

Diurnal Changing Patterns of the *In Situ* Size-Selective Feeding Activities of *Daphnia longispina hyalina* and *Eodiaptomus japonicus* in a Pelagic Area of Lake Biwa*

By

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Abstract. Size-selective feeding activities of *Daphnia longispina hyalina* and *Eodiaptomus japonicus* on natural phytoplankton composing of the large (150-70 μm), middle (70-25 μm) and small (<25 μm) fractions, which were separately labelled by ^{14}C , were examined 4-5 times a day in summer, autumn, 1976 and spring, 1977, under *in situ* condition. The changing patterns of feeding rates of both zooplankters showed no pronounced diurnal rhythm and had no relation to their vertical migration. From an economical viewpoint, or the daily carbon balance, a possible relationship between the nutritional state and the diurnal changing pattern of feeding activity in zooplankton was hypothesized. *Daphnia* selected consistently the small fraction, while *Eodiaptomus* exhibited the small selection in summer and autumn, and non-selection in spring. Such selective feedings were primarily consecutive throughout a day. The food-size selection of the zooplankters may be unchangeable during a day when the quantity and quality of food does not change diurnally.

1. Introduction

Diurnal variation in the feeding activity of zooplankton has a fundamental meaning for any attempt to understand energy flows and trophic interrelationships within pelagic environments. Since the work of Nauwerck (1959), the diurnal feeding activities of freshwater herbivores, particularly daphnids and diaptomid copepods, have been studied either through the direct measurement of their feeding and filtering rates under both *in situ* and laboratory conditions, or through the diurnal observation of their gut fullness in field. Consequently, the following three patterns of the diurnal feeding activities have been known; (1) unimodal change with the increased activities at night (Starkweather 1975; Hart 1977), (2) bimodal change with special rises of the activities either at twilight periods (Nauwerck 1959; Haney & Hall 1975; Duval & Geen 1976) or in no relation to such periods (Chisholm *et al.* 1975), and (3) no pronounced diurnal changes (Haney & Hall 1975; Gliwicz 1977). The existence of the diurnal changes has been discussed in relation to some factors such as endogenous rhythms (Starkweather 1975; Duval & Geen 1976), temperature (Chisholm *et al.* 1975), light (Haney & Hall 1975), vertical migration (Haney 1973; Haney & Hall 1975; Hart 1977) and nutritional history of zooplankters (Starkweather 1978).

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However, there is no satisfactory consistency among both these patterns and those relations to the endo- and exogenous factors. Such an inconsistency seems to be marked in the field works, in which no deep attention was given to the complexity of natural food condition and also to selective feeding of zooplankters.

Apparently, the small particles selection of *Daphnia* species is maintained by rejection against large particles (Gliwicz & Siedler 1980; Okamoto 1984), and the food selection of calanoid copepods is related to either rejection against unwanted particles or raptorial seizing of preferable ones (Alcaraz *et al.* 1980; Poulet & Marsot 1980). As pointed out by Vanderploeg (1981), feeding rate on natural phytoplankton must be measured together with food selection because of the strong interaction between these processes. However, there has been no field study treating of the whole phytoplankton assemblage, and in addition it has been hardly examined whether the selective feeding can be maintained over the 24-hour period.

Thus, the present study aims to examine the diurnal variations not only in the feeding rates but also in the size-selective feeding of dominant herbivorous zooplankters for a natural phytoplankton assemblage under *in situ* conditions in a pelagic area of Lake Biwa.

2. Materials and methods

Diurnal changes in size-selective feeding activities of *Daphnia longispina hyalina* (Cladocera) and *Eodiaptomus japonicus* (Calanoida Copepoda) for a natural phytoplankton assemblage were examined under the *in situ* condition in summer and autumn of 1976, and spring of 1977. The study site (44 m deep) was located in a pelagic area of the main basin of Lake Biwa (Fig. 1).

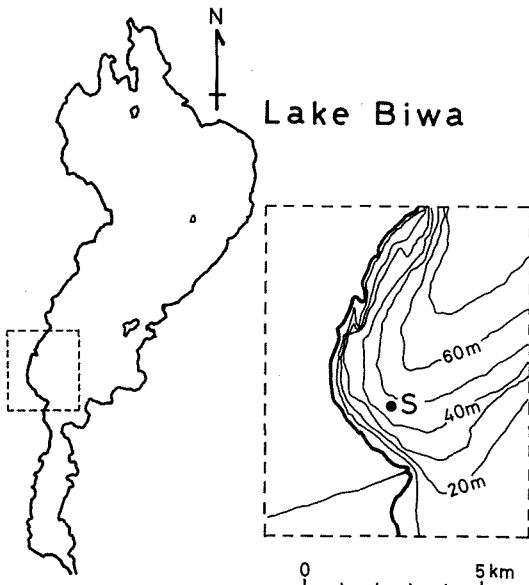


Fig. 1. The location of the experimental site (S) where the *in situ* feeding activities of zooplankters were determined.

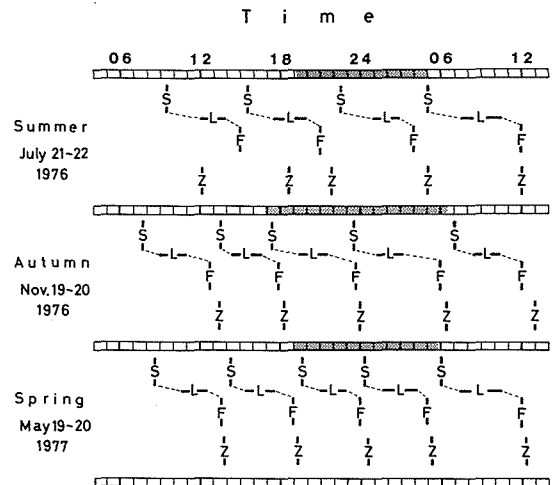


Fig. 2. Time schedule for the vertical zooplankton sampling (Z), the algal food sampling (S), the labelling of algae (L) and the performance of feeding (F).

Time schedule of the diurnal feeding experiment in the three seasons is shown in Fig. 2. The feeding rates of these zooplankters were measured at the depth of 5 m four times in a day in summer and five times in autumn and spring (Fig. 2). At the same time, vertical distribution of zooplankton population was examined with vertical hauls of a plankton net (67 μm aperture) in the summer experiment and with a Schindler-type zooplankton sampler (40 liter in volume with a net of 45 μm aperture) in the autumn and spring experiments.

Also to know the quantity of food resources for the zooplankters, the standing crop of phytoplankton was examined vertically at an interval of about 6 hours during a day. The phytoplankton sample was divided into three different size groups of <150 μm , <70 μm and <25 μm with screens, and chlorophyll *a* amount of each size group was measured by the method of Lorenzen (1967). Particulate organic carbon (POC) and nitrogen (PON) amounts of each group were also measured with a CHN analyzer (Yanako, MT-2 type). Amounts of chlorophyll *a* and POC in the three sized algal fractions of 150–70 μm (large), 70–25 μm (middle) and <25 μm (small) were calculated by subtraction between the respective two algal groups described above.

As environmental factors, water temperature and pH were measured vertically and transparency with a Secchi disk was measured. Light attenuation into the water was measured with an underwater-photometer except the spring experiment.

The procedure of the *in situ* feeding experiments is as follows. A natural phytoplankton assemblage from the 5 m depth was sampled about 5 hours before starting the feeding experiment. The phytoplankton assemblage was firstly filtered with a screen of 150 μm aperture to remove zooplankton. The filtrate was then divided into three different sized fractions consisting of 150–70 μm , 70–25 μm and <25 μm with screens. Each of these fractions was parted into the two portions; one is a group labelled with ^{14}C using $\text{NaH}^{14}\text{CO}_3$ solution and the other, a non-labelled. The two groups were incubated for about three hours under the saturated light condition. After incubation, one labelled fraction was mixed with the two other fractions non-labelled. Three kinds of food mixture in which either of the three size fractions was labelled with ^{14}C were prepared. The detailed process of preparation of the food mixture has been described by Okamoto (1984).

The zooplankters were collected at each experiment time by a vertical haul of a plankton net (150 μm aperture) from 10 m to the surface in the summer experiment, and at the 5 m depth by the Schindler-type zooplankton sampler (150 μm net) in both of the autumn and spring experiments. They were immediately put into a feeding glass chamber (1 liter in volume), in which the food mixture had been already prepared. Then, three feeding chambers with the respective food mixture were submerged immediately to the 5 m depth for 10 minutes. In summer, the experiments were carried out at the 15 m depth as well. After 10 minutes-feeding, the zooplankters were heat-killed and the radioactivities of them were measured following to the necessary process for treating them (cf. Okamoto 1984).

Feeding rate of each size class of *Daphnia* and *Eodiaptomus* was calculated on each of the three algal fractions in the way described by Okamoto (1984), but with no revision for rejection. Because, it was expected that the zooplankters in the lake might have been well acclimated to the natural food condition.

In summer, another *in situ* experiment using cultured alga (*Selenastrum* sp.) as food was

carried out eight times from July 22 to 23 in order to examine the diurnal change in the feeding rates in detail. The alga, being unicellular and approximately $8\ \mu\text{m}$ in size, appears to be favourable food for the zooplankters. The experimental time through a day and the food concentration of the cultured alga are shown in Table 1. The food concentration in each experiment was set up about $400\ \mu\text{gC}\cdot\text{l}^{-1}$, which corresponded to an almost half of the total concentration of the natural phytoplankton assemblage (cf. Table 2).

Table 1. The food concentrations of cultured algae used for the *in situ* feeding experiments on 22 and 23, July.

date	July 22					July 23			
time	16: 00	18: 30	21: 00	24: 00	03: 00	05: 00	07: 00	11: 30	
food concentrations ($\mu\text{gC}\cdot\text{l}^{-1}$)	363.2	403.4	394.1	390.8	413.6	359.7	422.7	368.4	

The experiment was carried out as follows; the cultured alga labelled with ^{14}C previously was suspended at a given concentration in a feeding chamber (1 liter in volume) filled with the filtered lake water (the Whatmann GF/C glass fiber filter was used for filtration of the lake water). The zooplankters sampled by a vertical haul from 10 m to surface were put into the chamber. Immediately, the chamber was put under the water depths of 5 m and 15 m. The feeding time and other treatment of organisms after the feeding experiment were same as those in the experiment using natural phytoplankton.

