

*Diel vertical migration of Daphnia in Lake Kizaki:
Difference in its pattern depending on
the daphnid's body size*

Takayuki HANAZATO¹, Shin'ichiro SAMBO² and Hidetake HAYASHI²

¹Suwa Hydrobiological Station, Shinshu University, Kogandori 5-2-4, Suwa,
Nagano 392-0027, Japan, and ²Faculty of Science, Shinshu University,
Asahi 3-1-1, Matsumoto, Nagano 390-0802, Japan

Abstract

The pattern of diel vertical migration (DVM) of *Daphnia galeata* was analyzed in summer in Lake Kizaki (a small mesotrophic lake) with maximum depth of 29.5 m. Juveniles, small adults and medium-sized adults stayed the whole day at 4-8, 8 and 14 m depths, respectively, and did not perform DVM, while large adults showed DVM between 14 m and near the bottom layer (26-27.5 m). Smaller adults had larger clutch sizes relative to their body size and allocated more energy to reproduction than larger adults. They might have compensated for loss due to predation by producing abundant offspring in the epilimnion where the food level was higher. On the other hand, the larger adults performed DVM to reduce mortality due to predation at the cost of reduced reproductivity induced by environmental factors in the hypolimnion (low concentrations of food and oxygen). The study thus demonstrated that even a single population of *Daphnia* can show different DVM patterns depending on body size (life stage).

1 Introduction

Diel vertical migration (DVM) of zooplankton, where the animals migrate downwards in the morning and upwards in the evening, have attracted attention of zooplankton ecologists for nearly a century, and its adaptive significance has been discussed (LAMPERT, 1989, 1993). The predator-avoidance hypothesis is now widely accepted. That is, the zooplankton perform downward migration by day to escape from mortality due to predation by the visually orienting predator fish, while ascend to the upper layer (epilimnion) by night to obtain food. This hypothesis is strongly supported by recent findings that DVM is induced by chemicals (kairomones) released from predators (DODSON, 1988 ; NEILL, 1990 ; LOOSE and DAWIDOWICZ, 1994).

Although DVM benefits zooplankton by reducing mortality in the presence of predators, there is an accompanying cost. The vertically migrating zooplankton have a reduced rate of growth and reproduction because they are exposed to unfavorable

environmental factors in the deep water layer (hypolimnion), such as low food concentration, low water temperature and low oxygen concentration (LOOSE and DAWIDOWICZ, 1994; HANAZATO and DODSON, 1995; HANAZATO, 1996). If the cost overcomes the benefit, the zooplankton cease DVM, as seen in the cladoceran *Daphnia longispina*, which stayed near the lake surface all day under food limited conditions (oligotrophic condition), but performed DVM when the water body was enriched with food particles (JOHNSEN and JACOBSEN, 1987). Zooplankton thus carry out DVM under a balance of cost and benefit (GLIWICZ and PIJANOWSKA, 1988).

Zooplankton may be expected to change their pattern of DVM depending on the environmental conditions, which affects the cost and benefit, and these in turn may be influenced by body size, because processes such as predation and feeding efficiency depend on the body size (BROOKS and DODSON, 1965; HALL *et al.*, 1976; O'BRIEN, 1979). A nice example of the influence of body size was demonstrated by STICH and LAMPERT (1981) for *Daphnia galeata* and *D. hyalina* in Lake Constance, where the smaller *D. galeata* stayed in the epilimnion for whole day while the larger *D. hyalina* performed DVM. Changes in pattern of DVM within a single species may also be expected, since zooplankton change their size with growth and this has been shown in examples where the smaller juvenile individuals do not carry out DVM but stay in epilimnion whole day, whereas the larger adult individuals do so (ZARET and SUFFERN, 1976; HANAZATO *et al.*, 1989).

The cladoceran *Daphnia* is the animal performing DVM in many lakes. As it continues to grow after maturation, we assumed that it might change its pattern of DVM after maturation. To test this, we analyzed DVM of *D. galeata* in Lake Kizaki.

