

琵琶湖におけるEodiaptomus japonicus(橈脚亜綱:カラヌス目)の個体数密度と分布

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Abundance and Distribution of *Eodiaptomus japonicus* (Copepoda : Calanoida) in Lake Biwa^{1), 2)}

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Abstract

Eodiaptomus japonicus was collected in the north basin of Lake Biwa at approximately weekly intervals from 1984 to 1986. Within the study area the horizontal distribution of the *E. japonicus* population was almost uniform. The population was distributed in the epilimnion during the stagnation period, and throughout the water column during the circulation period. No diel vertical migration was observed. Nauplii were distributed in layers at shallower depths than were those of copepodites. At the end of the stagnation period, adults were distributed in the same layers as nauplii. Eggs were laid throughout the year, except during the early circulation period. Small adult females and low egg production were observed in summer or autumn. Juvenile mortality was high in the spring of every year and in the summers of 1984 and 1985. Mortality was low in autumn. Individuals which achieved adulthood in November and December overwintered and laid eggs the following year.

The small freshwater calanoid copepod, *Eodiaptomus japonicus* (Burckhardt), is endemic to Japan and is widely distributed in lakes, reservoirs, ponds and brackish-water ponds (MIZUNO 1984). In Lake Biwa, *E. japonicus* is the sole calanoid species and a dominant zooplankton (NARITA & OKAMOTO 1984), which makes Lake Biwa a suitable site for studying the ecology of this species. Little work has previously been performed on its life history. In the present study, seasonal changes in the abundance of *E. japonicus*, and its horizontal and vertical distribution patterns were investigated in the north basin of Lake Biwa by a quantitative sampling regime conducted weekly over a 3-year period.

Materials and Methods

Regular Survey

Samples of *E. japonicus* were collected at Station O in the north basin of Lake Biwa (Fig. 1) at 10:00 hours at approximately weekly intervals (less frequently from December to April) on 102 dates from January 1984 to December 1986. Following capture with a Schindler-Patalas trap (capacity, 40l), samples were concentrated by filtration through a plankton net (mesh size, 40 μ m), anaesthetized with ice cubes or carbonated water, and fixed with 6% (final concentration) formalin. Duplicate samples were taken at 5-9 (mean, 6.4) depths at intervals of 2.5-5 m (10-20 m during the circulation period). No samples were taken from the hypolimnion during the stagnation period because preliminary surveys had shown few individuals to be there.

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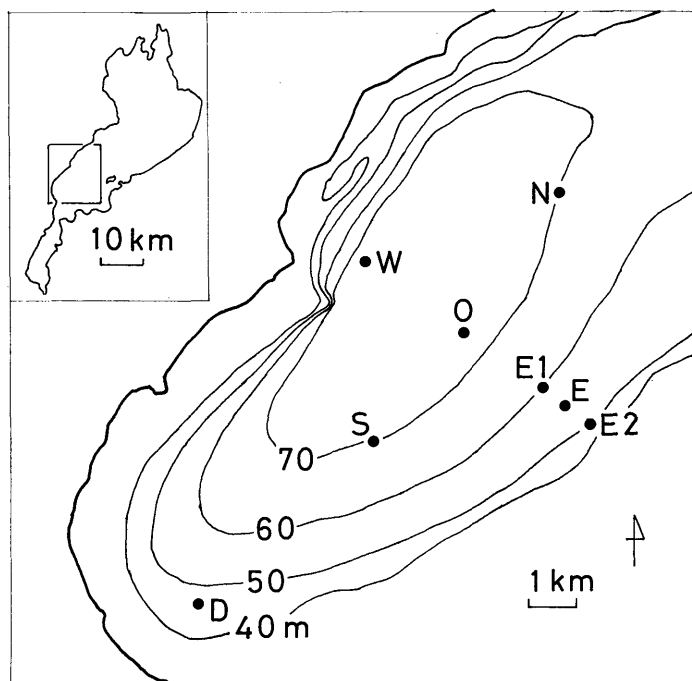


Fig. 1. Lake Biwa and sampling stations.

Water temperature at each depth was also recorded.

