Yoshinari ENDO

Laboratory of Aquatic Ecology, Graduate School of Agricultural Science, Tohoku University, Sendai, Miyagi 981-8555 Japan

(Received, March 4, 2002)

Summary

Seasonal changes in the abundance of plankton populations and resting eggs of marine cladocerans were surveyed in Onagawa Bay, and factors affecting the hatching of the resting eggs were examined experimentally.

Cladocerans have displayed remarkable seasonal succession in the water column. *Evadne nordmanni* appeared in summer, *Penilia avirostris* from summer to autumn, *Podon polyphemoides* and *E. tergestina* in autumn, *P. leuckarti* from winter to summer. The hatching rate was significantly higher in resting eggs collected from 0-4 cm than those collected from 4-8 cm of bottom sediment in *E. nordmanni*. Anoxic conditions in deeper layers probably inhibited the hatching of resting eggs. The hatching rate was not significantly different among 14 different combinations of temperature (5-20°C) and salinity (19-33 psu). However, the development time and half hatching period, the duration from the first development to 50% hatch, of the resting eggs decreased with increasing temperature. At a high temperature of 25°C, the resting eggs could not hatch. Light intensities expected to reach the bottom surface of this station do not seem to inhibit hatching of the resting eggs. The hatching rate was not significantly different between resting eggs collected in August and November, but the development time was longer in November than August. Factors that may inhibit the hatching of resting eggs of *E. nordmanni* in Onagawa Bay include slow development time at low temperatures and anoxic conditions in the sediment.

Because resting eggs of this species can hatch throughout the year, whether the plankton population can develop depends on the environmental conditions in the water column. The survival strategy of cladocerans, especially *E. nordmanni* was discussed.

Key words: cladocerans, Onagawa Bay, seasonal succession, resting eggs, hatchability

Introduction

There are more than 600 species of cladocerans, and many of them are freshwater species (1, 2). Cladocerans are very important zooplankton in a freshwater environment. Marine cladocerans, however, have only 8 species distributed among 3 genera (3–5). Although small in species number, marine cladocerans are widely distributed from estuarine areas to the open ocean. Marine cladocerans, like freshwater counterparts, reproduce by parthenogenesis and gamogenesis. When environmental conditions are suitable, eggs spawned into the brood chamber of females through parthenogenesis develop to become females. Females exiting the brood chamber continue parthenogenesis. The Family Podonidae performs paedogenesis in which the embryo in the brood chamber spawns eggs in its own brood chamber (5–7). By these reproductive characteristics, marine cladocerans sometimes predominate in the plankton community temporarily in warm and temperate waters (5, 8–11). Marine cladocerans are preyed on by fish larvae (12–19), chaetognaths (20) and cnidarians (21). Therefore, the population dynamics of marine cladocerans must be studied in order to better understand the energy flow of marine ecosystems.

When the environmental conditions become unsuitable for their reproduction, marine cladocerans form resting eggs through gamogenesis. A resting egg is very durable and lies on the sea bottom until environmental conditions become good. Resting eggs of marine cladocerans have been unknown for long, but many studies have been done on their geographical distribution, vertical distribution in the bottom sediment and morphology (5, 22–28) after the discovery of resting eggs in the Inland Sea of Japan by Onbé (22). However, there are few studies on seasonal changes in the abundance of resting eggs (29) and the effect of environmental factors on the hatching of resting eggs (5, 30–32). The resting eggs of marine cladocerans play an important role in the early process of the occurrence of their plankton populations in the water column (18, 29). Resting eggs as well as plankton should be investigated, therefore, to understand the fluctuations of populations of marine cladocerans. The studies of marine cladocerans in Japanese waters were mainly conducted in the southern part. In Onagawa Bay, although the seasonal fluctuations of plankton populations of marine cladocerans is reported (33), investigation of their resting eggs has not been conducted. In this study, in addition to seasonal changes in the abundance of plankton populations and resting eggs, factors affecting the hatching of resting eggs were examined experimentally. The survival strategy of cladocerans, especially *Evadne nordmanni*, was discussed.

Materials and Methods

Environmental factors

Sampling was carried out once or twice per month from 5 October, 2000 to 22 October, 2001 at a station (38°26.11′N, 141°27.81′E) in the innermost part of Onagawa Bay. The depth at the station was 17-21 m. Samplings were done between 9 : 00 and 14 : 00. The vertical profiles of temperature and salinity were determined by STD. Transparency was determined by the Secchi disk. Light intensity in the water column was calculated from the transparency and light intensity at the sea surface using the equation by Taniguchi (34)

$$I_z = I_0 e^{-kz}$$

where I_z denotes the light intensity at depth z (m), I_0 denotes the surface radiation and k denotes the extinction coefficient and is obtained using the Secchi disk depth (S.d.) as $k = 1.7$ S.d.$^{-1}$. The surface radiation was taken from the daily global radiation measured in Sendai and supplied by the Sendai District Meteorological Observatory. The day length was available from the Hydrographic Department, Japan Coast Guard. Mean daily global radiation was calculated for five days prior to each sampling date. The surface radiation was calculated by the equation below from the mean daily global radiation (I, in MJ m^{-2}) and mean day length for those five days (D, in second).

$$I_0 = I^* 10^6 \ D^{-1} \ (\text{w m}^{-2}\text{s}^{-1})$$

Mud surface (1 cm) temperature was measured using a mercury-filled Celsius thermometer immediately after the sediment was collected. Chlorophyll *a* concentration was determined for water samples collected from the surface down to 18 m depth at 3 m intervals with a Van Dorn water sampler. A subsample of 150 ml in blooming season, or 250 ml in other seasons, was taken and filtered through a Whatman GF/F filter. The filters were transferred to the laboratory and extracted at −20°C for 24 hours in 90% acetone, and fluorescence was determined before and after acidification on a Turner Designs fluorometer.

Seasonal variation in cladocerans in Onagawa Bay

Zooplankton samples were collected by a Norpac net (35) with a mesh aperture of 100 μm and preserved in 5% formalin-seawater solution. The net was hauled vertically by hand from 18 m depth to the surface. A flowmeter was not used; therefore, the volume of water filtered was calculated assuming 100% filtering efficiency. An aliquot of 1/8-1/16 was examined under a dissecting microscope for zooplankton identification and enumeration. Zooplankton were identified to orders, but cladocerans were identified to species. Sediment samples were collected by a midget Smith-McIntyre grab sampler. Four subsamples were

collected by sediment corers (3.7 cm diameter, 25 cm in length) from the top 2 cm, 2-4 cm, 4-6 cm and 6-7 cm and were carefully sliced off and stored at 5°C in the dark until further processing. The eggs were sorted from the sediment using a method introduced by Onbé (36) and modified by Marcus (37) : the samples were sonicated for 10 min, poured onto a 100 μm sieve and washed with GF/F-filtered seawater. The material remaining on the sieve was then centrifuged in a sugar solution (1 kg sucrose in 1 liter water) at 3,000 rpm for 5 min. The supernatant was transferred to a 100 μm sieve and thoroughly washed with filtered seawater. The procedure is reported not to induce bad effects on the resting eggs because there was no difference in the hatching rate between eggs sorted by this procedure and those sorted in the seawater (36). The eggs were then transferred to a counting chamber ; the species was identified according to Onbé (38) and counted under a dissecting microscope.

Environmental factors affecting hatching of resting eggs

Depth in the sediment

Sediment samples were collected from the mud surface down to 8 cm depth at 2 cm intervals on 10 July 2001 and stored at 5°C in the dark for 4 days. Resting eggs were sorted from the sediment as described earlier, and 12 resting eggs of *Evadne nordmanni* and 1-12 eggs each of *Podon leuckarti* and *Podon polyphemoides* were transferred to the wells of several tissue culture plates (Nunclon Multidish No. 150628) filled with 3 ml of filtered seawater. Resting eggs were incubated for 40 days, under the conditions of 15°C temperature, 33 psu salinity, a 12 h L : 12 h D photocycle, and 35 μE $m^{-2}s^{-1}$ light intensity. Once per 6 days, the resting eggs were transferred to the wells filled with fresh filtered seawater. The hatched eggs were checked daily in the light period in this experiment and the other experiments in the present study.

Temperature and salinity

Sediment samples were collected from the upper 2 cm on 20 August and 5 November 2001 and stored at 5°C in the dark for 2 days. Resting eggs were sorted from the sediment, and 10-12 eggs each were transferred to the wells filled with 3 ml of filtered seawater. Resting eggs were incubated at each of 17 combinations of temperature (10, 15, 20, and 25°C) and salinity (19, 24, 27, 30, and 33 psu) in August. In November, temperature and salinity were set to 5°C and 33 psu, respectively. Light conditions were a 12 h L : 12 h D photocycle and 23 μE $m^{-2}s^{-1}$ light intensity. The resting eggs were incubated for 30 or 40 days. Once per 6 days, the resting eggs were transferred to the wells filled with fresh filtered seawater. No hatched eggs were observed at 25°C in 30 days. Therefore, half of the eggs were transferred to the wells of 20°C and 4 respective salinity levels and incubated for additional 30 days. Once per 6 days, the resting eggs

were transferred to the wells filled with fresh filtered seawater. The rest of the eggs were incubated under the original conditions.

Light intensity

Sediment samples were collected from the upper 2 cm on 22 October and stored at 5°C in the dark for 2 days. The resting eggs of *Evadne nordmanni* were sorted, and twelve eggs each were transferred to the wells filled with 3 ml of filtered seawater. The light intensity was set to complete darkness, 6 and 42 μE $m^{-2}s^{-1}$ by changing the distance from the light source. Other conditions were 20°C temperature, 33 psu salinity, and a 12 h L : 12 h D photocycle. The resting eggs were incubated for only 13 days, because of malfunctioning of the incubator. Once per 6 days, the resting eggs were transferred to the wells filled with fresh filtered seawater.

Difference in hatching between August and November

Sediment samples were collected from the upper 2 cm on 5 November 2001 and stored at 5°C in the dark for 2 days. The resting eggs were sorted from the sediment, and 10 eggs each were transferred to the wells filled with 3 ml of filtered seawater. The resting eggs were incubated for 40 days, under the conditions of 15°C temperature, 33 psu salinity, a 12 h L : 12 h D photocycle, and 23 μE $m^{-2}s^{-1}$ light intensity. Once per 6 days, the resting eggs were transferred to the wells filled with fresh filtered seawater. The results were compared with those for resting eggs collected on 20 August 2001 and were incubated under the same conditions.