3. Results

3-1. Environmental conditions in the feeding experiments

Whenever the diurnal *in situ* feeding experiments were carried out, it was a fine day. Figure 3, showing the vertical distributions of water temperature and pH at the experimental site, suggests the water stratification in the summer experiment, the considerable vertical mixing of water in the autumn one, and a weak thermocline formation in the spring one.

The temperature at the experimental depth (5 m), where the feeding chambers were submerged, changed from 25°C in the daytime to 22°C in the nighttime in summer. However, it was constant during a day in autumn (14°C) and spring ($14\text{--}15^\circ\text{C}$).

In summer, the pH value changed diurnally from 8.4 to 9.2 in the epilimnion, tending to be slightly lower in the morning than in the afternoon. It was constant at 7.2 in autumn, and in a range of 7.4–7.6 in spring.

A Secchi disk reading changed from 4.1 m to 3.5 m in the summer experiment. The light extinction coefficient was calculated as $0.44\ \text{m}^{-1}$ in the former case and $0.55\ \text{m}^{-1}$ in the latter. In autumn, a Secchi disk depth of 6.2–6.5 m was recorded and the light extinction coefficient was approximately $0.30\ \text{m}^{-1}$. In spring when the light intensity in water was not measured, a Secchi disk recording was 3.9 m, suggesting that the extent of the light attenuation into water might be similar to that in summer.

Figure 4 shows the vertical distributions of chlorophyll *a* (chl. *a*) amount in the large ($150\text{--}170\ \mu\text{m}$), middle ($70\text{--}25\ \mu\text{m}$) and small ($<25\ \mu\text{m}$) fractions of phytoplankton assemblage

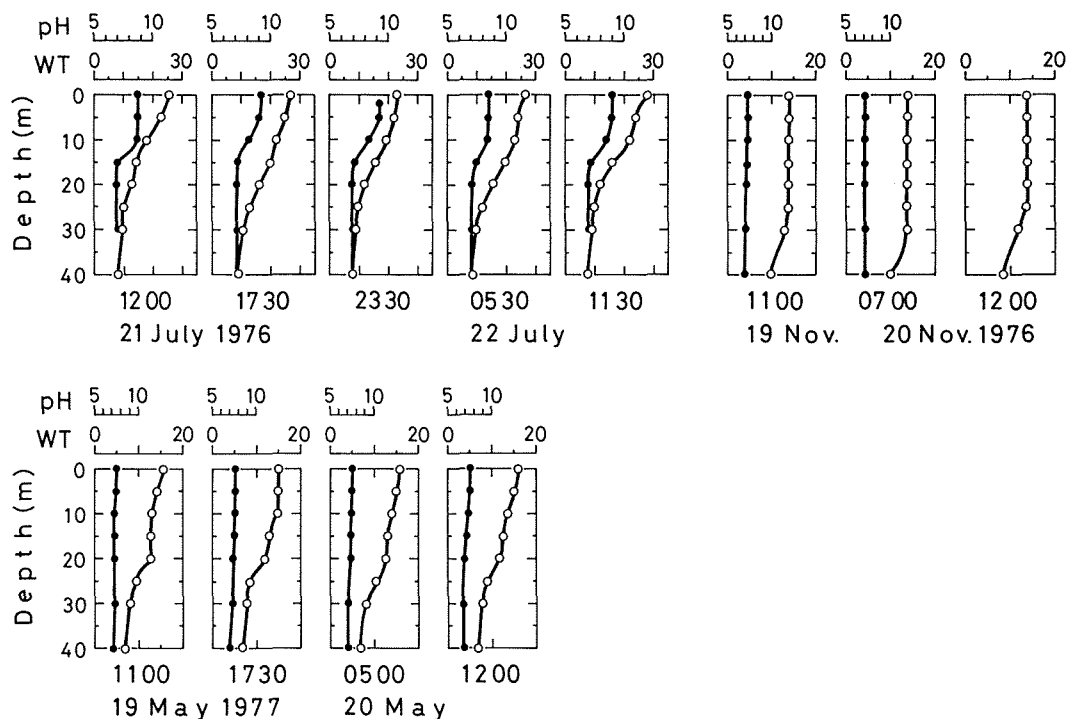


Fig. 3. Diurnal changes in the vertical distributions of water temperature (○) and pH (●) in the summer, autumn and spring experiments.

on the experimental day in summer, autumn and spring.

In summer, the chl. *a* amounts were very variable vertically, but not so much diurnally. A large amount of total chl. *a* was observed at the epilayer of 2.5 to 10 m. In the euphotic zone, 17% of the total chl. *a* amount on the daily average was occupied by the large fraction, 56.8% by the middle one, and 27.4% by the small one. The small fraction biomass was particularly high in the shallow layer above 5 m depth.

In the autumn phytoplankton assemblage, the chl. *a* amount in every fraction was nearly constant in the water stratum from surface to 35 m depth during a day. In the euphotic zone, the large fraction occupied 34.4% of the total chl. *a*, the middle one 23.4% and the small one 42.3%.

In spring, the chl. *a* amount in the upper layer above the 20 m depth was not largely variable in a range of 3 to 4.5 mg·m⁻³ at any depth. The small fraction was most abundant in the phytoplankton assemblage at any depth. It contributed to 66.2% of the total chl. *a* amount in the euphotic zone, while the large and middle fractions occupied 14.1 and 19.8%, respectively.

3-2. Vertical distribution of the zooplankters

In each experimental series, five vertical profiles of *Daphnia* and *Eodiaptomus* populations were determined over the 24 hours; noon, dusk, midnight, dawn and noon. All vertical

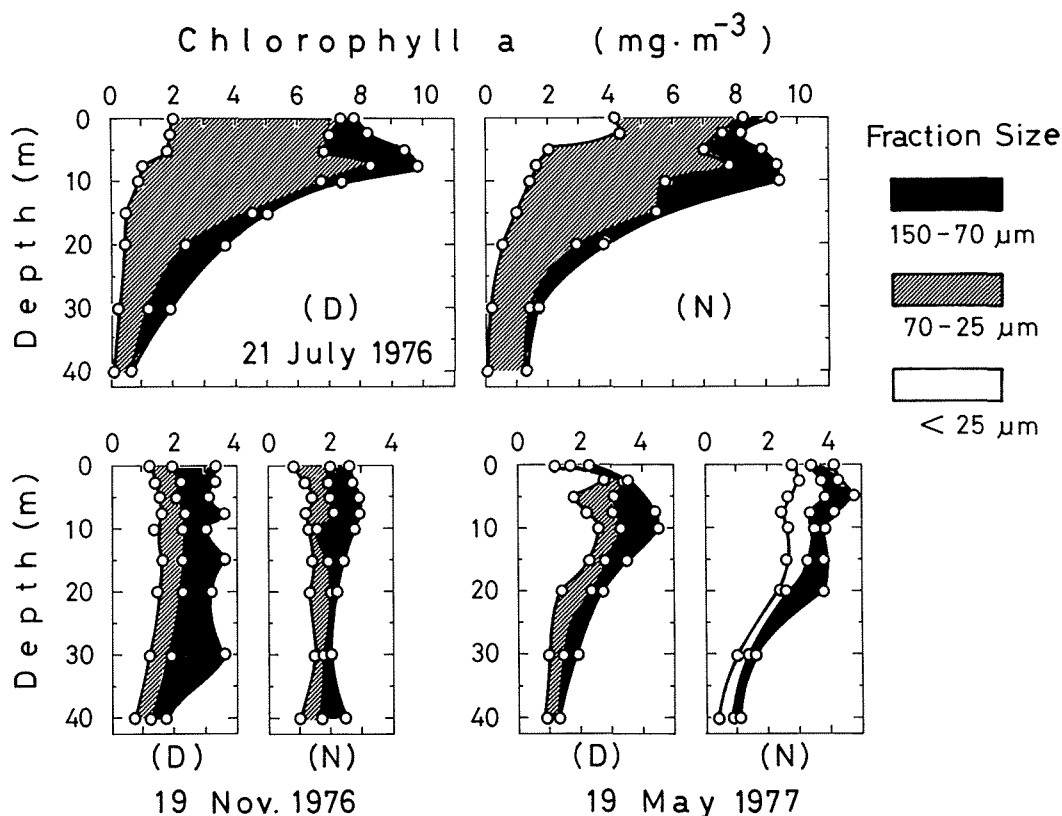


Fig. 4. The vertical distribution of chlorophyll *a* amount of the three algal fractions at noon (D) and midnight (N) in the summer, autumn and spring experiments.

distributions were expressed as a percentage of the entire population in the water column according to the depth (Figs. 5, 6 & 7).

(Summer). As shown in Fig. 5, *Daphnia* did not exhibit the diurnal vertical migration, but continued to stay mainly in the epilayer above 5 m depth during both the daytime and nighttime. More than 90% of the population was distributed in the column above 15 m depth. There were found few individuals in the deeper layer than 20 m. The minimum size class of a daphnid collected was 0.4–0.6 mm long, and the maximum, 1.4–1.6 mm long. The medium size daphnid (0.6–1.2 mm) comprised 80% of the population.

On the other hand, *Eodiaptomus* exhibited the diurnal migratory patterns of up- and downward moving. Nevertheless, most parts of the population (72–93%) were found above the depth of 15 m and only 2–8% of it, below the depth of 20 m, over the 24 hours. It indicated that the vertical migration of *Eodiaptomus* occurred mainly within the epilimnion above the thermocline. Four animal size classes (0.2–1.0 mm) were distinguished, while the large animals (0.6–1.0 mm) comprised more than 70% of the population.

(Autumn). Both of the *Daphnia* and *Eodiaptomus* populations were distributed over the whole water column throughout the day, and increased numerically at midnight (24:00), especially in the deep layer (Fig. 6).