Lake Kizaki is a small mesotrophic lake in a mountainous area (764 m above sea level) of central Japan. It has a surface area of 1.4 km² and a maximum depth of 29.5 m. *D. galeata* is the dominant zooplankton species, and its DVM has been studied by SEKINO and YOSHIOKA (1995) and AJISAWA (1996), who, however, have not analyzed the DVM pattern of the adult *Daphnia* depending on the body size.

2 Methods

The DVM of *D. galeata* was observed at the center of the lake in the summer of 1996 for 48 h from noon on 29 July to noon on 31 July. *Daphnia* were collected every 6 h from 8 different depths (0, 4, 8, 14, 18, 22, 26, 27.5 m) by taking 18 liters of lake water at each depth using a Van-Dorn sampler (6 liter in volume) and concentrated the sample using a plankton net (40 μ m mesh) on the boat. The concentrated sample was preserved with sugar formalin (HANEY and HALL, 1973).

At the sampling time, water temperature was measured with a thermistor thermometer at 1-m intervals from surface to lake bottom, and dissolved oxygen concentration was determined at depths of 0, 2, 4, 6, 8, 10, 14, 18, 22, 26 and 27.5 m by

the Winkler method. To assess the standing crop of total and edible phytoplankton, water samples were collected with a Van-Dorn sampler from the same depths as those where *Daphnia* was collected, and total particles and particles smaller than 40 μm in the sampled water were collected with Whatman GF/C filter. Chlorophyll *a* in the particles was then determined spectrophotometrically according to MARKER *et al.* (1980).

In the laboratory, the *Daphnia* individuals in the samples were counted under a microscope and were divided into juveniles and adults; the latter were the animals with well developed abdominal processes, while the former were the animals without them (LAMPERT, 1991). For the adult individuals, carapace length (CL), number of eggs in the brood chamber and size of the egg (shorter and longer diameters) were measured. Egg volume was estimated as a prolate spheroid using the shorter and longer diameters. To compare relative energy allocation to reproduction between different individual groups, we calculated ratio of total egg volume to body weight (E/B) for each adult individual as follows :

$$E/B = EV \times EN / CL^{2.56}$$

where, EV is mean volume of eggs in a brood chamber, EN is egg number in the chamber, and CL is carapace length. Because we did not measure body weight of the *D. galeata* individuals but DUMONT *et al.* (1975) has reported the body length-weight relationship of *D. galeata* as $W = 9.5 \times 10^{-8} L^{2.56}$ ($W = \mu\text{g}$ dry weight, $L = \mu\text{m}$), we assumed that the body weight of the present *D. galeata* is correlated with $CL^{2.56}$, and thus we used the $CL^{2.56}$ instead of actual body weight. The value of E/B could thus be used as an indicator of energy allocation to reproduction of individuals.

We tried to compare reproductivity of adult individuals of different size groups. To fulfill this, we calculated the instantaneous birth rate (PALOHEIMO, 1974) for each group and used it as an indicator of the rate of reproduction. This calculation required egg development time of *D. galeata*, which was estimated from the water temperature to which each *Daphnia* individual was exposed using the equation for *Daphnia* given by BOTTRELL *et al.* (1976). In this calculation, we used the data collected three times at noon (29, 30, 31 July) and the calculated values were averaged.

3 Results

At the sampling time, water temperature was about 25°C at the surface and below 8°C in the hypolimnion. Thermocline was present at the depths of 6-9 m. Dissolved oxygen concentration ranged from 9 to 11 mg O₂ l⁻¹ in epilimnion and metalimnion, but declined with increasing water depth in hypolimnion. At the depth of 26 m or deeper, a low oxygen layer (<2 mg O₂ l⁻¹) was present.

Chlorophyll *a* concentration of the total particles was between 4 and 9 $\mu\text{g l}^{-1}$ in the layers from surface to 10 m depth, but about 1 $\mu\text{g l}^{-1}$ in the deeper layer of the hypolimnion (Fig. 1). Chlorophyll *a* concentration of particles $< 40 \mu\text{m}$ decreased with increasing water depth from surface to near the bottom layer, with a maximum of 3 $\mu\text{g l}^{-1}$ at 2 m depth. This suggests that edible algae were most abundant in the epilimnion and that their amount decreased with increasing water depth.