Results

I. Seasonal variation in cladoceran community

Environmental factors

The seasonal change in temperature at 0, 9 and 15 m depths of the water column and the top 1 cm of the bottom sediment is shown in Fig. 1, and the seasonal change in the vertical profile of water temperature is shown in Fig. 2. Water temperature and the temperature of the top 1 cm of bottom sediment ranged from 5.2–22.0°C and 5.8–20.5°C, respectively. The highest sediment surface temperature, 20.5°C, was recorded in October 2000. After that, both water temperature and sediment surface temperature decreased, and their minimum values were recorded in March : 5.2°C for 1 m depth in the water column and 5.8°C for sediment surface. From April, both the water temperature and the sediment surface temperature increased, and the surface water temperature reached 22°C in August, the highest value in this study. Thermal stratification in the water column started to form in April and lasted until September. In other seasons, the

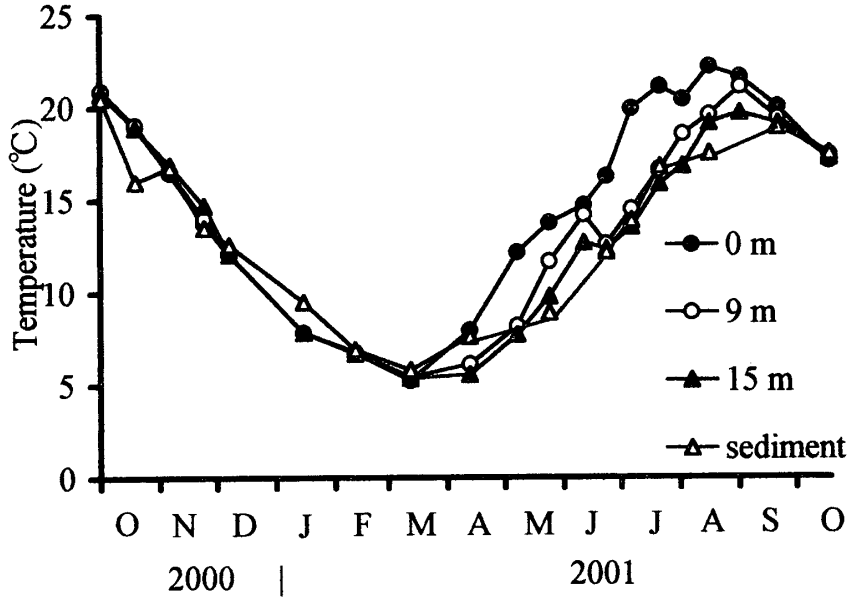

FIG. 1. Seasonal change in temperature (°C) at 0 m (●), 9 m (○), 15 m (▲) and the top 1 cm of the bottom sediment (△) at St. 1 in Onagawa Bay during the period from October 2000 to October 2001.

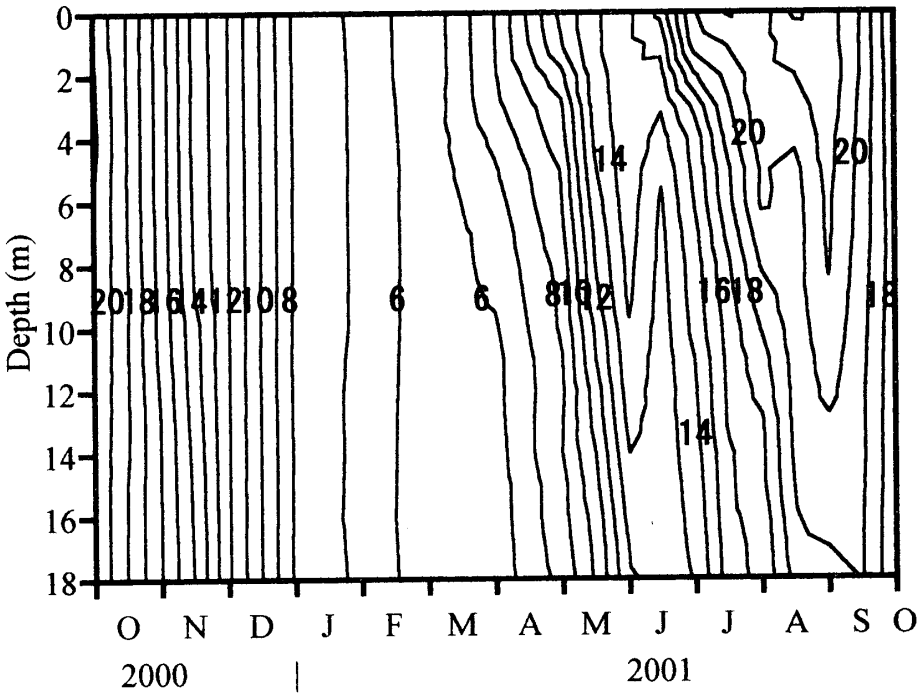

FIG. 2. Seasonal change in vertical profile of temperature (°C) at St. 1 in Onagawa Bay during the period from October 2000 to October 2001.

water column was well mixed vertically.

Salinity ranged from 28.3-33.8 psu. Although the salinity at 9 and 15 m depths varied within the range of 33.1-33.6 psu during the observation, salinity at 0 m showed low values in the period from April to September 2001 with the lowest value of 28.3 psu.

Transparency ranged from 3-10 m, with higher values in winter. The highest transparency was 10 m in December. Light intensity at the sea surface changed in the range of 841-1,761 μE $m^{-2}s^{-1}$. Although the light intensity at the sea surface in winter was low compared with that in summer, light reached the deeper layers in winter because the transparency was high in winter.

Chlorophyll *a* concentration varied in the range of 0.18-19.76 $\mu g\, l^{-1}$. High values of more than 10.00 $\mu g\, l^{-1}$ were recorded in October 2000 and from August to October 2001 at the surface, and in April 2001 in the middle layer. The highest value was recorded in April, which is indicative of the spring bloom.

Zooplankton

Seasonal changes in mean zooplankton abundance and the integrated chlorophyll *a* value over the water column from 0-18 m are shown in Fig. 3. Zooplankton abundance decreased with a fall in chlorophyll *a* from October 2000 and reached its minimum value, 1,736 indiv. m^{-3}, in March 2001. After that, the zooplankton abundance increased and attained its maximum, 30,039 indiv. m^{-3}, in June. Chlorophyll *a* reached its maximum in April, two months prior to the zooplankton maximum. From July onward, the zooplankton abundance was low and fluctuated between 5,000-15,000 indiv. m^{-3}.

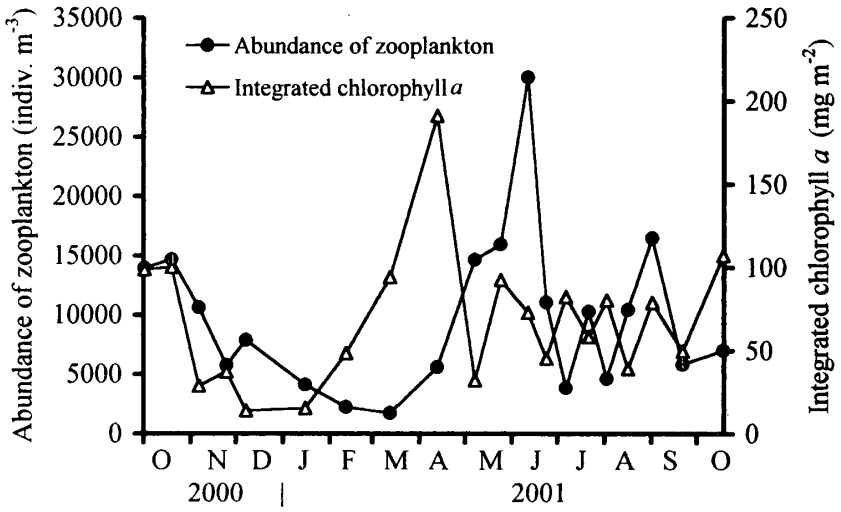

FIG. 3. Seasonal changes in mean zooplankton abundance (indiv. m^{-3}) and integrated chlorophyll a value (mg m^{-2}) over the water column from 0 to 18 m at St. 1 in Onagawa Bay during the period from October 2000 to October 2001.

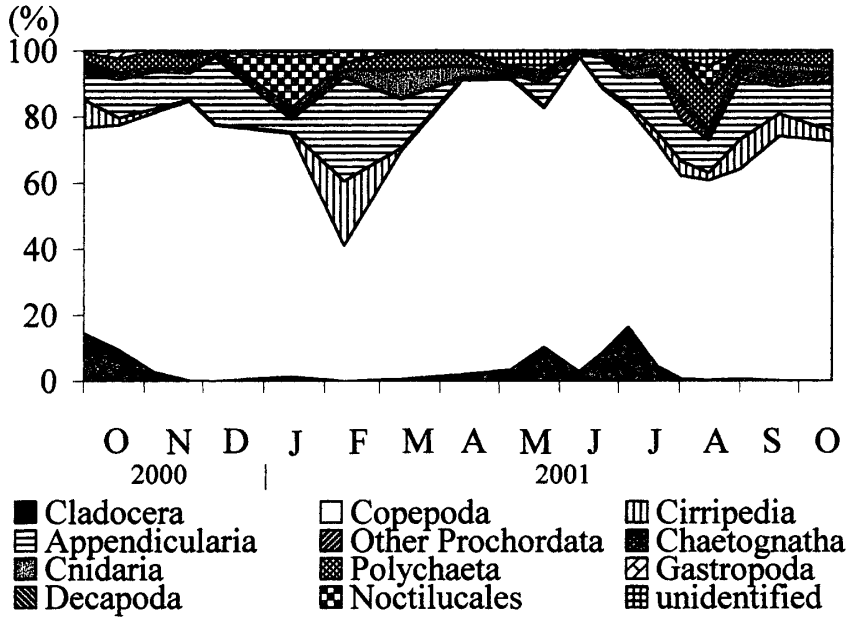

FIG. 4. Seasonal change in the composition of zooplankton taxonomic groups in the water column from 0 to 18 m at St. 1 in Onagawa Bay during the period from October 2000 to October 2001.