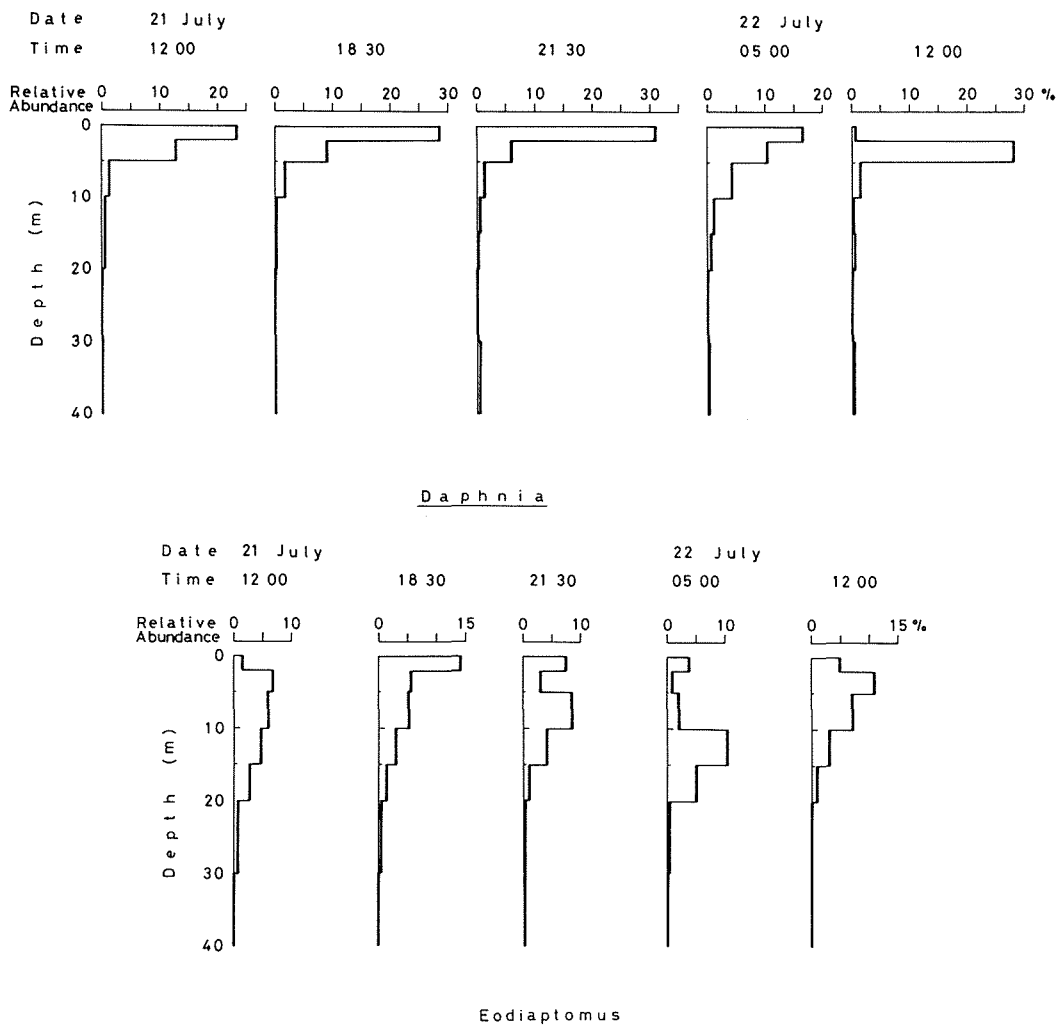


Fig. 5. Diurnal changes in the vertical distribution of relative abundance (%) of *Daphnia* and *Eodiaptomus* in summer.

Daphnia appeared to migrate vertically, but a considerably numerical population (more or less 10 animals·l⁻¹) was always present at the depth above 10 m over the 24 hours. This density was not so small when compared to the maximum density detected (14 animals·l⁻¹). It is seemed, therefore, that the diurnal vertical migration was not pronounced. About 50% of the population was comprised by the medium size daphnid (0.6–1.0 mm), and 30% by the small one (0.4–0.6 mm).

Eodiaptomus tended to avoid the residence in the epilayer above 2 m depth and to stay around at 10 m depth in the daytime, while it recovered the epilayer residence in the night-time. At the same time, however, the population density increased abruptly in the hypolimnion. It is uncertain whether this increase is due to a reverse migration (midnight sinking)

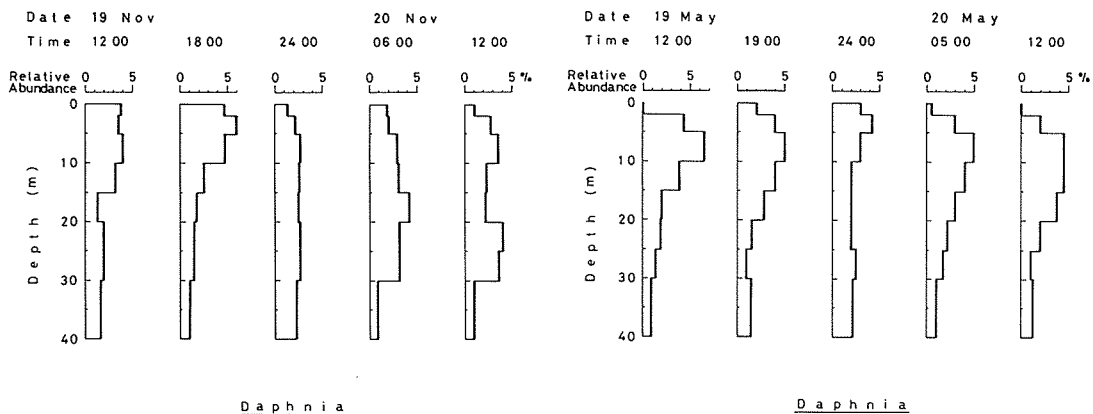
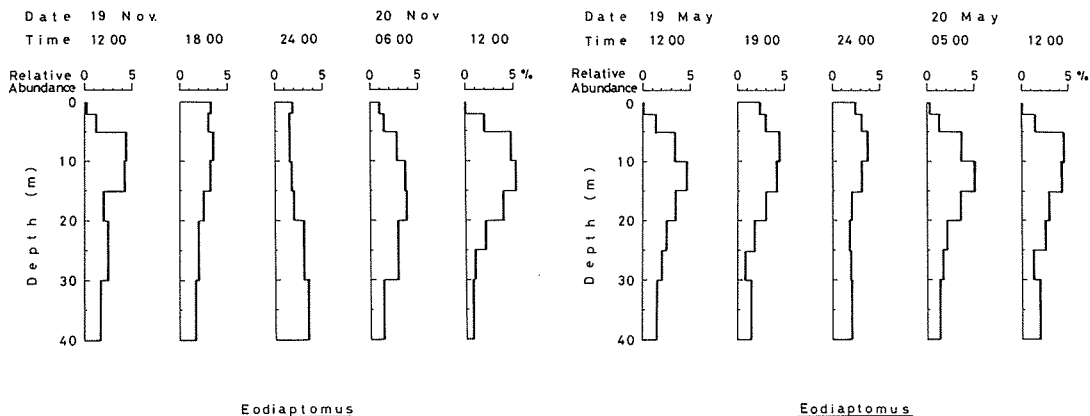
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Fig. 6. Diurnal changes in the vertical distribution of relative abundance (%) of *Daphnia* and *Eodiaptomus* in autumn.

Fig. 7. Diurnal changes in the vertical distribution of relative abundance (%) of *Daphnia* and *Eodiaptomus* in spring.

or not. A large part of the entire population was composed of the medium size animals (0.4–0.8 mm).

(Spring). *Daphnia* was distributed over the whole water column, while it disappeared from the epilayer at noon and turned up again in the nighttime (Fig. 7). A peak of the population density was found around at the depth of 5 to 10 m during the day. It suggested that the main part of *Daphnia* population migrated in a small scale within the epilimnion. More than 80% of the population consisted of the small animals (0.4–0.8 mm).

The vertical profile of *Eodiaptomus* was similar to that of *Daphnia* (Fig. 7). The disappearance from the epilayer took place at noon, while the night residence was recovered there. The depth at which the densest population was present varied from 5 to 10 m throughout the day. It suggested that a moderate migration of *Eodiaptomus* occurred within the epilimnion, as well as in *Daphnia*. The small copepod (0.2–0.6 mm) composed more or less 90% of the population.

3-3. Food conditions and algal compositions

Table 2 shows food concentrations of the large, middle, small and total fractions in POC amount per liter in the experiments. Both the concentrations and proportions of the three algal fractions were different among seasons.

Table 2. Food concentrations and food percentages of the three algal fractions in the summer, autumn and spring experiments.

		<i>Food Concentration</i> ($\mu\text{gC}\cdot\text{l}^{-1}$)				<i>Food Percentage</i>			
fraction size	time	July 21		July 22		average	average	range	
		15: 00	21: 00	04: 00	12: 00				
Summer	Large (150–70 μm)	535.9	574.0	544.2	462.7	529.2	60.9%	(57.8–64.3)	
	Middle (70–25 μm)	147.0	143.8	146.2	155.0	148.0	17.1%	(15.4–19.4)	
	Small (<25 μm)	150.8	218.2	216.8	183.1	192.2	22.1%	(18.1–23.9)	
	Total	833.7	936.0	907.2	800.8	869.4			
		Nov. 19		Nov. 20		average	average	range	
fraction size	time	12: 00	18: 00	24: 00	06: 00				12: 00
		Autumn	Large (150–70 μm)	41.7	43.0	46.0	52.0	47.3	46.0
Middle (70–25 μm)	70.4		72.4	76.5	67.4	52.5	67.8	25.9%	(22.5–27.3)
Small (<25 μm)	155.4		158.6	157.7	128.5	134.0	146.8	56.3%	(51.8–58.1)
Total	267.5		274.0	280.2	247.9	233.8	260.7		
		May 19		May 20		average	average	range	
fraction size	time	12: 00	19: 00	24: 00	04: 00				12: 00
		Spring	Large (150–70 μm)	70.3	69.1	71.8	66.2	77.4	71.0
Middle (70–25 μm)	93.1		105.3	94.7	79.3	80.9	90.7	23.4%	(20.8–27.4)
Small (<25 μm)	208.8		209.8	274.0	236.6	204.4	226.7	58.2%	(54.6–62.2)
Total	372.1		384.2	440.5	382.1	362.7	388.3		

In summer, the daily average concentration was about $530 \mu\text{gC}\cdot\text{l}^{-1}$ in the large fraction, $148 \mu\text{gC}\cdot\text{l}^{-1}$ in the middle one, and $192 \mu\text{gC}\cdot\text{l}^{-1}$ in the small one, resulting in $870 \mu\text{gC}\cdot\text{l}^{-1}$ in total. A large part of the food (61%) was composed of the large fraction, while 17% and 22% of it was occupied by the middle and small fractions, respectively.