Each sample was concentrated to 20 ml (40 ml or more when *E. japonicus* was abundant) and 3 subsamples of 1 ml each were taken with a large mouth pipette. The copepodites of *E. japonicus* and copepod nauplii, including cyclopoids, were counted with an inverted microscope.

After combining duplicate samples, copepodites (CI-CVI) were staged for at least 50 individuals from each of 1-7 (mean, 4.0) depth samples with an inverted microscope. Adults and CV were sexed, and the eggs carried by females were counted. The prosome length of copepodites (only adults in 1985 and 1986) was measured with an eyepiece micrometer. After combining data from all depths, the mean prosome length ($n \geq 10$), mean clutch size ($n \geq 10$), proportion of egg carrying females ($n \geq 19$), and proportion of females ($n \geq 40$) were calculated, as was Kendall rank correlation coefficient, τ , between clutch size and the body length of each egg carrying female ($n \geq 30$).

Nauplii (NI-NVI) were identified and staged for at least 50 individuals from each of 1-5 (mean, 1.5) depth samples with a differential interference microscope.

Abundance in unit water column was calculated assuming that abundance in unit volume changed linearly between successive depths. When the abundance of the *E. japonicus* population exceeded 10^6 animals m^{-2} , quartile depths were calculated. These divided the abundance into 4 equal parts, the second quartile depth being regarded as the median depth. Similar adjustments were made for nauplii and each copepodite stage when their abundance exceeded

10^5 animals m^{-2} .

Horizontal Distribution Survey

To study the horizontal distribution of *E. japonicus*, samples were collected at Stations W, O, E, N and S on May 29, 1985, and at Stations W, O, E1 and E2 on October 28, 1985, and July 1 and September 16, 1986 (Fig. 1). Methods were as in the regular survey, but a closing net (mesh size, $70\mu m$; mouth diameter, 15 cm) was used in May 1985.

Diel Vertical Distribution Survey

To study the diel change in the vertical distribution of *E. japonicus*, samples were collected at Station D (Fig. 1) at noon, dusk and dawn on August 30-31 and October 28-29, 1983, and January 25-26 and May 24-25 (excluding dusk), 1984. A single sample was taken at each depth. On September 3-4, 1985, duplicate samples were taken with the closing net at 12:00, 17:00, 19:00, 23:00, 04:00 and 07:00 hours (sunset, 18:20; sunrise, 05:30). Otherwise, methods were as in the regular survey.

Results

1. Horizontal Distribution

In May 1985, the *E. japonicus* population was less abundant at Station E than at the other stations (Fig. 2). In July 1986, early nauplii were more abundant at Stations E1 and E2 than at Station O. Excepting these occasions, the abundance and stage composition of the population was similar at all stations.

2. Vertical Distribution

The lake water was fully circulated during winter, and gradually stratified from April to May (Fig. 3). Thermal stratification was stable from June to September, and the lake water was mixed from October to December. The seasonal changes in the vertical distribution of the *E. japonicus* population were closely related to the water structure (Fig. 3). The population was confined to the epilimnion during the stagnation period, dispersed into deeper layers by water

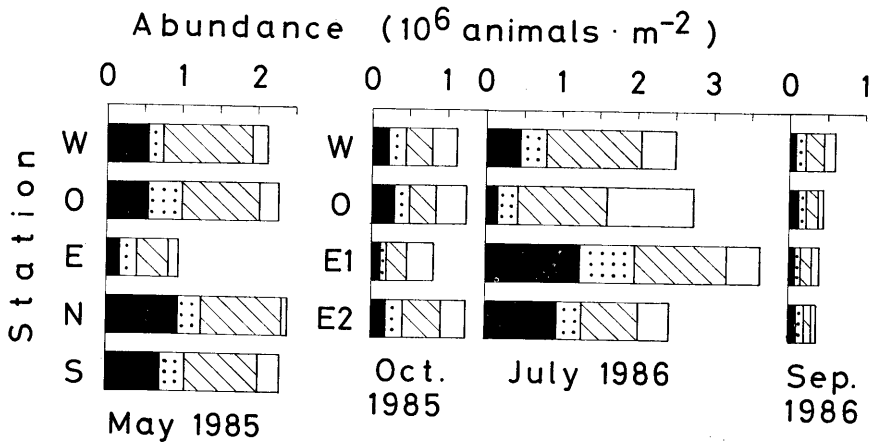


Fig. 2. Horizontal distribution of *Eodiaptomus japonicus* NI-NIII (solid), NIV-NVI (dotted), CI-CIII (shaded) and CIV-CVI (open).