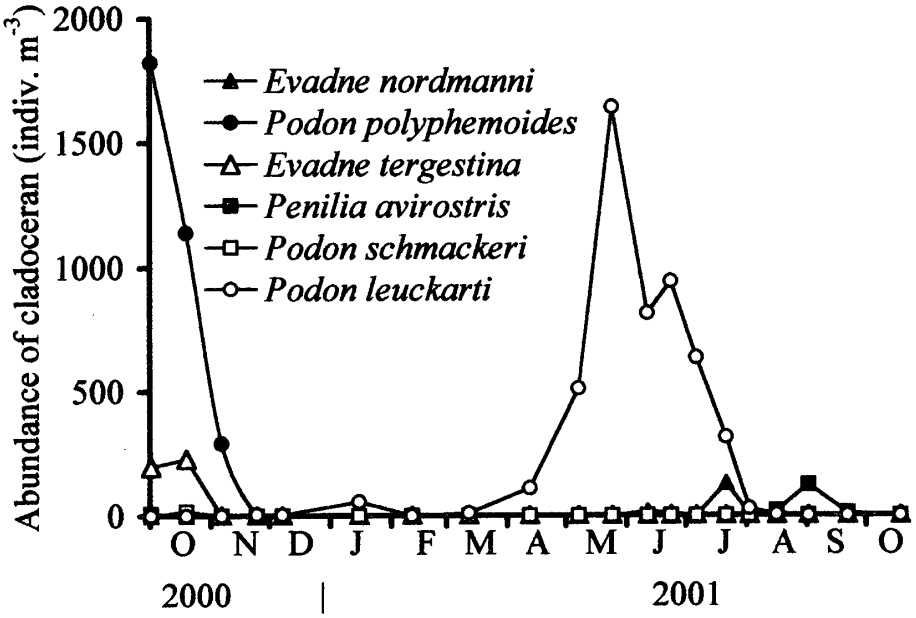

FIG. 5. Seasonal change in the abundance of each cladoceran species (indiv. m^{-3}) in the water column from 0 to 18 m at St. 1 in Onagawa Bay during the period from October 2000 to October 2001.

Seasonal change in the composition of zooplankton taxonomic groups in the water column is shown in Fig. 4. Copepods were the most dominant group throughout the year, occupying from 41.1-95.2% of the total zooplankton. The contribution of cladocerans varied from 0-16.5%. Cladocerans were the next most dominant plankton to copepods in October 2000 and May-July 2001.

The seasonal change in the abundance of each cladoceran species is shown in Fig. 5. A total of six species occurred and they showed remarkable seasonal succession. *Evadne tergestina* appeared in October 2000 with the maximum abundance of 229 indiv. m^{-3}. *Podon polyphemoides* appeared in October and November 2000 and August 2001 with the maximum abundance of 1,823 indiv. m^{-3} in October 2000. *Podon leuckarti* appeared from November 2000 to August 2001 with the maximum abundance of 1,644 indiv. m^{-3} in June 2001. *Evadne nordmanni* appeared from June to August 2001 with the maximum abundance of 131 indiv. m^{-3} in July. *Penilia avirostris* appeared from August to October 2001 with the maximum abundance of 123 indiv. m^{-3} in August. The occurrence of *Podon schmackeri* was observed for the first time in Onagawa Bay. However, its abundance was only 17 indiv. m^{-3} in October 2000.

The seasonal change in resting egg abundance of each cladoceran species is shown for the top 7 cm of sediment (Fig. 6) and for each depth layer of the sediment, namely, the top 2 cm, 2-4 cm, 4-6 cm, and 6-7 cm (Fig. 7). Resting eggs identified in the present study were of only three species, *Podon polyphemoides*, *Podon leuckarti*, and *Evadne nordmanni*. In addition, resting eggs

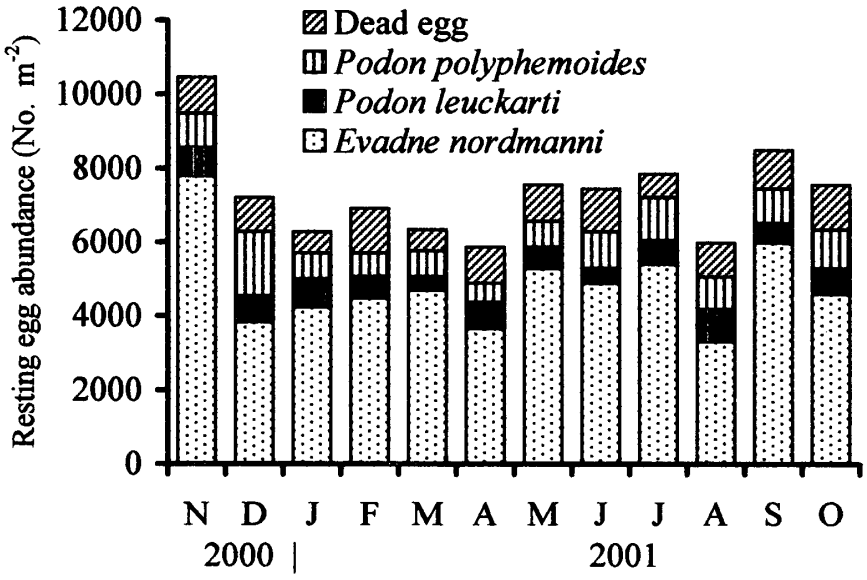

FIG. 6. Seasonal change in the resting egg abundance of each cladoceran species in the top 7 cm of the sediment at St. 1 in Onagawa Bay during the period from November 2000 to October 2001.

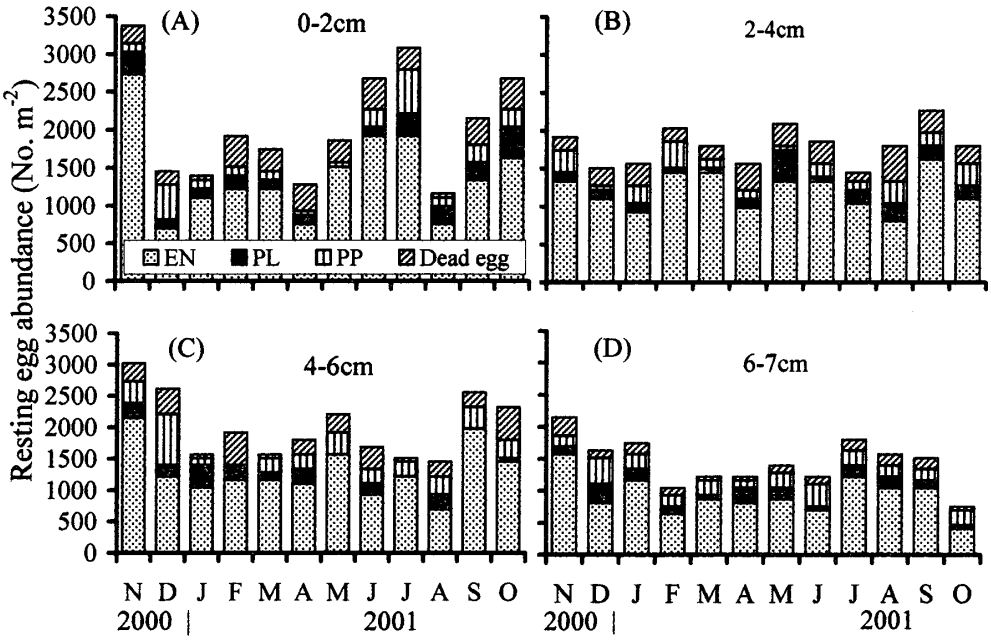

FIG. 7. Seasonal change in the resting egg abundance of each cladoceran species in (A) the top 2 cm (B) 2-4 cm (C) 4-6 cm and (D) 6-7 cm depth of the sediment at St. 1 in Onagawa Bay during the period from November 2000 to October 2001.

without protoplasm occurred and were judged to be dead eggs, because they lacked cleavage on the shell. The resting eggs of cladocerans existed in the bottom sediment throughout the year, and their abundance varied from 5,874–10,468 eggs m^{-2}. Resting eggs of *Evadne nordmanni* were the most numerous, ranging from 3,315–7,793 eggs m^{-2}, and their contribution was 53.2–74.4% of the total resting eggs. The next most abundant resting eggs belonged to *Podon polyphemoides* with an abundance of 523–1,744 eggs m^{-2}. The abundance of *Podon leuckarti* resting eggs ranged from 349–872 eggs m^{-2}.

There was no clear relationship between resting egg abundance and depth of the sediment (Fig. 7). Eggs were more or less evenly distributed in all depth layers. The seasonal variation in the abundance of resting eggs was most remarkable in the upper 2 cm. The species composition of resting eggs was similar at all depths, with *Evadne nordmanni* predominating in all seasons. The seasonal change in resting egg abundance in the upper 2 cm of the sediment and plankton abundance in the water column is shown for three species in Fig. 8. The top 2 cm was selected because the seasonal change in resting egg abundance was most remarkable at that depth. Onbé (29) reported that the resting egg abundance in the bottom sediment was the lowest shortly before the plankton appeared, and the highest just before the plankton disappeared. In the present study, a similar tendency was observed in *Podon leuckarti* and *Podon polyphemoides*, but the tendency was not clear in *Evadne nordmanni*.