All algal fractions showed the lowest food concentrations in autumn. The average POC amount was $261 \mu\text{gC}\cdot\text{l}^{-1}$ in total, some 56% of which was supported by the small fraction, 26% by the middle one and 18% by the large one.

In spring, the food amount (average: $390 \mu\text{gC}\cdot\text{l}^{-1}$) was a little more abundant than in autumn. The small fraction was most abundant and occupied 58% of it. The middle and large fractions accounted for 23% and 18% of it, respectively.

As shown in Table 3, the species composition of phytoplankton was distinctly different

Table 3. The species compositions and densities of phytoplankton in the three fractions used for the *in situ* feeding experiments. The density is shown in the number of cells per ml.

species	fraction size	July 22, 1976			Nov. 19, 1976			May 19, 1977		
		150-70 μm	70-25 μm	<25 μm	150-70 μm	70-25 μm	<25 μm	150-70 μm	70-25 μm	<25 μm
<i>Staurastrum dorsidentiferum</i>		269.1	42.1	3.8	—	0.8	—	0.9	*	—
<i>S. tohopekaligense</i>		2.2	—	—	3.3	—	—	—	—	—
<i>Closterium aciculare</i>		2.9	1.0	—	0.3	—	—	6.4	5.7	—
<i>Xanthidium hastiferum</i>		1.5	—	—	—	—	—	0.1	—	—
<i>Spyrogyra</i> sp.		6.6	—	—	—	—	—	—	—	—
<i>Oocystis</i> sp.		—	12.2	82.5	—	0.3	71.3	—	—	—
<i>Sphaerocystis schroeteri</i>		—	57.1	37.5	—	12.6	—	—	—	—
<i>Ankistrodesmus falcatus</i>		—	1.3	—	—	—	—	—	—	—
<i>Pediastrum Biwae</i>		—	—	—	37.8	—	—	—	—	—
<i>Coelastrum cambricum</i>		—	—	—	—	3.8	—	—	—	—
<i>Eudorina elegans</i>		—	10.5	—	—	—	—	—	—	—
<i>Asterionella formosa</i>		—	—	—	—	—	—	—	2.3	—
<i>Fragilaria crotonensis</i>		15.4	6.3	—	—	—	—	52.5	48.5	—
<i>Melosira granulata</i>		—	1.8	—	—	—	—	—	—	—
<i>M. italica</i>		5.1	—	—	—	—	—	—	—	—
<i>M. solida</i>		—	—	10.0	17.4	138.3	303.8	—	—	11.3
<i>Cocconeis</i> spp.		—	—	11.3	—	—	21.3	—	—	3.8
<i>Stephanodiscus carconensis</i>		—	—	—	—	0.6	—	—	—	2.5
<i>Merismopedia elegans</i>		—	5.3	—	—	—	—	—	—	—
<i>Aphanothece</i> sp.		—	2.1	—	—	—	—	—	—	—
<i>Microcystis aeruginosa</i>		—	—	—	—	(1.9)	—	—	—	—
<i>Ceratium hirundinella</i>		1.1	0.2	—	—	1.4	—	—	—	—
ultraplankton		—	—	1790.0	—	—	6480.0	—	—	2375.0
total cell number		304.0	139.8	1935.0	58.8	157.8	6876.3	59.9	56.5	2392.5

The parenthesis means colony number.

* The number of cells per ml was less than 0.1.

not only among the three fractions in a given experiment but also in a given fraction among the three seasons.

In summer, the large fraction consisted mainly of the large desmid, *Staurastrum dorsidentiferum*, which was followed by some diatoms and green algae with a few cell number like *Fragilaria crotonensis*, *Melosira italica* and *Spyrogyra* sp. The middle fraction included 11 species, the main members of which were *Sphaerocystis schroeteri* and *S. dorsidentiferum*. A few number of *Oocystis* sp., *Eudorina elegans*, *F. crotonensis* and *Merismopedia elegans* were also found. The small fraction contained a great number of unidentified ultraplancton, which dominated over 5 other unidentified species like *Oocystis* sp. and *S. schroeteri*.

In autumn, the chained diatom, *Melosira solida* appeared abundantly. The large fraction included *Pediastrum Biwae* and *M. solida* as the two main components. The most numerical

component in the middle fraction was *M. solida*. Seven other species except *S. schroeteri* were very scarce in number. The small fraction was occupied by a large number of ultraplankton, although it contained only a considerable number of the 3 species, small sized *M. solida*, *Oocystis* sp. and *Cocconeis* sp.

In spring, both of the large and middle fractions were dominated by the diatom, *F. crotonensis*. The small fraction consisted of ultraplankton, additionally containing a few number of some species.

3-4. Diurnal changes in feeding rates

Figures 8, 9 and 10 show the diurnal changes in feeding rates of *Daphnia* and *Eodiaptomus* on the three algal fractions in the summer, autumn and spring experiments, respectively. Both zooplankters of any size classes exhibited the continuous feeding throughout a 24-hour period in every experimental series. However, the pattern of diurnal change in the feeding rate was not consistent among the three seasons in both *Daphnia* and *Eodiaptomus*, while appeared to be similar between both the zooplankters in one series.

Summer Experiment. The feeding rates were determined at 5 m and 15 m depths. In the 5 m measurement, the daytime feeding rates tended to be higher than the nighttime ones in most of the size classes of both *Daphnia* and *Eodiaptomus*. The nighttime decreases were mainly caused by a remarkable decline of the feeding rate on the small fraction, although the rates on the two other fractions were slightly lowered in some cases. In *Daphnia* except the 0.6–0.8 mm size class, the average feeding rate on the small fraction in the nighttime (21:00, 04:00) was

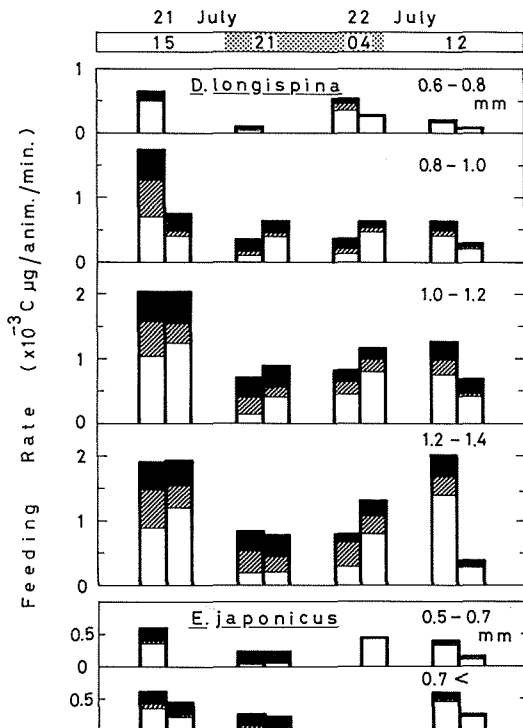


Fig. 8. Diurnal changes in the feeding rates of *Daphnia* and *Eodiaptomus* on a natural phytoplankton assemblage in summer. The left side column represents the rates measured at 5 m depth and the right side one, at 15 m depth. Shaded parts represent feeding rates on the large fraction, striped ones, on the middle fraction and open ones, on the small fraction.

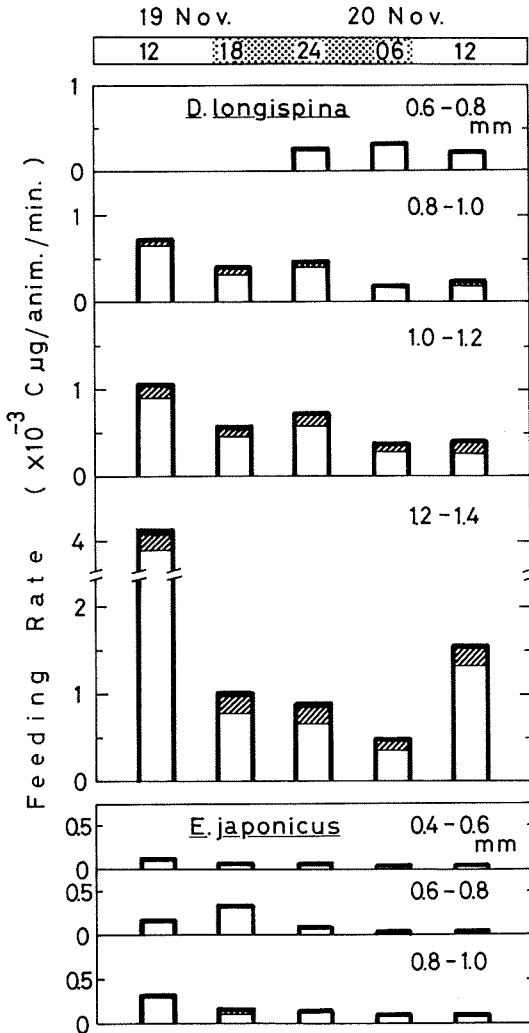


Fig. 9. Diurnal changes in the feeding rates of *Daphnia* and *Eodiaptomus* on a natural phytoplankton assemblage in autumn. The marks for the three algal fractions are same in Fig. 8.