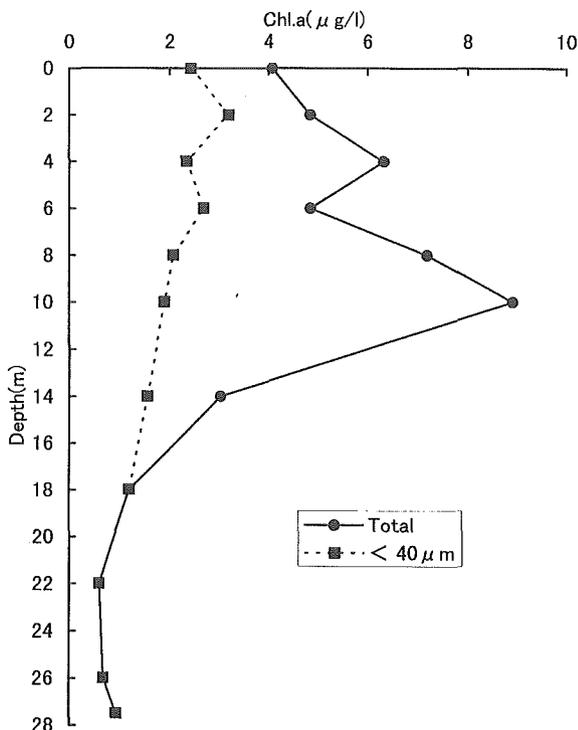


Fig.1 Vertical profile of chlorophyll *a* concentration for total particles and particles $< 40 \mu\text{m}$ in Lake Kizaki at the sampling time.

The analysis of vertical distribution of *Daphnia* individuals at 6-h intervals showed that juveniles were distributed in the epilimnion and metalimnion for whole day with the density peaks at 4-8 m (Fig. 2). Adult individuals showed two marked density peaks at the depths of 8 and 26 m at 12:00. However, the density peak at 26 m disappeared at midnight, when most adult individuals were at 8-14 m depth.

Analysis of body length (carapace length)-egg volume relationship showed that there were different size groups of adult individuals at noon at 8, 14 and 26-27.5 m depths (Fig. 3). Larger individuals stayed at deeper layers and had larger eggs. A similar analysis of individuals was made at noon and midnight at 8, 14 and 26-27.5 m depths (Fig. 4). At 8 m the size ranges of carapace length (mostly 600-900 μm) and egg