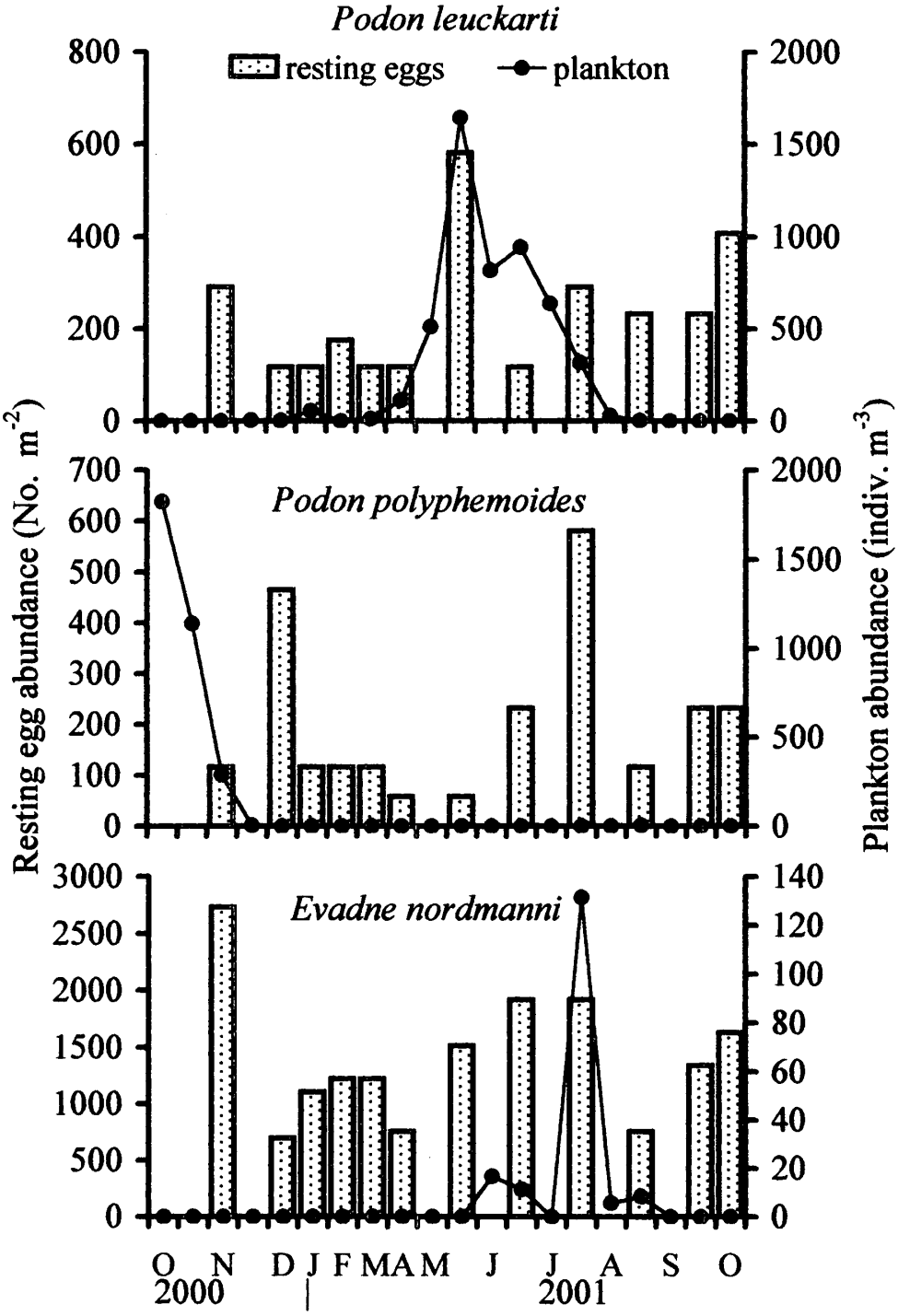

FIG. 8. Seasonal change in the resting egg abundance in the top 2 cm depth of the sediment and the plankton abundance in the water column from 0 to 18 m at St. 1 in Onagawa Bay during the period from October 2000 to October 2001.

II. Factors affecting the hatching of resting eggs

Depth in the sediment

The hatching rate of resting eggs collected from 4 depth layers in the top 8 cm of the sediment after incubation for 40 days is shown for the three species in Fig. 9. The hatching rate of *Evadne nordmanni* eggs was 29.6-55.6%. There was a significant difference in the hatching rate between depths (Mann Whitney U-test, $p<0.05$) : the hatching rate was high, 49.2-55.6%, in the upper 4 cm but low, 29.6-31.5%, in the deeper layers. The hatching rate of *Podon polyphemoides* eggs was 4.6-66.7%. The hatching rate of this species decreased gradually with depth. The hatching rate of *Podon leuckarti* eggs was 0-50.0%. Hatching did not occur in layers deeper than 4 cm in this species. Daily changes in the hatching pattern of resting eggs collected from 4 depth layers of the sediment are shown for the three species in Fig. 10. The development time and the half hatching period, the duration from the first development to 50% hatch, of the resting eggs collected from 4 depth layers of the sediment are shown in Table 1. A shorter half hatching period means that the development time of the resting eggs is more synchronized. The mean development time of *Evadne nordmanni* was 9.8-10.5 days, and there was no significant difference in development time among different depths in the sediment (Kruskal Wallis-test, $p>0.05$). The mean development time of the other 2 species was 8.0-10.6 days for *Podon polyphemoides* and 17-26.5 days for *Podon leuckarti*. The half hatching period of *Evadne nordmanni* was 1.1-2.0 days, and there was no significant difference in the half hatching period among depths in the sediment (Kruskal Wallis-test, $p>0.05$). The half hatching

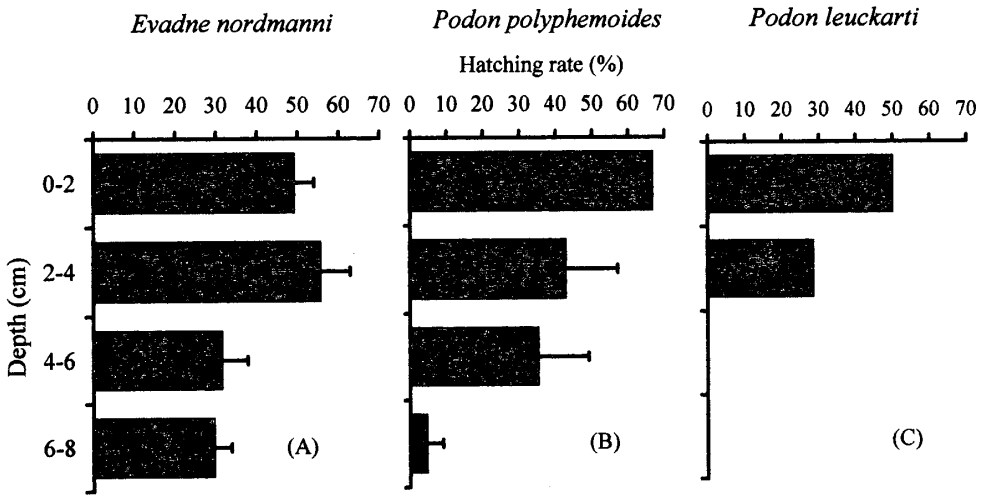

FIG. 9. The hatching rate of the resting eggs of (A) *Evadne nordmanni*, (B) *Podon polyphemoides* and (C) *Podon leuckarti* collected from 4 depth layers in the top 8 cm of the sediment in July. Horizontal bar represents +1 SE.

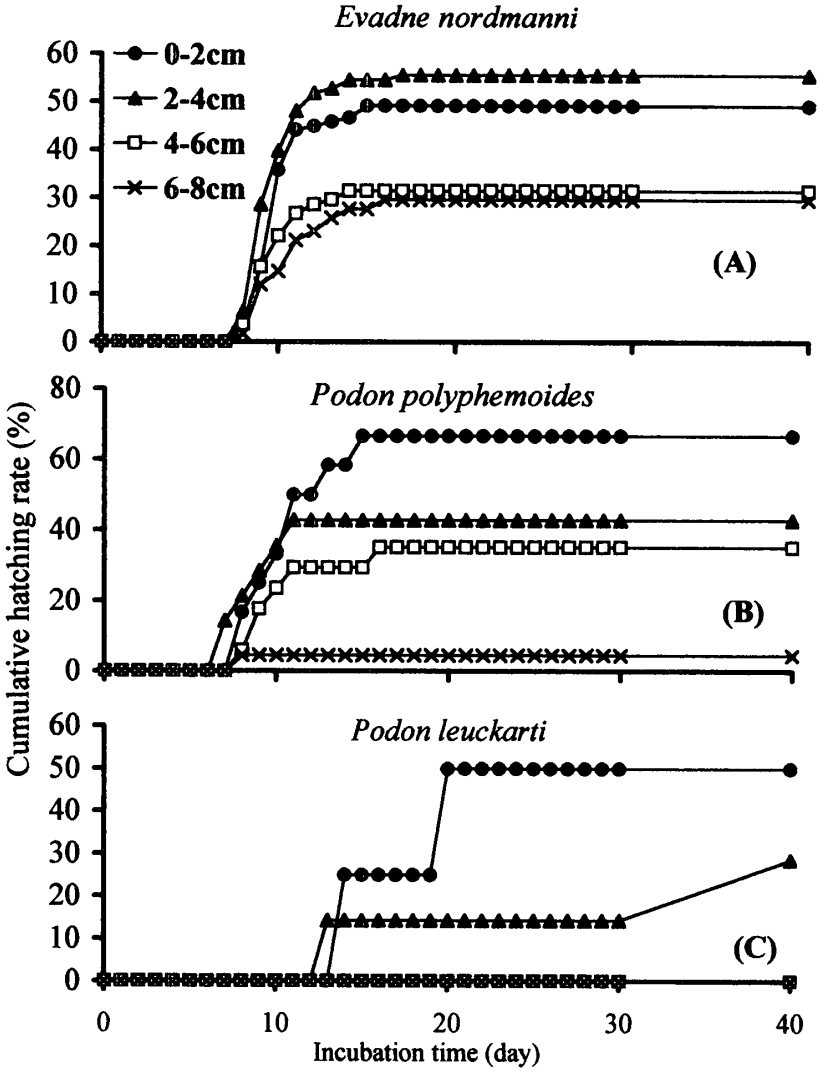

FIG. 10. Daily changes in cumulative hatching rate of the resting eggs of (A) *Evadne nordmanni*, (B) *Podon polyphemoides* and (C) *Podon leuckarti* collected from the top 8 cm of the sediment in July.

period of the other 2 species was 0.5–3 days for *Podon polyphemoides* and 1 day for *Podon leuckarti*. Because the number of resting eggs of the latter 2 species was small, no statistical test was conducted on them.

Temperature and salinity

The hatching rates of resting eggs of *Evadne nordmanni* under the conditions of 18 different combinations of temperature and salinity are shown in Fig. 11. The hatching rate was 44.4–72.2% except for 25°C, at which temperature hatching did not occur in 30 days, and there was no significant difference in hatching rate among these conditions excluding 25°C (Kruskal Wallis-test, $p > 0.05$). The mean development time at 5, 10, 15, and 20°C was 27.3, 15.2, 13.5, and 8.9 days, respec-

Table 1. Development time and half hatching period, the duration from the first development to 50% hatch, of the resting eggs of Evadne nordmanni, Podon polyphemoides *and* Podon leuckarti *collected from 4 depth layers in the top 8 cm of the sediment in July 2001. No hatching occurred in deeper layers than 4 cm in* Podon leuckarti.

Depth (cm)	Development time (day)	Half hatching period (day)
Evadne nordmanni		
0-2	10.2±0.3	2.0±0.4
2-4	9.8±0.3	1.5±0.2
4-6	9.9±0.3	1.1±0.1
6-8	10.5±0.4	1.6±0.4
Podon polyphemoides		
0-2	10.6	3
2-4	8.5±0.5	1.5±0.5
4-6	10±1.5	1.5±0.5
6-8	8	0.5
Podon leuckarti		
0-2	17	1
2-4	26.5	1
4-6	—	—
6-8	—	—

(mean±SE)

tively. There was a significant difference in any pair of development times at different temperatures (Mann Whitney U-test, $p<0.05$), and the relationship was expressed as an exponential function, $T_d=91.103*t^{-0.7518}$ ($r^2=0.960$, $p<0.05$, Fig. 12). However, there was no significant difference among development times at 5 salinity levels, 19, 24, 27, 30, and 33 psu (Kruskal Wallis-test, $p>0.05$). The relationship between the half hatching period of the resting eggs and temperature is shown in Fig. 13. The mean value of the half hatching period at 5, 10, 15 and 20°C was 3.3, 2.5, 2.4 and 1.5 days, respectively. The half hatching period at 20°C was significantly different from that at any other temperatures (Mann Whitney U-test, $p<0.05$). Moreover, a significant correlation was also seen between the half hatching period and temperature ($r^2=0.914$, $p<0.05$). However, there was no significant difference in the half hatching period among 5 salinity levels (Kruskal Wallis-test, $p>0.05$).