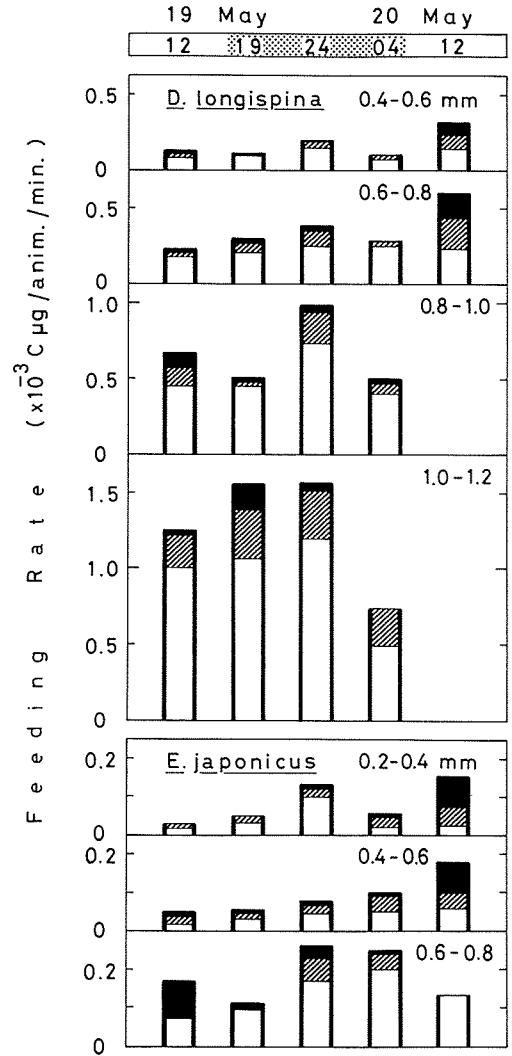


Fig. 10. Diurnal changes in the feeding rates of *Daphnia* and *Eodiaptomus* on a natural phytoplankton assemblage in spring. The marks for the three algal fractions are same in Fig. 8.

equivalent to 13–34% of the daytime rate (15: 00, 12: 00), resulting in reduction of the total feeding rate to more or less 40% of the daytime rate. In *Eodiaptomus*, similarly, the nighttime feeding rate on the small fraction was lowered to be close to 10% of the daytime one, resulting in the total nighttime feeding rate declined to 44% of the daytime one.

The diurnal changing pattern of feeding rates at 15 m depth seemed to be similar to that at 5 m depth, except the facts that the feeding rates at noon were not heightened but lowered and the extent of the nighttime decrease in the rates was less. Combining the results in both

the 5 and 15 m measurements, it appeared that the feeding rate of *Daphnia* was particularly high at 15:00, decreased at night and afterwards remained at a low level with a little fluctuation.

In *Eodiaptomus*, it was difficult to compare the feeding rates between the two measurements in detail, because some of the rates could not be determined due to no samples.

In the experiment using the cultured alga (Fig. 11), the pattern of diurnal changes in feeding rates of *Daphnia* and *Eodiaptomus* was completely different from that found in the series using natural phytoplankton: In every size class of both zooplankters, the feeding rate was maintained at a nearly constant level throughout the diurnal period in both the measurements at 5 m and 15 m depths. Also, its level was almost same between both depths, suggesting that such a small difference in depth has only a minor influence on the feeding rates.

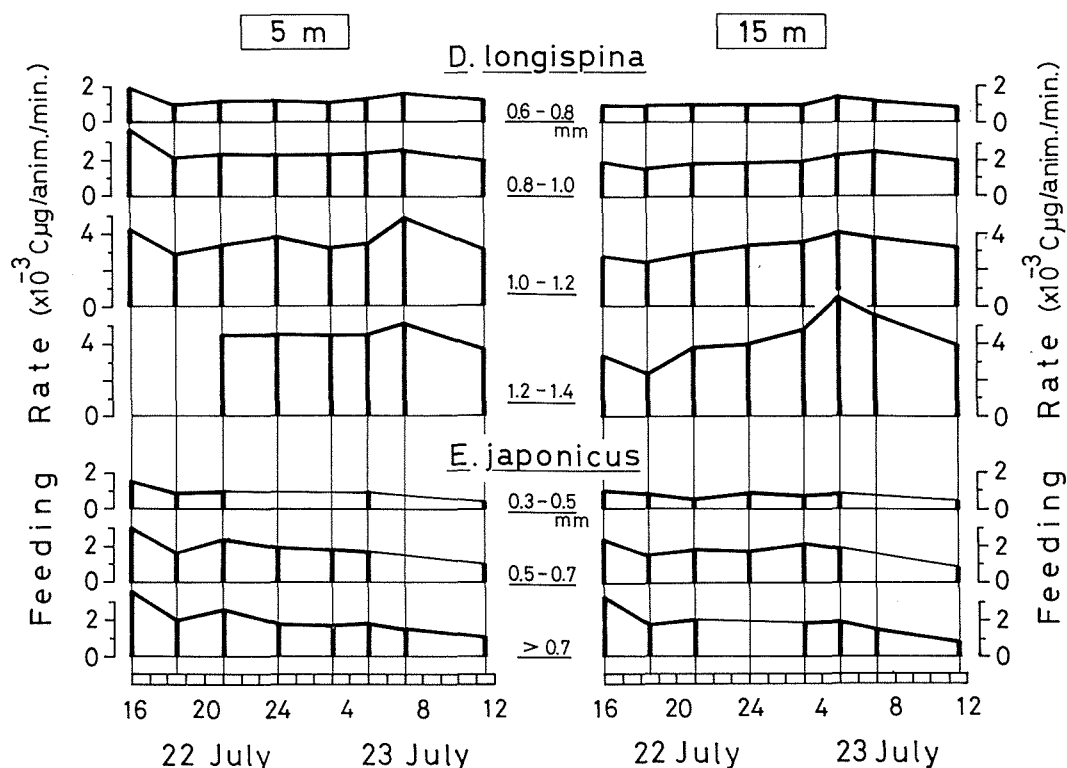


Fig. 11. Diurnal changes in the feeding rates of *Daphnia* and *Eodiaptomus* on the cultured alga, *Selenastrum* sp., at 5 and 15 m depths in summer.

The daily average rate of feeding on the cultured alga was about 3-4 times higher than that on the natural food in any size class of the daphnid and diaptomid, despite that the former food concentration was below a half of the latter one. It indicates that the feeding process of the zooplankters in the natural phytoplankton assemblage was strikingly obstructed probably due to intensive rejection against unwanted food particles in the assemblage, resulting in the lower feeding rate.

Autumn Experiment. In both *Daphnia* and *Eodiaptomus*, the feeding rates tended to decrease with time from the first noon to the second noon, except the 1.2–1.4 mm daphnid (Fig. 9). Only this size class exhibited a nighttime decrease and daytime increase pattern of the feeding rate.

Spring Experiment. In both zooplankters, there were no remarkable changes in the feeding rates throughout a 24-hour period (Fig. 10), except an increase in the feeding rate on the large fraction at the second noon in some size classes.

A Relation of Feeding Activity to Animal Size. Whether the allometric relation of feeding activity was kept during a day was examined (Tables 4, 5, 6 & 7). In all of the three seasons, the feeding rate of *Daphnia* on every fraction was highly dependent on the animal size (weight) at

Table 4. The relationships of feeding rates of *Daphnia longispina* with animal size in the *in situ* experiments carried out at 5 and 15 m deep during a day in summer, 1976. The relationships are expressed in a following equation; $F = aW^b$, where F is feeding rate ($\times 10^{-4} \mu\text{gC} \cdot \text{anim.}^{-1} \cdot \text{min.}^{-1}$), W, animal weight ($\mu\text{gC} \cdot \text{anim.}^{-1}$) and a and b, constants.

date		July 21		July 22		
time		15: 00	21: 00	04: 00	12: 00	
depth	fraction size					
(5 m)	150–70 μm	a	1.570	1.072	1.004	0.639
		b	0.864	0.921	0.369	1.311
		r^2	0.883	0.872	0.608	0.920
	70–25 μm	a	7.520	0.293	1.196	0.421
		b	–0.198	1.970	0.683	1.543
		r^2	0.728	0.956	0.788	0.911
	<25 μm	a	5.910	0.360	2.657	2.639
		b	0.395	1.343	0.089	1.187
		r^2	0.809	0.893	0.015	0.995
	total	a	9.377	1.760	5.047	3.489
		b	0.676	1.274	0.324	1.319
		r^2	0.747	0.930	0.408	0.987
(15 m)	150–70 μm	a	1.763	1.051	0.704	0.367
		b	0.805	1.075	0.954	1.198
		r^2	0.815	0.925	0.945	0.670
	70–25 μm	a	0.235	0.508	0.147	0.344
		b	1.990	0.932	2.348	–0.227
		r^2	0.956	0.943	0.962	0.037
	<25 μm	a	3.234	5.435	3.245	1.056
		b	1.064	–0.564	0.772	1.014
		r^2	0.770	0.831	0.920	0.783
	total	a	6.053	6.506	4.153	3.229
		b	0.906	0.183	0.937	0.349
		r^2	0.867	0.341	0.953	0.185

most of the experimental times. The b exponent in the power function was much time-variant in summer (Table 4), while less variable in both autumn and spring (Tables 5 & 6). On the other hand, the summer experiment using the cultured alga exhibited the relatively stable b exponents throughout the diurnal period; 0.756 and 0.817 on the average at 5 m and 15 m depths, respectively (Table 7). These values are well consistent with those known for some *Daphnia* species fed on cultured algae (Burns 1969). It is suggested, therefore, that the summer feeding of *Daphnia* in nature was remarkably unstable although the size-dependent feeding was maintained.