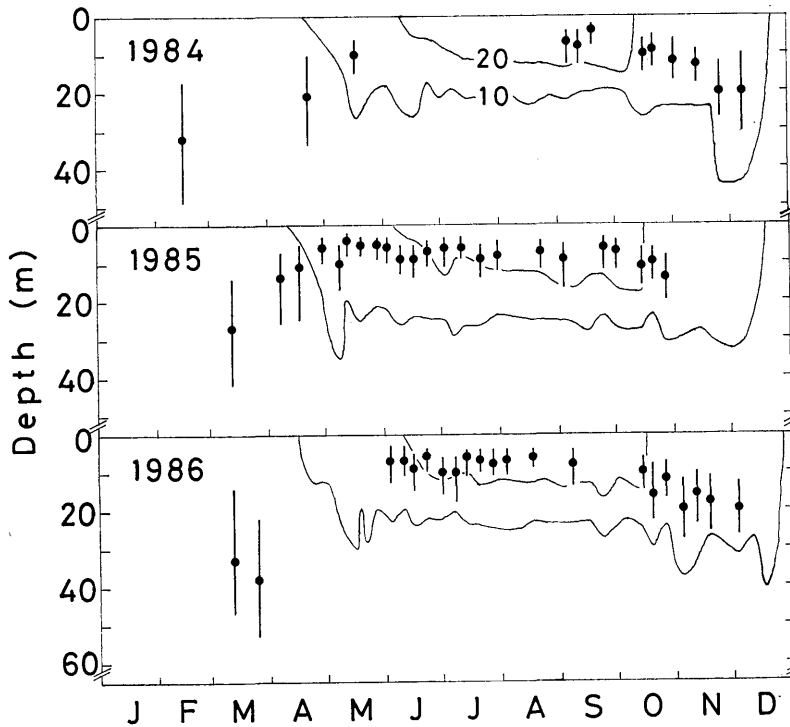


Fig. 3. Seasonal changes in median depth (plots) and interval from the first to third quartile depth (bars) of the *Eodiaptomus japonicus* population. Lines show isotherms in °C.

TABLE 1. MEDIAN DEPTHS (m) OF NAUPLII AND EACH COPEPODITE STAGE OF *Eodiaptomus japonicus*. VALUES ARE MEANS \pm SD WITH NUMBER OF DATA IN PARENTHESES.

	Nauplii	CI	CII	CIII	CIV	CV	CVI
June-August	5.5 \pm 1.3(33)	7.0 \pm 2.9(7)	9.3 \pm 2.8(6)	10.4 \pm 3.5(8)	10.6 \pm 3.0(11)	9.2 \pm 2.2(8)	9.6 \pm 2.7(17)
October	8.7 \pm 2.6(11)	10.3 \pm 1.9(9)	12.4 \pm 3.8(8)	14.7 \pm 2.7(9)	18.3 \pm 2.3(7)	21.1 \pm 1.8(4)	9.0 \pm 2.7(8)
November	13.6 \pm 4.1(9)	15.3 \pm 3.9(3)	14.6 \pm 4.3(5)	16.7 \pm 4.1(6)	17.7 \pm 3.9(7)	20.4 \pm 4.4(8)	19.8 \pm 5.2(7)

mixing, and distributed throughout the water column during the circulation period.

During the stagnation period, the median depth at which nauplii were encountered was less than that of CII and the later stages (Table 1). CI showed an intermediate value. In October, the median depth at which stages were encountered increased respectively from nauplii to CV, but adults showed almost the same values as nauplii. In November, adults were again distributed in deeper layers than nauplii. Only slight differences in the median depth were evident among nauplii and between sexes.