The resting eggs incubated at 25°C did not hatch in 30 days. Half of those eggs were transferred to the culture plate at 20°C and the respective salinity levels and incubated for additional 30 days. The hatching rate and formation rate of the compound eye of the resting eggs are shown in Fig. 14. Both rates are shown for additional 30 days. The resting eggs could hatch only under the conditions of

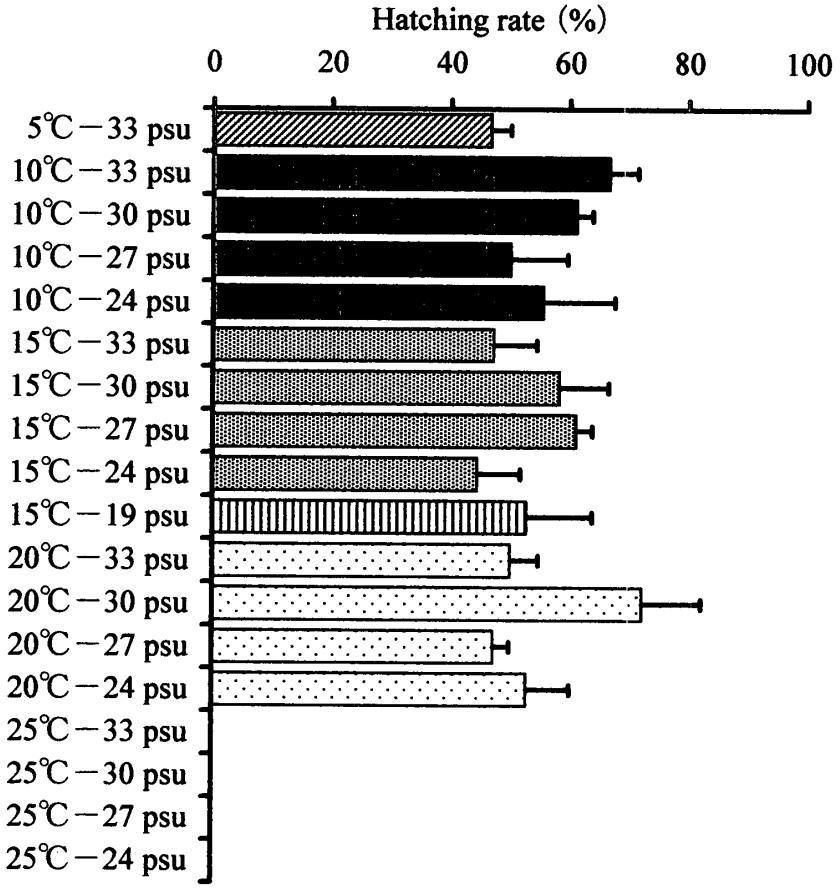

FIG. 11. The hatching rate (%) of the resting eggs of *Evadne nordmanni* for each of 18 different combinations of temperature (°C) and salinity (psu). Horizontal bar represents +1 SE. Hatching rate was 0 at 25°C.

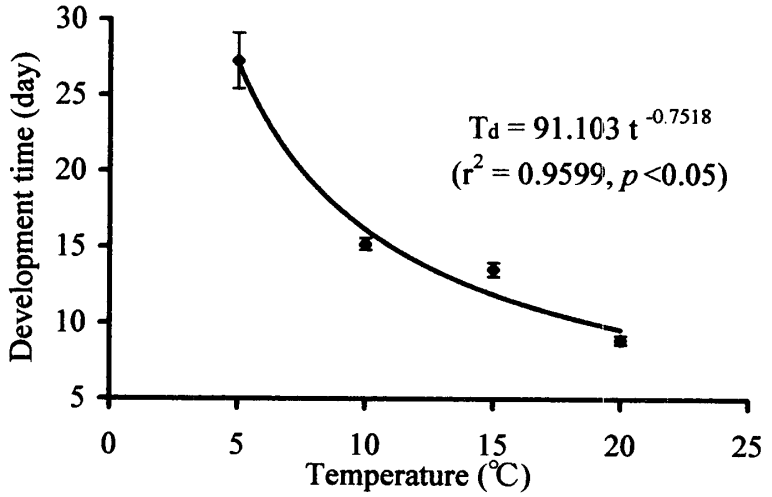

FIG. 12. Relationship between development time of the resting eggs of *Evadne nordmanni* and temperature (°C). Vertical bar represents ±1 SE.

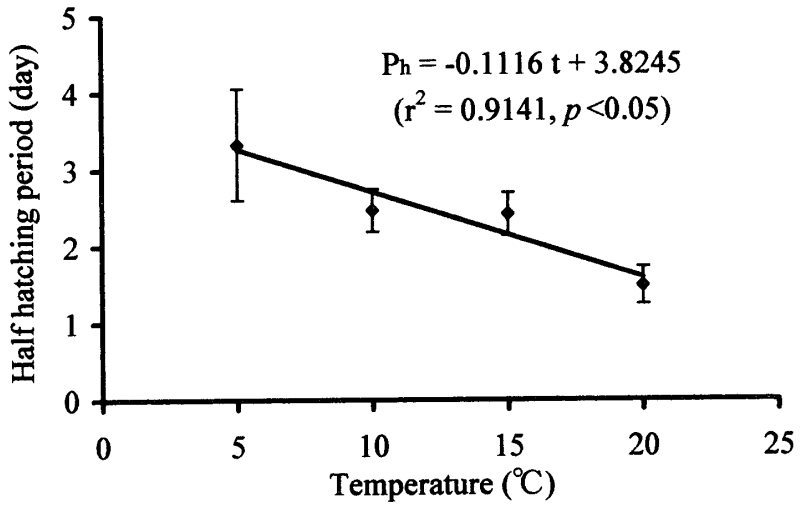

FIG. 13. Relationship between temperature (°C) and the half hatching period (day), the duration from the first development to 50% hatch, of the resting eggs of *Evadne nordmanni*. Vertical bar represents ±1 SE.

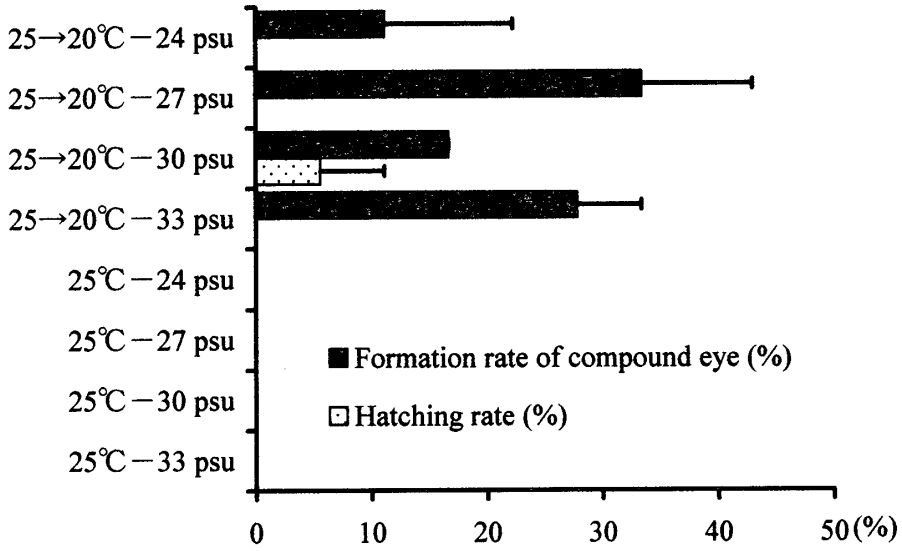

FIG. 14. The hatching rate (%) and formation rate of the compound eye (%) of the resting eggs of *Evadne nordmanni*. Eggs were incubated at 25°C and 4 salinity levels for the first 30 days. Half of the eggs were transferred to the culture plates at 20°C and the respective salinity levels and incubated for additional 30 days. The rest of the eggs were incubated under the original condition. The rates were shown for additional 30 days. No hatching occurred at 25°C. Horizontal bar represents +1 SE.

20°C −30 psu with a very low hatching rate of 5.6%. The compound eye was formed only in those resting eggs that were transferred to 20°C. The formation rate of the compound eye was 11.1-33.3%, and there was no significant difference in the rate among 4 salinity levels (Kruskal Wallis-test, $p > 0.05$).

Light intensity

The calculated light intensity at the bottom surface of our sampling station in Onagawa Bay ranged from 0.06-42 μE $m^{-2}s^{-1}$. Daily changes in the hatching pattern of the resting eggs of *Evadne nordmanni* under different light intensities are shown in Fig. 15. The hatching rate, development time and formation rate of the compound eye of the resting eggs of *Evadne nordmanni* under different light intensities are shown in Table 2. The hatching rate in the dark, at 6 and 42 μE $m^{-2}s^{-1}$ was 33.3, 36.1 and 16.7%, respectively. The development time of the resting eggs in the dark, at 6 and 42 μE $m^{-2}s^{-1}$ was 9.4, 8.9 and 9.6 days, respectively and there was no significant difference among light intensity levels (Kruskal Wallis-test, $p>0.05$). The formation rate of the compound eye in the dark, at 6 and 42 μE $m^{-2}s^{-1}$ was 11.1, 19.4 and 30.6%, respectively and there was a significant difference between darkness and 42 μE $m^{-2}s^{-1}$ (Mann Whitney U-test, $p<0.05$).

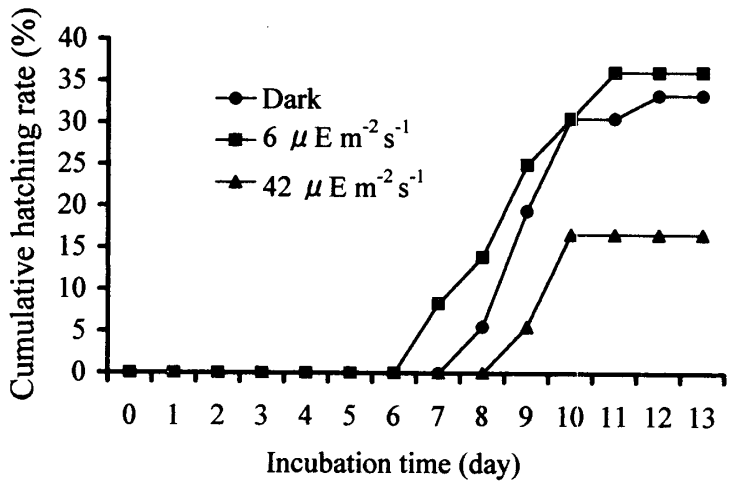

FIG. 15. Daily change in cumulative hatching rate (%) of the resting eggs of *Evadne nordmanni* under different light intensities.