Table 5. The relationships of feeding rates of *Daphnia longispina* and *Eodiaptomus japonicus* with animal sizes in the *in situ* experiments carried out during a day in autumn, 1976. The relationships are expressed in the equation, $F=aV^b$ (See Table 4).

date			Nov. 19			Nov. 20	
time			12: 00	18: 00	24: 00	06: 00	12: 00
zooplankter	fraction size						
<i>Daphnia</i>	150-70 μm	a	0.070	0.041	0.065	0.101	0.090
		b	1.229	1.672	1.709	0.583	0.967
		r^2	0.997	0.906	0.982	0.964	0.759
	70-25 μm	a	0.452	0.532	0.343	0.211	0.407
		b	1.211	1.035	1.572	0.960	1.048
		r^2	0.986	0.963	1.000	0.771	0.919
	<25 μm	a	4.793	2.944	3.515	1.484	1.800
		b	1.488	0.692	0.582	0.751	0.504
		r^2	0.800	0.941	0.967	0.990	0.999
	total	a	5.318	3.404	4.001	1.751	2.315
		b	1.473	0.813	0.791	0.804	0.638
		r^2	0.831	0.950	0.993	0.968	0.987
<i>Eodiaptomus</i>	150-70 μm	a	0.028	0.037	0.013	0.014	
		b	1.839	-2.957	1.466	1.317	
		r^2	0.976	0.786	0.911	0.323	
	70-25 μm	a	0.071	0.124	0.040	0.011	0.019
		b	0.307	1.573	1.272	1.539	1.070
		r^2	0.994	0.726	0.621	0.965	0.309
	<25 μm	a	1.512	0.721	0.553	0.203	0.231
		b	1.227	2.469	1.722	1.999	1.192
		r^2	0.842	0.558	0.999	0.693	0.789
	total	a	1.616	1.131	0.608	0.231	
		b	1.200	1.678	1.684	1.943	
		r^2	0.847	0.522	0.995	0.700	

In summer, *Eodiaptomus* showed the obvious size-dependent feeding on the cultured alga at any experimental times during a day (Table 7), but the general feature of the allometric relation in feeding on the natural phytoplankton could not be ascertained due to few available sets of the feeding rate-body weight relations. The relatively stable size-dependent feeding during a day was found in autumn (Table 5), but not in spring when the b exponents for the large and middle fractions varied largely (Table 6).

Table 6. The relationships of feeding rates of *Daphnia longispina* and *Eodiaptomus japonicus* with animal sizes in the *in situ* experiments carried out during a day in spring, 1976. The relationships are expressed in the equation, $F=aW^b$ (See Table 4).

date		May 19			May 20			
time		12: 00	19: 00	24: 00	04: 00	12: 00		
zooplankter	fraction size							
<i>Daphnia</i>	150-70 μm	a	0.346	0.331	0.295	0.174	2.363	
		b	0.414	1.149	0.594	1.438	1.346	
		r^2	0.232	0.860	0.997	0.955	0.993	
	70-25 μm	a	0.555	0.407	1.119	0.415	2.470	
		b	1.136	1.425	1.090	1.369	1.318	
		r^2	0.968	0.787	0.945	0.987	0.980	
	<25 μm	a	2.243	2.453	3.463	2.075	3.400	
		b	1.324	1.273	1.122	0.902	1.324	
		r^2	0.979	0.969	0.980	0.764	1.000	
	total	a	3.221	3.244	4.914	3.082	5.329	
		b	1.216	1.292	1.072	1.400	1.322	
		r^2	0.976	0.964	0.961	0.889	0.648	
	<i>Eodiaptomus</i>	150-70 μm	a	0.273	0.108	0.216	0.099	
			b	2.123	0.579	0.808	0.052	
			r^2	0.973	0.990	0.809	0.596	
70-25 μm		a	0.242	0.174	0.434	0.388		
		b	0.720	0.457	0.915	0.292		
		r^2	0.827	0.621	0.757	0.967		
<25 μm		a	0.325	0.531	1.291	0.825	0.745	
		b	0.774	0.567	0.673	1.246	0.964	
		r^2	0.596	0.596	0.502	0.911	0.969	
total		a	0.895	0.818	1.959	1.401		
		b	1.067	0.548	0.736	0.821		
		r^2	0.804	0.670	0.597	0.902		

Table 7. The relationships of feeding rates of *Daphnia longispina* and *Eodiaptomus japonicus* with animal sizes in the *in situ* experiments using the mono-cultured alga, *Selenastrum* sp. The *in situ* experiments were carried out at 5 and 15 m deep eight times in a day on July 22–23, 1976. The relationships are expressed in a following equation; $F=aW^b$, where F is feeding rate ($\times 10^{-4} \mu\text{gC}\cdot\text{anim.}^{-1}\cdot\text{min.}^{-1}$), W, animal weight ($\mu\text{gC}\cdot\text{anim.}^{-1}$) and a and b, constants.

zooplankter	depth	date time	July 22				July 23				
			16: 00	18: 30	21: 00	24: 00	03: 00	05: 00	07: 00	11: 30	
<i>Daphnia</i>	5 m	a	2.450	1.307	1.570	1.641	1.508	1.716	2.058	1.555	
		b	0.690	0.908	0.789	0.782	0.798	0.709	0.720	0.649	
		r ²	0.868	0.959	0.982	0.980	0.981	0.995	0.946	0.986	
	15 m	a	1.282	1.185	1.300	1.352	1.380	1.802	1.720	1.338	
		b	0.741	0.586	0.806	0.854	0.932	0.895	0.867	0.858	
		r ²	0.981	0.907	0.992	0.976	0.991	0.994	0.996	0.968	
<i>Eodiaptomus</i>	5 m	a	1.701	0.880	1.041			0.926		0.377	
		b	0.626	0.632	0.804			0.594		0.912	
		r ²	0.997	0.988	0.963			0.958		0.940	
	15 m	a	1.085	0.856	0.623		0.895	0.936		0.398	
		b	0.902	0.574	1.025		0.718	0.632		0.661	
		r ²	1.000	0.977	0.925		0.815	0.952		0.917	

3-5. An estimation of the daily rations and the daily carbon balance

Daily Rations. Table 8 shows the daily food intake from each algal fraction and the total rations of *Daphnia* and *Eodiaptomus*. The total rations were compared with body carbon weight of the zooplankters.

Both zooplankters relied a large part of their rations on the small fraction, the average contribution of which was 53.7% in summer, 85.7% in autumn and 64.8% in spring in *Daphnia*, and 54.8%, 86.6% and 54.9% in *Eodiaptomus*, respectively. These high contribution indicates the definite food selection of both animals for the small fraction except the spring diaptomid, when compared with its contribution to total food concentration; 22.1% in summer, 56.3% in autumn and 58.2% in spring.

The percentage of the large fraction to the rations was 22.0% (summer), 2.5% (autumn) and 14.4% (spring) on the average in *Daphnia*, while 38.0% (summer), 5.8% (autumn) and 21.1% (spring) in *Eodiaptomus*. The large fraction seemed to be a little more available food for *Eodiaptomus* than for *Daphnia*. The average contribution of the middle fraction to the rations ranged from 8.7 to 22.5% in the daphnid and from 3.3 to 28.9% in the diaptomid among the three seasons, suggesting no remarkable difference in the availability for this fraction between both zooplankters.

An average ratio of the total rations to body weight in summer, autumn and spring was 66.8%, 53.0% and 64.0% in *Daphnia*, and 18.4%, 12.1% and 16.6% in *Eodiaptomus*, respectively (Table 8). The extremely low values in the latter animal might have been underestimated. However, the ratios (range: 7.9–20.3%) are comparable to those (range: 2.2–23.9%)

Table 8. The estimated daily rations of *Daphnia longispina* and *Eodiaptomus japonicus* in summer, autumn and spring, in comparison with the animal body weights.

zooplankter	<i>Daphnia</i>					<i>Eodiaptomus</i>			
	animal size class (mm)	0.4-0.6	0.6-0.8	0.8-1.0	1.0-1.2	1.2-1.4	0.4-0.6	0.6-0.8	0.8-1.0
July, 1976									
daily rations (large fraction)		0.097	0.258	0.432	0.420		0.184	0.218	
(μgC) (middle fraction)		0.047	0.351	0.454	0.590		0.027	0.050	
(small fraction)		0.369	0.486	0.863	0.997		0.269	0.310	
total		0.513	1.095	1.749	2.007		0.480	0.578	
animal body weight (μgC)		0.71	1.42	2.55	4.09		2.36	3.53	
total rations/body weight (%)		72.3	77.1	68.6	49.1		20.3	16.4	
November, 1976									
daily rations (large fraction)		0.007	0.012	0.024	0.055	0.007	0.002	0.005	
(μgC) (middle fraction)		0.037	0.053	0.149	0.199	0.005	0.006	0.019	
(small fraction)		0.382	0.465	0.661	1.590	0.039	0.173	0.172	
total		0.426	0.530	0.834	1.844	0.051	0.181	0.196	
animal body weight (μgC)		0.62	1.08	2.11	3.37	0.65	1.16	1.55	
total rations/body weight (%)		68.7	49.1	39.5	54.7	7.9	15.6	12.7	
May, 1977									
daily rations (large fraction)		0.039	0.069	0.154			0.032	0.054	
(μgC) (middle fraction)		0.050	0.114	0.218			0.037	0.060	
(small fraction)		0.143	0.324	0.826			0.059	0.199	
total		0.232	0.507	1.198			0.128	0.313	
animal body weight (μgC)		0.50	0.76	1.52			0.90	1.65	
total rations/body weight (%)		46.4	66.7	78.8			14.2	19.0	

in some marine calanoid copepods fed on natural food (Ikeda 1971; Poulet 1974; Dagg & Grill 1980). There has been no comparable study on the daily ingestion of freshwater calanoid copepods in nature.

Daily Carbon Balance. Table 9 represents the daily carbon balance between the estimated rations and respiration, in which the surplus or shortage is judged on the basis of the assimilation efficiency reported by Gulati (1976); the assimilation efficiency of filter feeders on natural food varied from 28 to 60% depending on the circumstances where they lived.

Daphnia in summer might be in debt in the carbon metabolism even at the high assimilation efficiency (60%), except a small size class. The same situation was found from the autumn daphnids at the low assimilation efficiency (28%), but not from the spring ones. However, the food selection of *Daphnia* for the small fraction implied that the higher respiratory loss than the estimated one might be caused by the rejectory behaviour against the other fractions (Porter *et al.* 1982). Accordingly, a possibility that *Daphnia* in the three seasons might live on a subsistence level can be inferred.

Table 9. An estimation of the daily carbon balance between food incomes and metabolic expenditures by *D. longispina* and *E. japonicus* in summer, autumn and spring.