Figure 4 shows the diel changes in the vertical distribution of nauplii and copepodites at Station D. Although their abundance fluctuated, the vertical profile showed no diel change. Neither nauplii nor copepodites showed a clear diel vertical migration.

3. Body Length

The body length of adult females was small from September to October 1984, and from July to September 1986 (Fig. 5). The high water temperature in summer did not always result in a small body size (Fig. 3). The seasonal changes in body length of the earlier stages preceded those of adult females (Fig. 5). Males were smaller than females, the difference being 0.12 ± 0.02 mm (mean \pm SD, $n=81$) in adults and 0.07 ± 0.02 mm ($n=11$) in CV.

4. Egg Production

Few eggs were laid in November and December each year (Fig. 6). Both clutch size and the proportion of egg carrying females were small in September 1984 and 1985, and in August 1986. In September 1984 and August 1986, the body length of adult females was also small (Fig. 5). A significant correlation was found between clutch size and the body length of each egg carrying female on 6 out of 16 dates tested ($p < 0.01$; $\tau = 0.02-0.52$, mean = 0.24). The low egg production was probably a consequence of the small body size of adult females.

5. Population Dynamics

In 1984 and 1985, most individuals achieved adulthood before January, began to lay eggs in February, and survived until May (Figs. 7 and 8). The overwintering individuals in 1986 showed a similar cycle one month earlier (Fig. 9). The greatest number of overwintering adults and eggs laid in spring was seen in 1985.

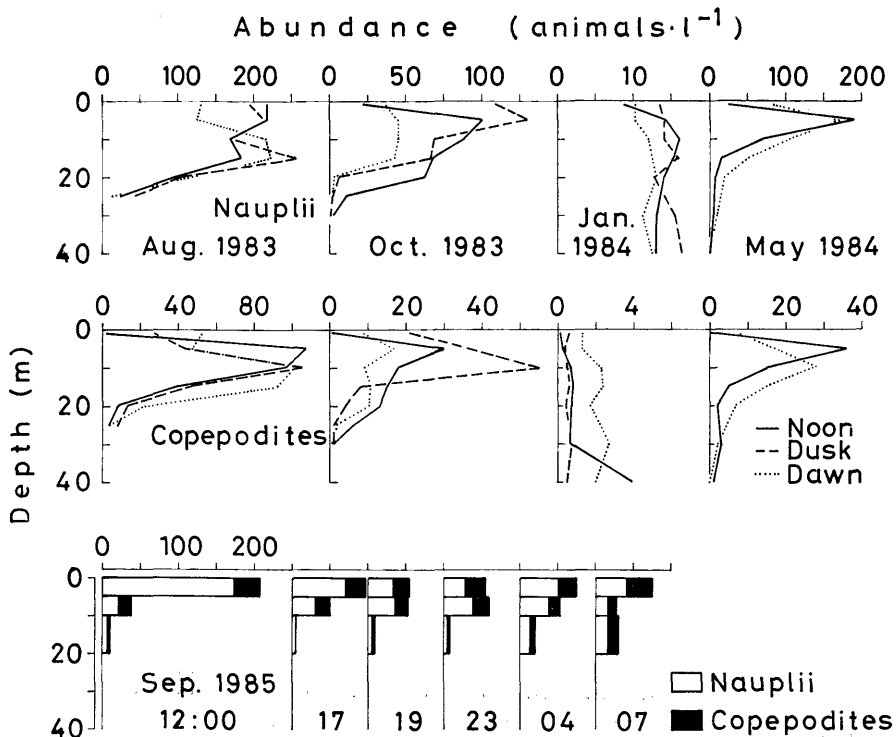


Fig. 4. Vertical distribution of *Eodiaptomus japonicus* nauplii and copepodites at Station D.