Table 2. Hatching rate, development time and formation rate of the compound eye of the resting eggs of Evadne nordmanni *under different light intensities.*

Light intensity (μE $m^{-2}s^{-1}$)	Hatching rate (%)	Development time (day)	Formation rate of the compound eye (%)
Dark	33.3±4.8	9.4±0.4	11.1±2.8
6	36.1±2.8	8.9±0.1	19.4±2.8
42	16.7±4.8	9.6±0.3	30.6±2.8

(mean±SE)

Difference in hatching between August and November

The hatching rate of resting eggs of *Evadne nordmanni* collected in August and November and incubated under the same conditions was 46.7 and 47.2%, respectively, and no significant difference was found between them (Mann Whitney U-test, $p>0.05$). The development time of resting eggs collected in August and November was 12.2 and 14.8 days, respectively and a significant difference was found between them (Mann Whitney U-test, $p<0.05$). The half hatching period of resting eggs collected in August and November was 1.9 and 2.4 days, respectively, and no significant difference was found between them (Mann Whitney U-test, $p>0.05$).

Discussion

I. Seasonal variation in cladoceran community

Plankton

Cladocerans sometimes dominate in a zooplankton community temporarily in temperate and warm waters (5, 8-11). In Otuchi Bay in Iwate Prefecture, cladocerans dominate temporarily (39, 40). Cladocerans were the next most dominant zooplankton group in October 2000 and May-July 2001 following copepods in the present study. There was not much difference in the season of occurrence for each cladoceran species between the present study and the study by Uye (33). The only species whose abundance exceeded the value reported by Uye (33) was *Podon polyphemoides* : the abundance of the other species was lower than that reported by Uye. The years of 2000 and 2001 may be the ones when cladoceran abundance was low, because Uye (33) reported that there were large year-to-year differences in cladoceran abundance. *Podon schmackeri*, which is an oceanic species, was recorded for the first time in Onagawa Bay in this study. It is indicative of the intrusion of oceanic water into Onagawa Bay in this season. The maximum occurrence of each species did not overlap seasonally (Fig. 5). Especially, *Evadne* and *Podon* are reported not to appear concurrently (5, 8, 24, 29, 41-43), which is thought to be a strategy to avoid competition for food (43), because these two genera eat the same food organisms (44).

Resting eggs

Abundance of the resting eggs of cladoceran species in the present study was within the range reported previously (Table 3). Among the resting eggs, those of *E. nordmanni* predominated in the present study (Figs. 6 and 7), which is in sharp contrast to the dominance of warm water species such as *Penilia avirostris*, *Podon polyphemoides* and *Evadne tergestina* in the previous studies on resting eggs in Japanese waters (5, 22-24). This is probably because these studies were made in warmer areas, and therefore, resting eggs of a cold water species *E. nordmanni* were

Table 3. Abundance of the resting eggs of cladoceran species in Onagawa Bay. Reported values for other areas in Japanese waters were also tabulated.

Species	Location	Number of resting eggs ($\times 10^3$ m^{-2})	Reference
Evadne nordmanni	Onagawa Bay	3.3-7.8	Present study
	Ise Bay	11.2	Onbé (1978)
	Uragami Bay	0.4	Onbé (1978)
	Sensui Island	1.7	Onbé (1985)
	The Sea of Hiuchi	6.1	Onbé (unpubl)
	Hiroshima Bay	1.9	Onbé (unpubl)
Podon leuckarti	Onagawa Bay	0.35-0.87	Present study
	The Sea of Hiuchi	1.1	Onbé (unpubl)
	Hiroshima Bay	0.4	Onbé (unpubl)
Podon polyphemoides	Onagawa Bay	0.52-1.74	Present study
	Ise Bay	65	Onbé (1978)
	Uragami Bay	0.7	Onbé (1978)
	Sensui Island	18.2	Onbé (1985)
	The Sea of Hiuchi	5.9	Onbé (unpubl)
	Hiroshima Bay	0.9	Onbé (unpubl)

not abundant. In colder areas such as the Baltic Sea and the northern California coast, the resting eggs of cold water species such as *Evadne nordmanni* and *Podon leuckarti*, or a temperate species *Podon polyphemoides* dominated (27, 28, 45).

In the present study, *Evadne nordmanni* dominated as resting eggs but was scarce as plankton, while *Podon polyphemoides* and *Podon leuckarti* were abundant as plankton but scarce as resting eggs. Two possible explanations can be possible for this discrepancy. 1) Different species composition in the past. The abundance of *Evadne nordmanni* as plankton was much lower than that of *Podon polyphemoides* or *Podon leuckarti* in the present study. However, Uye (33) reported that *Evadne nordmanni* was the most dominant plankton in cladocerans in 1976. Therefore, the resting eggs of this species in the present study may have been spawned in the previous years. 2) Difference in the ability of sexual reproduction among species. The percentage of sexually reproducing individuals is variable among species: in the Inland Sea of Japan, it is 30% for *Evadne nordmanni*, 15-20% for *Podon polyphemoides*, and 10% for *Penilia avirostris* (5). It is possible that *Evadne nordmanni* produce a larger percentage of sexually reproducing individuals and therefore more resting eggs than *Podon polyphemoides* and *Podon leuckarti*.

The seasonal change in the abundance of resting eggs was most conspicuous in the upper 2 cm of the bottom sediment. Factors affecting the seasonal abundance of resting eggs include spawning, hatching, concentration or dispersion by

current (24, 37), vertical displacement in the sediment through the sedimentation process (29) and by bioturbation (37, 46), predation by other animals (24, 29, 47), and death caused by lethal environmental conditions (24, 29, 47, 48). Resting eggs decreased in number from November to December 2000 in the present study. If downward replacement of resting eggs in the sediment or eggs being buried in the sedimentation process are responsible for the decrease in resting eggs in the upper 2 cm of the sediment, the abundance and species composition of resting eggs in the deeper layers of the sediment must change. However, both of them were similar between November and December. Therefore, factors other than downward replacement or sedimentation must be responsible for the reduction of eggs in the upper 2 cm.

Resting egg abundance in the layers deeper than 2 cm did not vary very much seasonally, suggesting little physical and biological perturbation. Resuspension of resting eggs in the layers deeper than 2 cm, therefore, may not occur often.

Marcus *et al.* (27) reported that cladoceran resting eggs existed as deep as 21 cm in the bottom sediment in the Baltic Sea. Considering that the resting eggs were fairly abundant in the deepest layer in the present study, the abundance may be underestimated. The fact that resting eggs occurred abundantly in the bottom sediment throughout the year and that eggs collected from 8 cm depth hatched suggest the presence of an egg bank of cladocerans in Onagawa Bay.

II. Factors affecting the hatching of resting eggs

Depth of occurrence

The hatching rate of three cladoceran species was higher in the upper layer than in the lower layer of the sediment (Fig. 9). The color of the sediment differed by the depth of the sediment: brown in the upper 4 cm and black in the lower depths. It is indicative that the lower layers were anoxic (49). Because a low oxygen concentration is reported to inhibit hatching of cladoceran resting eggs (25, 29), the lower hatching rate observed in the lower layers may be caused by low oxygen concentration. The hatching rate of *Evadne nordmanni* and *Podon leuckarti* decreased abruptly below 4 cm depth, but in *Podon polyphemoides*, hatching decreased gradually by depth. This suggests that tolerance to oxygen deficiency may be different from species to species.

Development time and the half hatching period, the duration from the first development to 50% hatch, did not vary with the depth in *Evadne nordmanni* (Table 1). The effect of low oxygen appeared only on hatching rate, not on the development time or half hatching period, which suggests that low oxygen did not delay development of the resting eggs but imposed cessation of development or death. The effect of low oxygen on the development time and half hatching period was not clear for the other two cladoceran species, because the number of resting eggs was small. The effect of low oxygen, however, is not always nega-

tive : some freshwater cladocerans live longer by reducing respiratory loss under lower oxygen (50).

No clear relationship, however, was reported between the depth of the sediment and hatching rate in *Evadne nordmanni*, *Podon leuckarti* or *Podon polyphemoides* (26-28, 45). The difference between these studies and the present one seems to stem from the difference in the oxygen concentration in the sediment.

Temperature and salinity

Iwasaki *et al.* (30) examined the effects of temperature and salinity on the hatching of resting eggs of *Evadne* spp. collected from Ise Bay. The hatching rate generally increased with decreasing temperature from 21°C to 15°C, but the salinity effect was not clear in the range from 13 to 28 psu, with the highest hatching rate of 60% at 19 psu. They reported that 15°C and 19 psu were the best conditions. The hatching rate was as low as less than 20% under the other conditions of temperature and salinity.

The hatching rate of *Evadne nordmanni* resting eggs at 15°C and 19 psu in the present study was 52.8%, similar to the value, 60%, reported by Iwasaki *et al.* (30). However, we obtained more than 44.4% for other temperature and salinity conditions except 25°C. Two possible causes can be pointed out for the difference between the results of Iwasaki *et al.* and ours. Firstly, the genus *Evadne* contains warm water species, *E. spinifera* and *E. tergestina*, and a cold water species, *E. nordmanni* (3-5). Iwasaki *et al.* (30) carried out experiments on two or more species of different distributional characteristics. Secondly, they did not cite the depth of sediment from which the resting eggs were collected. As shown previously, the hatching rate of resting eggs could differ with the depth and their results may reflect the depth difference.

The hatching rate did not differ significantly among 14 combinations of temperature (5-20°C) and salinity (19-33 psu) in the present study. The development time and half hatching period, however, depended on temperature : they decreased with increasing temperature (Figs. 12 and 13). High temperature may accelerate the speed of enzymatic reactions necessary for development. Onbé (10) reported similar results for *Podon polyphemoides* : hatching rates were similar at temperatures ranging from 13 to 20°C and salinities ranging from 7.3 to 31.3 psu. The resting eggs of *Penilia avirostris* showed different results : the hatching rate was higher at 17-20°C and 24-30.6 psu than other values of temperatures ranging from 12 to 23°C and salinities ranging from 7.2 to 30.6 psu (5, 30). Therefore, the effect of temperature and salinity on the hatching rate may differ from species to species.

The resting eggs of *Evadne nordmanni* never hatched after 30 days incubation at 25°C. After being transferred to 20°C, the formation of the compound eye was observed in some eggs, but most of the eggs did not hatch in 10 days after

compound eye formation. These eggs may be dead because *Penilia avirostris* resting eggs needed about 100 hours from the first cleavage to hatching at 19.4°C (5). The high temperature of 25°C may be lethal to the resting eggs of *Evadne nordmanni*. Because some eggs formed a compound eye, the high temperature did not seem to inhibit the first steps in cleavage but to inhibit development after eye formation. A fungus, *Lagenidium* sp., is known to inhibit the development of a freshwater cladoceran, *Moina macrocopa* (51). A similar phenomenon is reported for marine cladocerans such as genera *Podon* and *Evadne* that died after eye formation (32). They died probably because their resistance to fungus was lowered or the activity of the fungus increased at high temperature. In Onagawa Bay, mud temperature never rises to as high as 25°C, but in the Inland Sea of Japan, the period of high temperature higher than 25°C lasts more than 1 month (29). The fact that *Evadne nordmanni* appear as plankton every year in the Inland Sea of Japan (29) shows that not all the eggs of the species die from high temperatures. This species may have adapted to the warmer temperatures there.