		<i>Daphnia</i>				<i>Eodiaptomus</i>			
			animal size			animal size			
Summer	body weight (BW)	(μgC)	0.71	1.42	2.55	4.09	2.36	3.53	
	daily rations (F)	(μgC)	0.513	1.095	1.749	2.007	0.480	0.578	
	respiration* (R)	(μgC)	0.243	0.658	1.096	1.923	1.116	1.454	
	F/BW	(%)	72.3	77.1	68.6	49.1	20.3	16.4	
	R/BW	(%)	34.2	46.3	43.0	47.0	47.3	41.2	
	R/F	(%)	47.4	60.1	62.7	95.8	232.5	251.6	
	economical balance**	A	—	—	—	—	—	—	
	B	+	+—	—	—	—	—		
Autumn	body weight (BW)	(μgC)	0.62	1.08	2.11	3.37	0.65	1.16	1.55
	daily rations (F)	(μgC)	0.426	0.530	0.834	1.844	0.051	0.181	0.196
	respiration* (R)	(μgC)	0.117	0.213	0.371	0.613	0.205	0.300	0.363
	F/BW	(%)	68.7	49.1	39.5	54.7	7.9	15.6	12.7
	R/BW	(%)	18.9	19.7	17.6	18.2	31.5	25.9	23.4
	R/F	(%)	27.5	40.2	44.5	33.2	402.0	165.8	185.2
	economical balance**	A	+—	—	—	—	—	—	—
	B	+	+	+	+	—	—	—	
Spring	body weight (BW)	(μgC)	0.50	0.76	1.52		0.90	1.65	
	daily rations (F)	(μgC)	0.232	0.507	1.198		0.128	0.313	
	respiration* (R)	(μgC)	0.056	0.153	0.286		0.276	0.411	
	F/BW	(%)	46.4	66.7	78.8		14.2	19.0	
	R/BW	(%)	11.2	20.1	18.8		30.7	24.9	
	R/F	(%)	24.2	30.2	23.9		215.6	131.3	
	economical balance**	A	+	—	+		—	—	
	B	+	+	+		—	—		

* The respiratory oxygen consumption of *D. longispina* and *E. japonicus* was estimated on the basis of the relationship between oxygen consumption and temperature in *D. hyalina* (Blázka 1966) and the Comita's formula (1968) for the respiration of some diaptomid species, respectively. Then, the metabolic carbon loss was determined assuming $RQ=1.0$.

** The economical balance was judged on the assumption of assimilation efficiency as follows; 28% at A and 60% at B (Gulati 1976).

In *Eodiaptomus*, the respiratory carbon loss was surprisingly larger than the rations income in all of the seasons (Table 9). This discrepancy cannot be explained, although the summer experiment using the cultured alga shows that the summer diaptomids had potentially the high feeding activity enough to cover the estimated respiratory loss. In any case, the diaptomid seemed to be at least under a poor nutritional condition.

3-6. Selective feeding on the three fractions

The size-selectivity of *Daphnia* and *Eodiaptomus* for the three algal fractions, expressed by the Jacobs' index (Jacobs 1974), is shown in Fig. 12.

Daphnia. In summer, patterns of diurnal changes in the size-selective feeding were different

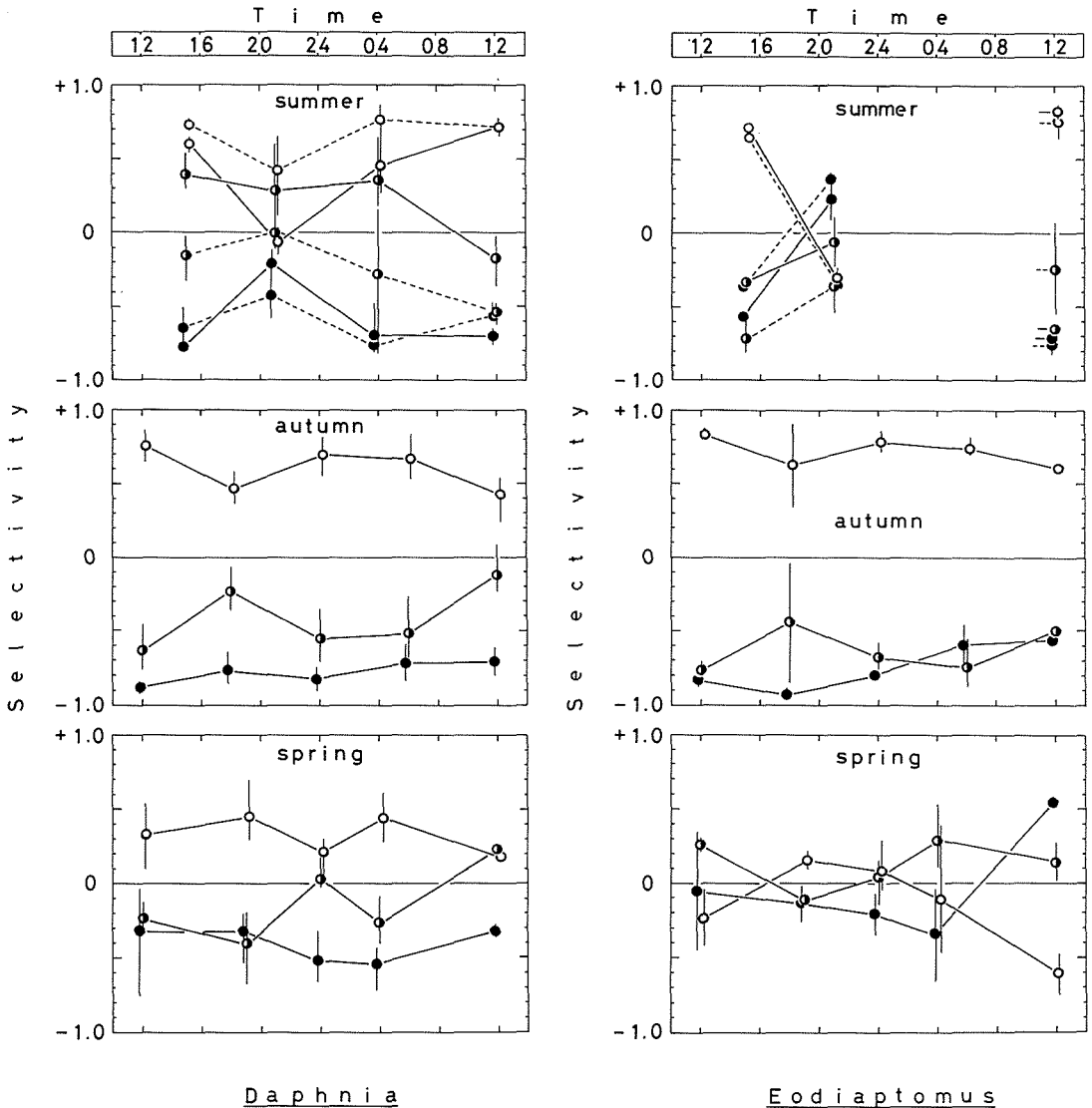


Fig. 12. Diurnal changes in the food size-selectivities of *Daphnia* and *Eodiaptomus* in feeding on a natural phytoplankton assemblage. The selectivity is shown by the Jacobs' index. A solid line shows the experiment at 5 m depth, and a dotted one, at 15 m depth. Food size: ●-large, ◐-middle, ○-small.

between the experimental series at 5 m and 15 m depths. The latter series showed no marked changes in the selectivity during a day; highly positive selection for the small fraction, weak negative or non-selection for the middle one and strong negative selection for the large one. In the 5 m experiment, however, both the small and middle fractions tended to be positively selected during a day except at 21:00 and noon, although the selectivities for the large fraction were consistently negative. The tendency of the positive middle-fraction selection found only at the 5 m depth seemed to be concerned with either the higher feeding rate on this fraction or

the lower rate on the small fraction, or with both, than the rate on the respective fraction at the 15 m depth (Fig. 8). The distinct change from positive to non-selection for the small fraction at 21:00 and from that to negative selection for the middle one at noon was mainly caused by the abrupt decrease and the increase in the feeding rate on the small fraction, respectively (Fig. 8).

The autumn daphnids exhibited continuously positive selection for the small fraction all over the day, while negative selection for both the middle and large ones. This pattern of the food size-selection was similarly seen from noon to 06:00 in spring, but turned to be completely reversed at the next noon. This reverse seemed to be resulted from striking increases in the feeding rates on the middle and large fractions.

Eodiaptomus. In summer, the changing pattern of the size-selectivity seemed to be similar between the 5 m and 15 m experimental series; positive small-selection in the daytime, while reversely positive large-selection in the nighttime (21:00). The middle fraction was almost negatively selected during a day. In autumn, on the contrast, the selectivity was always highly positive for the small fraction, but negative for the other two fractions over a 24-hour period. In spring, the selectivities for any of the three fractions were variable between the positive and negative values during a day, and most of them were distributed around the center line showing non-selection. It suggested that the definite food-size selection was not demonstrated, that is, the non-selective feeding.

4. Discussion

4-1. The summer night decrease in the feeding rates

In summer, the feeding rates of *D. longispina* and *E. japonicus* in nature decreased at 21:00 as compared with those at 15:00, and afterwards remained on the low level or tended to recover gradually until the next noon. Such night decrease was especially remarkable in *Daphnia*. Throughout the day- and nighttime, both the food concentration and temperature were nearly constant. The estimated mean density of the zooplankters in the water from surface to 10 m depth was not different between the experiments at 15:00 (21 animals·l⁻¹) and 21:00 (19 animals·l⁻¹). Therefore, these three factors can be discarded from possible causes on the night decrease.

On the other hand, the pH condition, one of the factors affecting feeding rate (Ivanova 1969), changed from 8.4 to 9.2. The high pH above 9.0 is known to reduce severely feeding rate of herbivorous zooplankton, and such a reduction occurs abruptly in the narrow range of pH from 8.0 to 9.0 (Kring & O'Brien 1976). In field, also, O'Brien and deNoyelles (1972) observed reduced feeding rate due to photosynthetically elevated pH in an outburst of natural phytoplankton.

In the present study, the pH value increased to 9.2 in the afternoon on July 21, and remained on the high level during the night. This increase was marked in the upper layer than 10 m depth where the phytoplankton was much abundant, suggesting the photosynthetically elevated pH during the daytime. As a possible cause on the night decrease in the feeding rates, therefore, such high pH condition which remained during the night can be inferred.