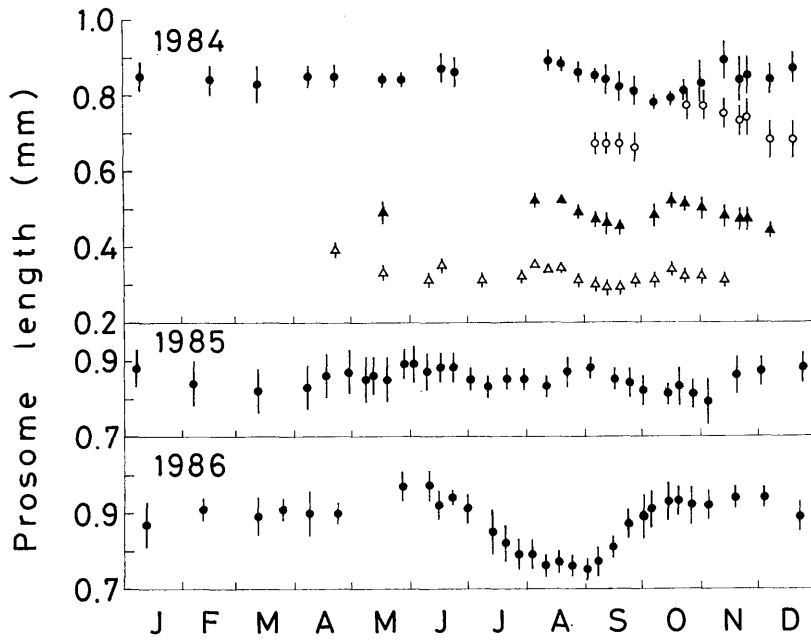


Fig. 5. Seasonal changes in prosome length (plots, mean; bars, SD) of *Eodiaptomus japonicus* adult females (solid circles), CV females (open circles), CIII (solid triangles) and CI (open triangles).

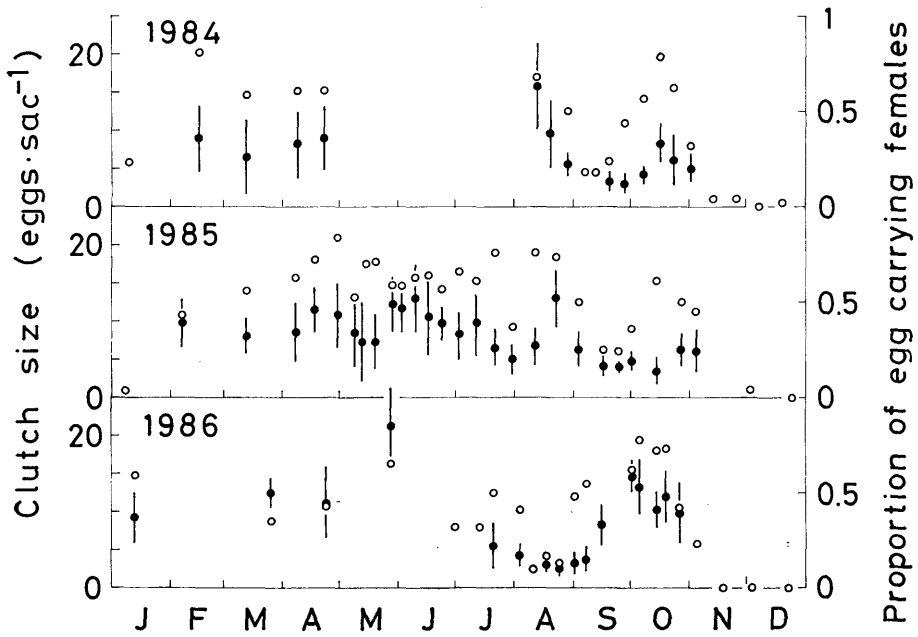


Fig. 6. Seasonal changes in clutch size (solid circles, mean; bars, SD) and proportion of egg carrying females (open circles) of *Eodiaptomus japonicus*.