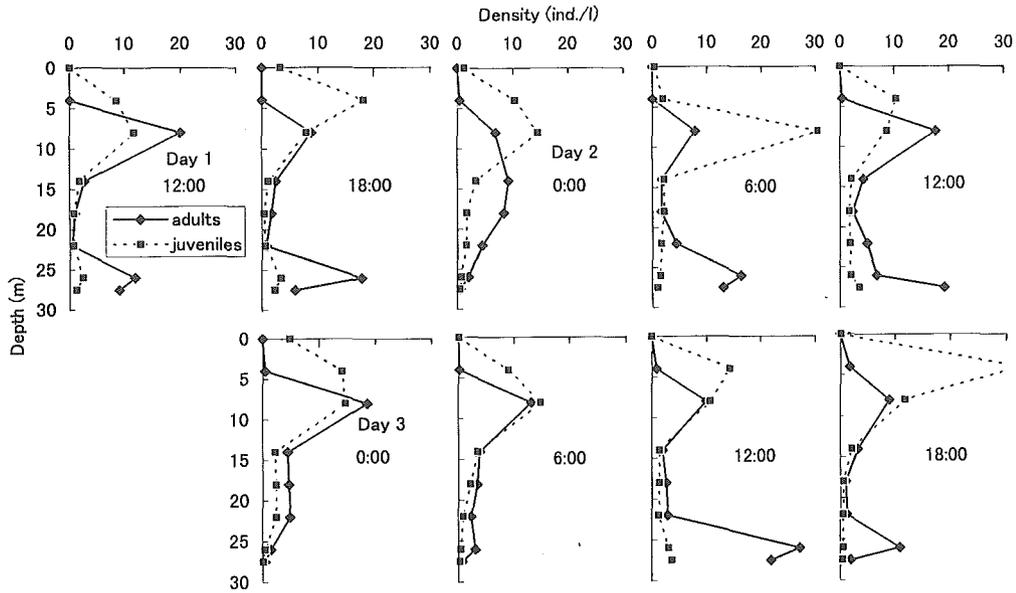


Fig. 2 Changes in vertical profiles of density of juveniles and adults of *D. galeata* in Lake Kizaki from 12:00 on 29 July (Day 1) to 12:00 on 31 July (Day 3) 1996.

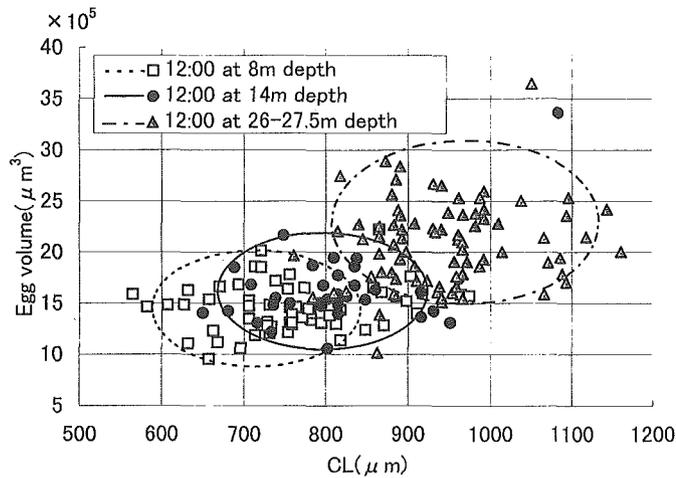


Fig. 3 Egg volume-carapace length (CL) relationship in adult individuals of *D. galeata* distributed at 8 m, 14 m and 26-27.5 m depths at 12:00 during the study period. Circles in the figure were drawn by eye to indicate approximate ranges of egg volume and carapace length in the individual groups at different depths.

volume (mostly around $15 \times 10^5 \mu\text{m}^3$ or less) at noon overlapped with those of the individuals at midnight (upper panel of Fig. 4). This indicates that the individuals distributed at 8 m depth stayed at that depth for whole day. At 14 m the ranges of carapace length (650–950 μm) and egg volume (mostly $15\text{--}20 \times 10^5 \mu\text{m}^3$) at noon were separated from those (CL: mostly $>850 \mu\text{m}$, egg volume: mostly $15\text{--}30 \times 10^5 \mu\text{m}^3$) of the individuals at 26–27.5 m at the same time (lower panel of Fig. 4). However, the ranges for individuals at 14 m at midnight covered the ranges for both 14 and 26–27.5 m at noon. This suggests that the individuals at 14 m at noon did not migrate vertically, but that the individuals distributed at 26–27.5 m at noon migrated up to 14 m depth at midnight.

Carapace length and clutch size showed a positive correlation, meaning that larger adult individuals had more eggs in the brood pouches (Fig. 5). However, the regression equation for the carapace length-clutch size relationship differed among the individuals at three different depths (8, 14, 26–27.5 m): the y-axis intercept was highest for the individuals at 8 m depth while lowest for the individuals at 26–27.5 m depth, indicating