This inference can be supported by the fact that the feeding rates on the cultured alga did

not change in the period from 16:00 on July 22 to 11:30 on July 23 during which the pH level was constant at 9.2. In this experiment, also, the allometric relation of feeding rate was stable throughout the day. It suggests that the unstable allometric relation detected in the feeding rate on the natural phytoplankton assemblage is reflective of the high and changeable pH condition on 21–22, July.

A similar night decrease in the *in situ* filtering rate has been found from *D. longispina* var. *hyalina* in Lake Erken in summer when the phytoplankton was highly abundant (Nauwerck 1959, 1963), although it was not explained.

Since the high pH condition probably due to the outburst of phytoplankton was a peculiar phenomenon observed in the summer in Lake Biwa, the night decrease in the feeding rates would have been a singular result restricted to such season. As observed in both the autumn and spring experiments, however, the pattern with no pronounced periodicity may be often found for the diurnal change in the feeding rates of *Daphnia* and *Eodiaptomus* on a natural phytoplankton assemblage in a pelagic area of lake Biwa.

4-2. A possible condition inducing non-diurnal feeding pattern in zooplankters; poor nutritional state

The non-diurnal change in the feeding rates of *D. longispina* and *E. japonicus* do not agree with most of the accumulated evidences since the work of Nauwerck (1959); the feeding or filtering rate of freshwater herbivorous zooplankters changes diurnally both in the field and under laboratory conditions. The negative evidence like the present study has been reported by Gliwicz (1977), but he did not explain at all this phenomenon.

Diurnal change in the feeding and filtering rates of *Daphnia* species is often related to vertical migration and light change in the field (Haney 1973; Haney & Hall 1975), but they exhibit rhythmic feeding changes of unimodal or bimodal with no relation to migration even under laboratory conditions with (Starkweather 1975) or without 24-hours photocycles (Chisholm *et al.* 1975; Starkweather 1975; Duval & Geen 1976). Water temperature and food condition are also effective on the diurnal change (Chisholm *et al.* 1975; Starkweather 1978). Thus, the diurnal feeding patterns are associated with both environmental and internal factors. However, possible interrelationships between the factors have not been defined.

In the present study, migration is not a decisive factor for *D. longispina*, since the daphnid migrated vertically in some distance in both the autumn and spring experiments. Under the condition of the constant water temperature and food concentration, the endogenous rhythmic diurnal feeding (Starkweather 1975) should be expected, but was not in fact found in the present study. It can be suspected, therefore, that some environmental (exogenous) factor would have concealed the endogenous rhythmic activity of *Daphnia*, resulting in non-diurnal feeding pattern, in Lake Biwa.

Chisholm *et al.* (1975) pointed that adaptation or acclimatization of zooplankters to environmental conditions affects to the diurnal feeding pattern. Starkweather (1978) found that *Daphnia pulex* which had been held under a starved condition exhibited different diurnal patterns in the intensity of the appendage movement from the daphnid fed on plentiful food. Therefore, he suspected that such different response would be caused by the food shortage. Consequently, the nutritional history of zooplankters is very important for controlling the

feeding activity and modifies a general rhythmic pattern such as bimodal of diurnal feeding changes, and also their nutritional state must be taken into account.

An estimation of the daily carbon balance suggested a poor nutritional state of *Daphnia*. It is very doubtful that even under such poverty, *Daphnia* would still maintain the diurnal feeding rhythm with a low activity in the daytime. It is rather reasonable and acceptable to postulate that the animal would continue to feed at a certain rate as high as possible throughout a day to obtain enough ration for sustaining the life. In other words, *Daphnia* would not exhibit the periodical change in diurnal feeding activity. To collect algal food as efficiently as possible, moreover, it is more advantageous for the daphnid to stay in the epilimnion, where phytoplankton is plentiful during a day. Consequently, no pronounced diurnal vertical migration would be observed.

To ascertain this postulation, it may be useful to compare the food quantity of Lake Biwa with that of the Michigan lakes where two *Daphnia* species showed apparent periodical diurnal feeding pattern (Haney & Hall 1975). In Three Lakes, one of the Michigan lakes, the POC amount of 0.45–31 μm sized particles is nearly $1.5 \text{ mg}\cdot\text{l}^{-1}$, which is about twice higher than even the maximum total food concentration and more than 7-fold of the small fraction in Lake Biwa. Also, the light attenuation coefficient of water is 0.0102 cm^{-1} in Wintergreen Lake, another part of the Michigan lakes (Haney & Hall 1975), while the coefficient value is apparently low in Lake Biwa ($0.0030\text{--}0.0055 \text{ cm}^{-1}$). It indicates that those Michigan lakes contain much more amount of small suspended particles than Lake Biwa.

In addition, most of the studies that have defined the diurnal rhythmic change in the filtering and feeding rates were carried out under sufficient food conditions both *in situ* and in the laboratory (Starkweather 1975; Duval & Geen 1976). A starved daphnid exhibits the different response of the appendage movement to the light-dark changes from the daphnid well fed (Starkweather 1978). It can be suspected, therefore, that the diurnal feeding rhythm may be characteristic of the feeding activity of zooplankters living under a favourite condition of plentiful food.

Therefore, a possible relationship between the diurnal feeding pattern and the nutritional state can be hypothesized as follows; *Daphnia* may possess the endogenous rhythm in feeding activity which rises in the nighttime (Starkweather 1975). Such a rhythm can be modified or disappeared by the influence of environmental factors, especially food condition. Under so plentiful food condition that *Daphnia* can gather enough rations to sustain both of the metabolic and reproductive demands during a night period, the animal feeds mainly in the nighttime in accordance with the endogenous rhythm. It is more efficient to feed in the epilimnion with more abundant food than in the hypolimnion. After finishing the necessary intake of food, the animal does not need to feed actively and to stay in the epilimnion. Resultingly, it moves downwards and becomes inactive, or resting in the hypolimnion with lower water temperature. This case may correspond with the diurnal feeding pattern of *Daphnia* in the Michigan lakes.

On the contrary, under so scarce food condition that *Daphnia* cannot gain the rations enough to satisfy the daily demands by the nocturnal feeding alone, it must continue to feed even in the daytime until it collects enough food materials for the sustenance. To do so, the animal has to remain in the epilimnion even in the daytime, resulting in no pronounced vertical migration. This case can be just applied to the diurnal feeding pattern of *Daphnia* in Lake Biwa.

It can be expected that non-periodical diurnal feeding pattern would be generally observed in daphnids which live not only in a clear water (complete oligotrophic lakes and a clear water period even in mesotrophic lakes), but also under specially poor nutritional condition which may be caused by a large increase in unfavourable algae for daphnids.

Eodiaptomus exhibited non-rhythmic change in the feeding rate during a day, and was inferred to be under a poor nutritional situation. As well as *Daphnia*, the diaptomid would be obliged to feed continuously throughout a day. It appears, therefore, that the non-rhythmic diurnal feeding pattern may be a reflection of this economical situation. A similar observation was reported by Gauld (1953); when the natural food particles were very scarce, *Calanus pacificus*, a marine calanoid, continued to feed in the upper layer throughout a day, resulting in no pronounced diurnal changes in both the feeding activity and vertical distribution.

However, *Eodiaptomus* migrated vertically within the epilimnion, despite exhibiting no pronounced diurnal changes in the feeding rate. A similar result has been found from *Diaptomus pallidus* in the Michigan lakes (Haney & Hall 1975).

In general, the feeding activities of marine calanoid copepods may be accelerated in accordance with the nocturnal upward migration (Gauld 1953; Mackas & Bohrer 1976). In freshwater, *Pseudodiaptomus hessei* demonstrated the nocturnal increase in the gut fullness, which occurred with the upward migration (Hart 1977). However, this diaptomid, which is a bottom dweller in the daytime and alters to a migrator at night, is completely different in daytime behaviour from *Eodiaptomus* and *D. pallidus*. Such specified behaviour of it seems to cause the night increase in the gut fullness. It is conceivable, therefore, that a connection of the diurnal feeding activity with the diurnal vertical migration in a short distance is not decisive in diaptomids.

Additionally, *Eudiaptomus graciloides* showed another feeding pattern; the high filtering rate in the daytime (Nauwerck 1959). Thus, the diurnal feeding pattern of freshwater calanoid copepods may be possibly species-specific, or highly variant depending on the differences in circumstances where copepods live. Furthermore analytical studies in relation to physico-chemical and biological factors will be needed to define the characteristics of the diurnal feeding of diaptomids in nature.

4-3. Diurnal variation in size-selective feeding

In *D. longispina*, the selection of food size was almost consistent and less variable during one diurnal period in every experiment, except rare drastic changes in selectivity. Such changes were connected with either a striking decrease or increase in feeding rate on a given algal fraction. However, those changes are exceptional, and the selective feeding of *Daphnia* in diurnal cycle is characterized by the consecutive small selection.

According to Gliwicz (1977), *D. longispina* and *D. cucullata* in Lake Mikołajskie showed no pronounced changes in their filtering rates and kept the small particles selection throughout a day in nature. It can be generally said, therefore, that selective feeding of daphnids may be stable during a day when feeding and filtering rates vary gradually according to time.

In *E. japonicus*, the food size selection during one diurnal cycle was consecutively stable in autumn, and almost obscure in spring, but a little changeable in summer. But, such changes were derived from unexplainable alteration of the feeding rate, differing from those in *Calanus*

helgolandicus which depends on qualitative and quantitative changes in food (Richman & Rogers 1969). Gliwicz (1977) reported the diurnally invariant selection for food size by *Eudiaptomus graciloides*. Except for the above derivative changes, thus, it should be understood that the food-size selection of *Eudiaptomus* may be unchangeable throughout a day in each season when the quantity and quality of food does not change diurnally, although it changes seasonally with relation to the food quality (Okamoto, in preparation).

When marine and freshwater herbivorous zooplankton exhibit definite diurnal changes in feeding and filtering rates on natural phytoplankton, however, whether or not such changes may be accompanied with changes in the food size selection has never been examined in detail. Thus, these two activities must be studied together in nature.

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