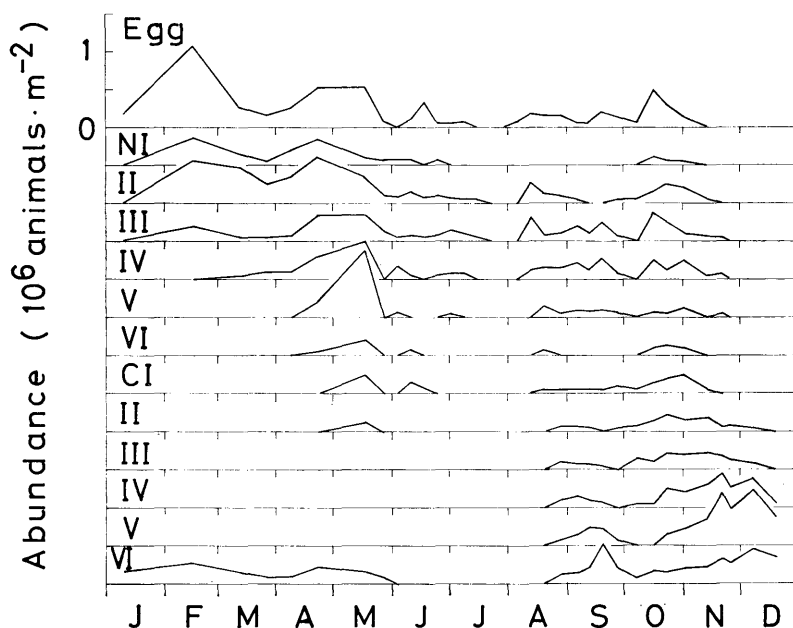


Fig. 7. Seasonal changes in abundance of *Eodiaptomus japonicus* in 1984.

In spring, many individuals survived to NV in 1984, and NIV in 1986, but most of them died during the later developmental stages (Figs. 7 and 9). In the spring of 1985, the abundance of early nauplii was high, but this decreased from NIV onward (Fig. 8). High spring mortality was seen in the late nauplius and early copepodite stages every year. The greatest number of individuals to achieve adulthood in spring was seen in 1985.

In every year, individuals born in spring laid eggs in June of that year (Figs. 7, 8 and 9). In 1984 and 1985, high summer mortality rates were seen. In 1984, mortality occurred mainly during the early stages, whereas in 1985 it occurred in NIV and the later stages. In 1986, however, juvenile mortality was low, and large numbers of individuals achieved adulthood in July and August.

High egg production was seen from August to October every year (Figs. 7, 8 and 9). Mortality was low in autumn and those individuals which achieved adulthood in November and December overwintered and laid eggs the following year.

The proportion of females fluctuated, but was near 0.5 on most dates (Fig. 10). The life cycle was probably the same in both sexes.

Discussion

The horizontal distribution of the *E. japonicus* population was sometimes heterogenous at eastern shallower stations (Figs. 1 and 2). For *E. japonicus*, the environment at the margin of the pelagic area may have differed from that within the pelagic area, where the population was uniformly distributed (Fig. 2). Therefore, horizontal migration was negligible as a cause of the seasonal changes in abundance of *E. japonicus* at Station O.