Light intensity

Light intensity is reported to be an important factor regulating hatching of resting eggs for freshwater cladocerans (52, 53). Iwasaki *et al.* (30) examined whether there is such an effect on marine cladocerans, *Evadne* spp., and found that the hatching rate was the highest at 1,000 lux (42 μE $m^{-2}s^{-1}$), 60%, among three light conditions, namely, darkness, 1,000 and 5,000 lux (208 μE $m^{-2}s^{-1}$). The hatching rate at darkness was 40%.

In the present study, the incubation period, 13 days, was not long enough to judge which light intensity was the best because many unhatched eggs formed a compound eye at the end of the incubation (Table 2). It is not certain whether these eggs are dead or alive because the incubation period was not long. However, hatching took place at both 6 and 42 μE $m^{-2}s^{-1}$, and darkness did not inhibit hatching of the *Evadne nordmanni* resting eggs. It is also reported by Iwasaki *et al.* (30) and Madhupratap (45) that darkness does not inhibit hatching.

The sinking rates of resting eggs of copepods, *Acartia clausi* (now, *A. omorii* and *A. hudsonica*) and *Acartia steueri*, were 31 m d^{-1} and 58 m d^{-1}, respectively (54). The specific gravity of cladoceran resting eggs is heavier than that of copepods because of the thick egg capsule and the large amount of yolk substances with a value of 1.12-1.13 for *Penilia avirostris* (5). The resting eggs of *Evadne nordmanni*, therefore, are expected to sink to the bottom in less than half a day, even if resuspended by chance at the present station in Onagawa Bay. Light intensity does not seem to be a regulating factor on hatching of this species given that the light intensity is 42 μE $m^{-2}s^{-1}$ or less at the bottom.

Difference in hatching between August and November

In the Inland Sea of Japan, the hatching rate of resting eggs of *Penilia avirostris* is high in June-August when the plankton population of the species appears, but very low in September when the plankton disappears (55). On the other hand, the hatching rate of *Podon polyphemoides* resting eggs is constantly high throughout the year (55). In the present study, the hatching rate of *Evadne nordmanni* resting eggs was not different between August when the plankton population appeared and November when there were no planktonic form. However, there was a significant difference in the development time between August and November with longer development time in November by 2.6 days. Therefore, resting eggs in November take longer to hatch due to staying on the sea bottom and thereby increasing their susceptibility to predation and the possibility of being buried in the bottom sediment. This may be because the eggs experienced high temperatures in summer, but the detailed mechanisms were unknown.

III. Survival strategy of Evadne nordmanni

The known ranges of water temperature and salinity in Onagawa Bay reported previously (e.g., 56) are within the values used in the incubation experiments in the present study. Namely, the salinity range in Onagawa Bay does not seem to affect the hatching of resting eggs of *Evadne nordmanni*. Nor does the light intensity at the sea bottom inhibit hatching of resting eggs of the species. Our results showed that there was no significant difference in the hatching rate of resting eggs of the species among temperatures ranging from 5 to 20°C, which means that these eggs can hatch in any season of the year in Onagawa Bay. The evidence for this is exemplified by Uye (33) who showed that plankton of this species occurred, although small in number, in February and March 1982 in the bay. The water temperature was 6°C at that time.

Plankton of this species occurred only from June to August in the present study. In the Inland Sea of Japan, *Evadne nordmanni* begin to appear as plankton in February-April when the water temperature has a minimum value of 8-10°C, disappear in June when the temperature exceeds 21-22°C and do not appear until February when the temperature drops to 20°C or less (5). In Akkeshi Bay, Hokkaido, plankton of this species appears in July when the water temperature exceeds 10°C and disappears in November when the temperature drops to below 10°C (57). Why don't they appear as plankton throughout the year in Onagawa Bay, in spite of their ability to hatch over a wide temperature range from 5 to 20°C ? Seven possible causes can be pointed out. Firstly, we assume that *Evadne nordmanni* can hatch throughout the year but cannot sustain a plankton population. 1) Food shortage. The important food items of the species are the diatoms, *Skeletonema costatum*, *Chaetoceros* spp., *Thalassiosira allenii*, *Cyclotella meneghiniana*, *Coscinodiscus* spp., *Navicula* spp., *Thalassiothrix*

sp., dinoflagellates, *Prorocentrum triestinum*, *P. dentatum*, *Ceratium kofoidii*, *Ceratium furca*, *Peridinium* spp., *Gonyaulax excavata*, tintinnids, *Tintinnopsis* spp., and copepod eggs and nauplii (6, 20, 44, 58, 59). If the resting eggs hatch when these food organisms are scarce, newly hatched young will die. 2) Predation. *Evadne nordmanni* is reported to be preyed on by chaetognaths and cnidarians (20). Hatched plankton may be eliminated by heavy predation pressure of these predators. 3) Defeated by the animals in the same niche in the competition for food. Cladoceran species are reported to have food organisms in common (44). *Evadne nordmanni* may be defeated by *Podon polyphemoides*, *Podon leuckarti* and *Penilia avirostris* in the competition for food during the period when the plankton of *Evadne nordmanni* does not appear. 4) *Evadne nordmanni* may not be able to reproduce by parthenogenesis because of the low temperature.

Secondly, we assume that hatching does not take place. 5) Resuspension of the bottom sediment does not occur. Uye *et al.* (60) reported that resting eggs of copepods can hatch when they are on the surface of the bottom sediment, but the hatching was inhibited when buried in the sediment. So, effective resuspension may not have occurred for the *Evadne nordmanni* resting eggs to hatch. 6) Lowered hatching rate during the period when the plankton population cannot develop. This hypothesis was proven invalid by our experiment showing that there is no significant difference in the hatching rate between August and November. 7) Increase in development time may lower the hatching rate. There was a significant difference in the development time among different temperatures in the present study. If resting eggs stay longer on the bottom sediment, the possibility of predation and being buried in the sediment increases. Therefore, the lower the temperature, the lower the possibility of survivorship and hatching of resting eggs. Development time was longer in November than in August. Because the incubation conditions were the same, the environmental conditions that the resting eggs experienced prior to the incubation, such as day length and cumulative temperature, may be responsible for the difference.

This last hypothesis can explain the absence of plankton of this species in the period from August to next June in Onagawa Bay. Low temperature does not inhibit hatching but decreases the apparent hatching rate. Therefore, if the resting eggs can stay on the mud surface long enough to develop at low temperatures, they do hatch. After hatching, whether they can maintain a plankton population depends on other factors such as food availability, and the abundance of predators and animals that share the same niche. If these factors are favorable, *Evadne nordmanni* can develop a plankton population even in February as exemplified by Uye (33) in Onagawa Bay. It is reported that *Bosmina longispina* could hatch in the period when the plankton population could not develop in the Baltic Sea (61). To better understand the seasonal variation in the

Evadne nordmanni population, it is necessary to study factors affecting the possibility of maintaining a plankton population such as seasonal variation in food availability and the abundance of predators and animals that share the same niche.

The reason why *Evadne nordmanni* selected the reproductive strategy to hatch throughout the year may be to establish a plankton population making use of a scant possibility, if any, and perform sexual reproduction. To increase the possibility of survival, cladocerans have special functions: individuals hatched out from resting eggs have a larger size than those from parthenogenesis and are superior in swimming and feeding ability which leads to a higher survival rate. Newly hatched young have yolk substances in their body and again have a higher survival rate (25). The fact that the half hatching period becomes longer with decreasing temperature means that the resting eggs hatch for a longer period at low temperatures. This prolonged hatching period can be an adaptive feature (62). Newly hatched young, if hatched simultaneously at low temperature, cannot develop the plankton population because of food scarcity and reduced physiological activities. However, if the hatching takes place asynchronously over a longer period, some young can have better chances of survival than others.

Dinoflagellates, *Scrippsiella* spp. in Onagawa Bay, are reported to have a similar survival strategy (56). High germination rates or synchronized mass germination of the cysts is not necessary for bloom initiation. The presence of vegetative cells in the water column is important for vegetative growth. However, the bloom is dependent on vegetative growth rather than recruitment of newly germinated cells.

Acknowledgements

We are greatly indebted to Prof. A. Taniguchi and other members of the Laboratory of Aquatic Ecology, Tohoku University. The authors are also grateful to technical staff of the Education and Research Center of Marine Bioresources at Onagawa, Tohoku University, for their help with the samplings.

References

1) Schram, F.R., *Crustacea*. Oxford Univ. Press, New York, 606 pp. (1986).
2) Korovechinsky, N.M., How many species of Cladocera are there? *Hydrobiologia*, **321**: 191-204 (1996).
3) Dolgopolskaya, M.A., Morskie Cladocera Cernogo Morya (Marine Cladocera in the Baltic Sea). *Tr. Sevastop. Biol. Stn.*, **120**: 27-75 (1958) (in Russian).
4) Della Croce, N., Cladocera. *Cons. Intern. l'Explor. Mer, Zooplankton Sheet*, **143**: 1-4 (1974).