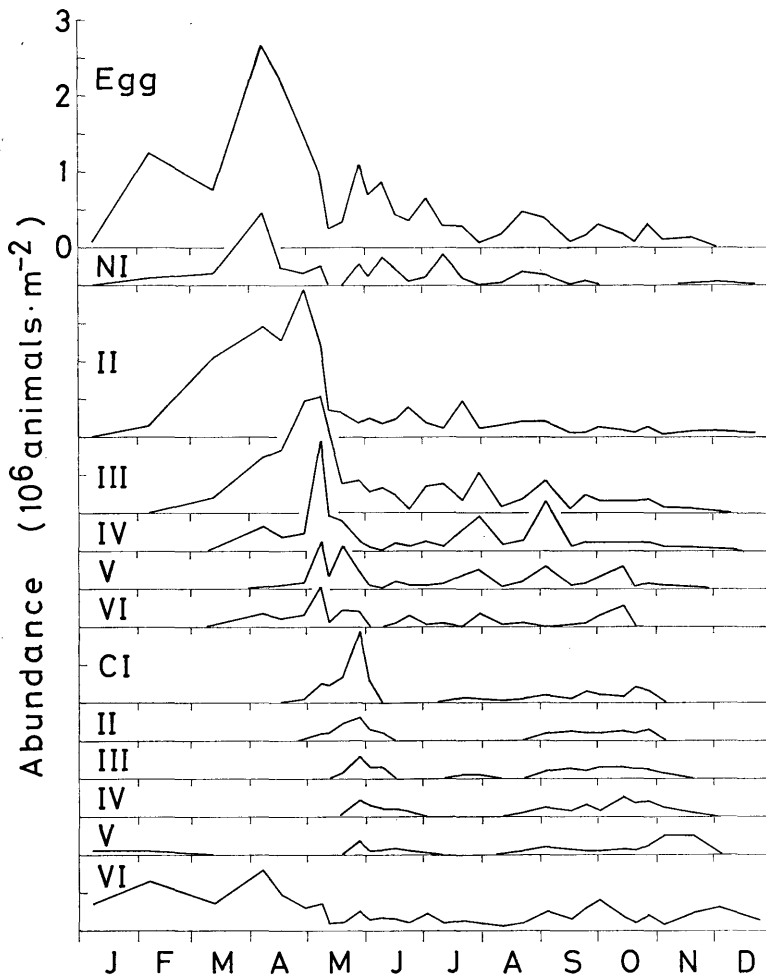


Fig. 8. Seasonal changes in abundance of *Eodiaptomus japonicus* in 1985.

A simple cohort analysis was not applicable to the *E. japonicus* population in Lake Biwa because its generations were overlapping (Figs. 7, 8 and 9). Furthermore, a quantitative population analysis requires a knowledge of the natural development time (HAIRSTON & TWOMBLY 1985). Therefore, only a qualitative analysis was made in the present study. A high mortality was seen in the late nauplius and early copepodite stages of *E. japonicus* in the spring of every year (Figs. 7, 8 and 9). In summer, mortality of these stages was high in 1984 and 1985, but not in 1986. Food shortage and predation are probable causes of the juvenile mortality. The findings of UCHIMA & HIRANO (1986) that, under conditions of low food concentration cyclopoid copepod larvae die while under development suggest that food shortage during the early stages may have caused the high juvenile mortality of *E. japonicus*.

In the study area, *Mesocyclops leuckarti* (Claus) was a dominant invertebrate predator in the spring of all years, and in the summers of 1984 and 1985 (KAWABATA unpubl.). The preda-

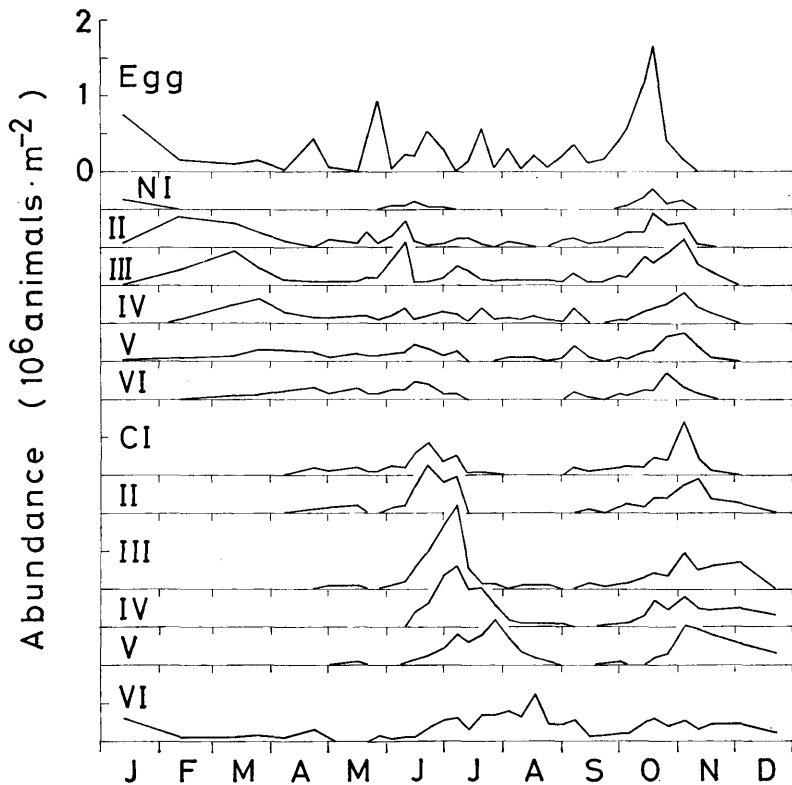


Fig. 9. Seasonal changes in abundance of *Eodiaptomus japonicus* in 1986.

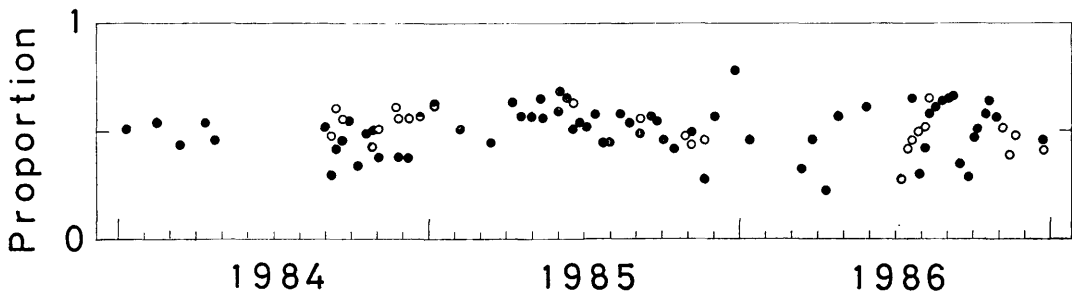


Fig. 10. Seasonal changes in proportion of females in adults (solid circles) and CV (open circles) of *Eodiaptomus japonicus*.

tion rate of *M. leuckarti* on calanoid copepods is highest on nauplii and lowest on adults (JAMIESON 1980) and therefore, *M. leuckarti* was probably an important predator on juvenile *E. japonicus*. Conversely, piscine planktivores prefer later stages of a copepod (BROOKS 1968, ZARET & SUFFERN 1976). For example, *Chaenogobius isaza*, a planktivorous fish in Lake Biwa, preys upon *E. japonicus* and selects only late copepodites (TAKAHASHI & HIDAKA 1984). It is probable that predation by fishes was negligible for juvenile *E. japonicus*.

In the present study, *E. japonicus* copepodites showed no clear diel vertical migration (Fig. 4), reflecting the findings of KIKUCHI (1930) and OKAMOTO (1984) on *E. japonicus* in the same study area. OKAMOTO (1984) calculated the daily carbon balance of *E. japonicus* copepodites and concluded that poor food conditions made them stay in the epilimnion throughout a day. Within the epilimnion, copepodites were distributed in deeper layers than nauplii (Table 1) and this may have been advantageous in terms of resource partitioning.

During the stagnation period, *E. japonicus* adults were distributed in layers about 4 m deeper than nauplii (Table 1), indicating that newly-hatched nauplii must have swum the distance upward. In October, *E. japonicus* was dispersed into deeper layers by water mixing (Fig. 3) and CV was distributed in layers at about 12 m deeper than that of nauplii (Table 1). Newly-hatched nauplii would have to swim a greater distance upward in October than in the stagnation period if adults were distributed in the same layers as CV. Actually, however, adults were distributed in almost the same layers as nauplii in October (Table 1). This behaviour reduced the energy loss of newly-hatched nauplii and probably contributed to high juvenile survival in autumn (Figs. 7, 8 and 9). In November, adult females laid no eggs (Fig. 6) and were again distributed in deeper layers (Table 1).

Both body length and clutch size are reported to become small at low food concentration in *Eudiaptomus graciloides* (WEGLENSKA 1971) and *Diaptomus dorsalis* (ELMORE 1982). In the present study also, clutch size was sometimes correlated with the body length of the egg carrying female. It is suggested that two factors bring about low egg production. One is food shortage after the maturation of females, and another is the small size of adult females resulting from a food shortage during their development. It seems that both factors operated in September 1984 and August 1986, and that only the former operated in September 1985 (Figs. 5 and 6).

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