5) Onbé, T., Studies on the ecology of marine cladocerans. *J. Fac. Fish. Anim. Husb. Hiroshima Univ.*, **13**: 83-179 (1974) (in Japanese with English summary).
6) Bainbridge, V., Some observations on *Evadne nordmanni* Loven. *J. Mar. Biol. Ass. U.K.*, **37**: 349-370 (1958).
7) Kim, S.W. and Onbé, T., Observations on the biology of the marine cladoceran *Podon schmackeri*. *J. Crust. Biol.*, **9**: 54-59 (1989).
8) Gieskes, W.W.C., Ecology of the Cladocera of the North Atlantic and the North Sea, 1960-1967. *Netherlands J. Sea Res.*, **5**: 342-376 (1971).
9) Della Croce, N. and Venugopal, P., *Penilia avirostris* Dana in the Indian Ocean (Cladocera). *Int. Rev. Gesamten Hydrobiol.*, **58**: 713-721 (1973).
10) Onbé, T., The biology of marine cladocerans in a warm temperate water. *Proc. Symp. Warm Water Zoopl. Spec. Publ. UNESCO/NIO (Goa)*, 383-398 (1977).
11) Yoo, K.I. and Kim, S.W., Seasonal distribution of marine cladocerans in Chinhae Bay, Korea. *J. Oceanol. Soc. Korea*, **22**: 80-86 (1987).
12) Lebour, M.V., Feeding habits of some young fish. *J. Mar. Biol. Ass. U. K.*, **12**: 9-47 (1919).
13) Lebour, M.V., The food of young fish. *J. Mar. Biol. Ass. U. K.*, **12**: 261-324 (1920).
14) Lebour, M.V., The food of planktonic organisms. *J. Mar. Biol. Ass. U.K.*, **12**: 644-677 (1922).
15) Marshall, S.M., Nicholls, A.G. and Orr, A.P., On the growth and feeding of the larval and post-larval stages of the Clyde herring. *J. Mar. Biol. Ass. U. K.*, **22**: 245-267 (1937).
16) Wickstead, J.H., The cladocera of the Zanzibar area of the Indian Ocean, with a note on the comparative catches of two plankton nets. *East African Agricul. Forest. J.*, **29**: 164-172 (1963).
17) Anraku, M. and Azeta, M., The feeding habits of larvae and juveniles of the yellowtail, *Seriola quinqueradiata* Temminck et Schlegel, associated with floating seaweeds. *Bull. Seikai Reg. Fish. Res. Lab.*, **33**: 15-45 (1965) (in Japanese).
18) Brakio, V.D., K biologii zimuyushchikh yaits *Penilia avirostris* DANA. (Biology of the winter eggs of *Penilia avirostris* DANA). *Dokl. Akad. Nauk SSSR*, **164**: 1187-1189 (1965) (in Russian).
19) Selvakumar, R.A., Cladoceran swarm in relation to mackerel fishery along the west coast of India. *Current Science*, **39**: 481-482 (1970).
20) Gieskes, W.W.C., *The cladocera of North Atlantic and the North Sea : Biological and ecological studies*. Ph. D. thesis, McGill University, Montreal, 204 pp. (1970).
21) Ishii, H. and Tanaka, F., Food and feeding of *Aurelia aurita* in Tokyo Bay with an analysis of stomach contents and a measurement of digestion times. *Hydrobiologia*, **451**: 311-320 (2001).
22) Onbé, T., Occurrence of the resting eggs of a marine cladoceran, *Penilia avirostris* Dana on the sea-bottom. *Bull. Japan. Soc. Sci. Fish.*, **38**: 305 (1972).
23) Onbé, T., Preliminary note on the biology of the resting eggs of marine cladocera. *Bull. Plankt. Soc. Jap.* **20**: 74-77 (1973).
24) Onbé, T., Distribution of the resting eggs of marine cladocerans in the bottom sediment of Ise Bay and Uragami Inlet, central Japan.

Bull. Japan. Soc. Sci. Fish., **44**: 1053 (1978).

25) Onbé, T., Some aspects of the biology of resting eggs of marine cladocerans. p. 41-55. In: Wenner, A., Kuris, A. (eds) *Crustacean Egg Production*, Crustacean Issues. 7. A.A. Balkema, Rotterdam (1991).

26) Marcus, N.H., Calanoid copepod, cladoceran, and rotifer eggs in sea-bottom sediment of the northern Californian coastal waters: identification, occurrence and hatching. *Mar. Biol.*, **105**: 413-418 (1990).

27) Marcus, N.H., Lutz, R., Burnett, W. and Cable, P., Age, viability, and vertical distribution of zooplankton resting eggs from an anoxic basin: evidence of an egg bank. *Limnol. Oceanogr.*, **31**: 206-210 (1994).

28) Viitasalo, M. and Katajisto, T., Mesozooplankton resting eggs in the Baltic Sea: identification and vertical distribution in laminated and mixed sediments. *Mar. Biol.*, **120**: 455-465 (1994).

29) Onbé, T., Seasonal fluctuations in the abundance of populations of marine cladocerans and their resting eggs in the Inland Sea of Japan. *Mar. Biol.*, **87**: 83-88 (1985).

30) Iwasaki, H., Takami, A. and Onbé, T., Studies on the cultivation of marine Cladocera-I. Factors affecting the hatch of resting eggs. *Bull. Plankt. Soc. Jap.*, **24**: 62-65 (1977).

31) Onbé, T., Mitsuda, T. and Murakami, T., Some notes on the resting eggs of the marine cladoceran *Podon polyphemoides*. *Bull. Plankt. Soc. Jap.*, **24**: 9-17 (1977).

32) Takami, A., Iwasaki, H. and Nagoshi, M., Studies on the cultivation of marine cladocera. II. Cultivation of *Penilia avirostris*. *J. Fac. Fish., Pref. Univ. Mie*, **5**: 47-68 (1978).

33) Uye, S., Seasonal cycles in abundance of major holoplankton in the innermost part of Onagawa Bay, Northeast Japan. *J. Fac. Applied Biol. Sci., Hiroshima Univ.*, **21**: 1-10 (1982).

34) Taniguchi, A., The sea and the plankton-12. Physical Environmental Factors-7. *Aquabiology.* **10**: 82-89 (1988) (in Japanese).

35) Motoda, S., North Pacific Standard Plankton Net. *Inform. Bull. Planktol. Jap.* No. 4, 13-15 (1957) (in Japanese).

36) Onbé, T., Sugar flotation method for sorting the resting eggs of marine cladocerans and copepods from sea-bottom sediment. *Bull. Japan. Soc. Sci. Fish.*, **44**: 1411 (1978).

37) Marcus, N.H., Recruitment of copepoda nauplii into the plankton: importance of diapause egg and benthic processes. *Mar. Ecol. Prog. Ser.*, **15**: 47-54 (1984).

38) Onbé, T., Cladocera. p. 609-624. In: Chihara, M., Murano, M. (eds) *An Illustrated Guide to Marine Plankton in Japan*. Tokai University Press, Tokyo (1997) (in Japanese).

39) Aizawa, Y., Plankton of Otsuchi Bay. *Gekkan Kaiyo Kagaku* (*Marine Sciences Monthly*), **12**: 625-633 (1980) (in Japanese).

40) Terazaki, M., Zooplankton in Otuchi Bay. *Otsuchi Mar. Res. Cent. Rep., Univ. Tokyo*, No. 6: 1-5 (1980) (in Japanese).

41) Gieskes, W.W.C., The succession of two *Podon* (Crustacea, Cladocera) species in the North Sea. *Netherlands J. Sea Res.*, **5**: 377-381 (1971).

42) Erikkson, S., The occurrence of marine Cladocera on the west coast of

Sweden. *Mar. Biol.*, **26**: 319-327 (1974).
43) Onbé, T. and Ikeda, T., Marine cladocerans in Toyama Bay, southern Japan Sea: seasonal occurrence and day-night vertical distribution. *J. Plankt. Res.* **17**: 595-609 (1995).
44) Kim, S.W., Onbé, T. and Toon, Y.H., Feeding habits of marine cladocerans in the Inland Sea of Japan. *Mar. Biol.*, **100**: 313-318 (1989).
45) Madhupratap, M., Nehrig, S. and Lenz, J., Resting eggs of zooplankton (Copepoda and Cladocera) from the Kiel Bay and adjacent water (southwestern Baltic). *Mar. Biol.*, **125**: 77-87 (1996).
46) Marcus, N.H. and Schmidt-Gengenbatch, J., Recruitment of individuals into the plankton: The importance of bioturbation. *Limnol. Oceanogr.*, **31**: 206-210 (1986).
47) Kasahara, S., Onbé, T. and Kamigaki, M., Calanoid copepod eggs in the sea-bottom muds. III. Effect of temperature, salinity and other factors on the hatching of resting eggs of *Tortanus forcipatus*. *Mar. Biol.*, **31**: 31-35 (1975).
48) Uye, S., Yoshiya, M., Ueda, K. and Kasahara, S., The effect of organic sea-bottom pollution on survivability of resting eggs of neritic calanoids. *Crustaceana, Suppl.*, **7**: 390-403 (1984).
49) Albertsson, J. and Leonardsson, K., Impact of burrowing deposit-feeder, *Monoporeia affinis*, on viable zooplankton resting eggs in the northern Baltic Sea. *Mar. Biol.*, **136**: 611-619 (2000).
50) Carvalho, G.R. and Wolf, H.G., Resting eggs of lake-*Daphnia*. I. Disrtibution, abundance and hatching of eggs collected from various depths in lake sediments. *Freshwat. Biol.*, **22**: 459-470 (1989).
51) Murakami, Y., Studies on the winter eggs of the water flea, *Moina macrocopa* STRUS. *J. Fac. Fish. Anim. Husb., Hiroshima Univ.*, **3**: 323-346 (1961).
52) Pancella, J.R. and Stross, R.G., Light-induced hatching of *Daphnia* resting eggs. *Chesapeake Sci.*, **4**: 135-140 (1963).
53) Stross, R.G., Light and temperature requirements for diapause and development and release in *Daphnia*. *Ecology*, **47**: 368-374 (1966).
54) Uye, S., Development of neritic copepoda *Acartia clausi* and *A. steueri*. I. Some environmental factors affecting egg development and nature of resting eggs. *Bull. Plankt. Soc. Jap.*, **27**: 1-9 (1980).
55) Onbé, T., Mass culture of marine cladocerans. *Report of the special feasibility study on Agriculture and Fisheries*, 25-38 (1976).
56) Ishikawa, A. and Taniguchi, A., Contribution of benthic cysts to the population dynamics of *Scrippsiella* spp. (Dinophyceae) in Onagawa Bay, northeast Japan. *Mar. Ecol. Prog. Ser.*, **140**: 169-178 (1996).
57) Koyama, A., *Studies on zooplankton community in Akkeshi Bay, Hokkaido*. Ph. D. thesis, Hokkaido Universtiy (1979) (in Japanese).
58) White, A.W., Recurrence of kills of Atlantic herring (*Clupea harengus harengus*) caused by dinoflagellate toxins transferred through herbivorous zooplankton. *Can. J. Fish. Aquat. Sci.*, **37**: 2262-2265 (1980).
59) Eofonoff, P.W., *Marine Cladocerans in Narragansett Bay*. Ph. D. Dissertation, University of Rhode Island, Kingston, USA, 54 pp. (1994).
60) Uye, S., Kasahara, S. and Onbé, T., Calanoid copepod eggs in sea-bottom muds. IV. Effects of some environmental factors on the hatching of

resting eggs. *Mar. Biol.*, **51** : 151-156 (1979).
61) Kankaala, P., Resting eggs, seasonal dynamics, and production of *Bosmina longispina maritime* (P.E. Muller) (Cladocera) in the northern Baltic proper. *J. Plankt. Res.*, **5** : 53-69 (1983).
62) Hanazato, T., *Cladocerans, Their Ecology and Environmental Problems of Lakes*. University of Nagoya Press, 230 pp. (1998) (in Japanese).