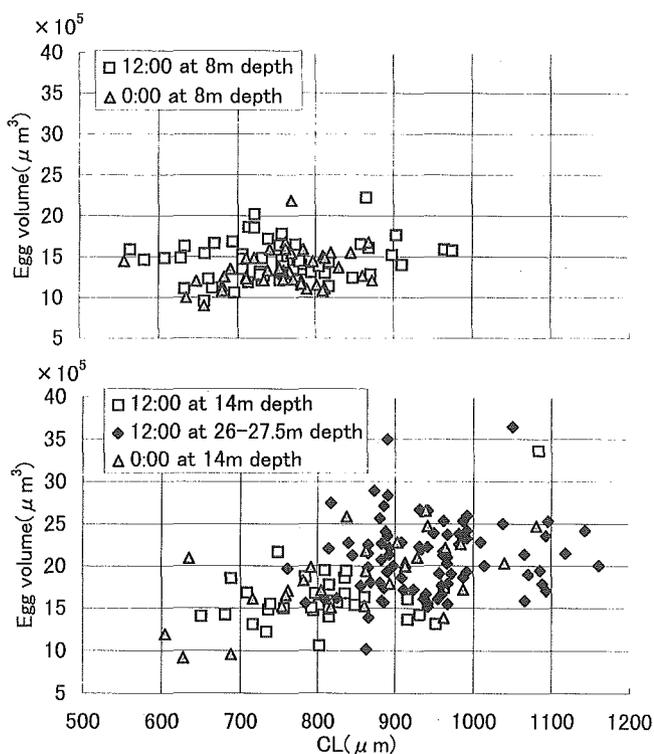


Fig. 4 Egg volume-carapace length (CL) relationship of adult individuals of *D. galeata* distributed at 8 m depth at 12:00 and 0:00 (upper panel) and at 14 and 26–27.5 m depths at 12:00 and 0:00 (lower panel).

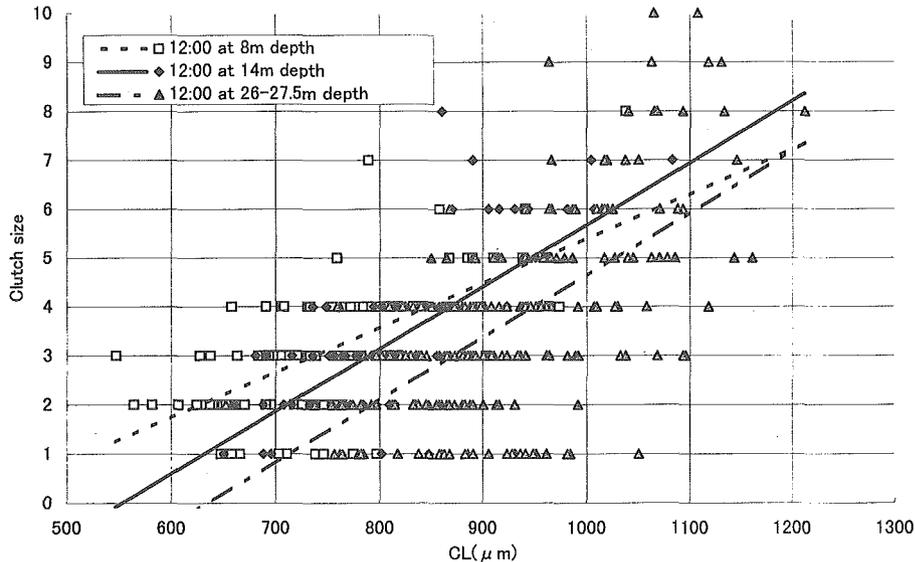


Fig. 5 Clutch size-carapace length (CL) relationship of adult individuals of *D. galeata* distributed at 8, 14 and 26–27.5 m depths at 12:00. The regression equations for the groups at 8, 14 and 26–27.5 m are, respectively $Y=0.009X - 3.760$, $Y=0.013X - 7.012$ and $Y=0.013X - 8.118$

that the individuals at shallower depths had larger clutch sizes relative to their body size than the individuals at deeper depths.

The birth rates calculated for the individual groups at 8, 14 and 26–27.5 m depths at noon were 0.18, 0.09 and 0.09, respectively. The group at 8 m had a much higher value than the other groups. The high value of the 8-m depth group was due to a relatively large clutch size and the higher water temperature to which the individuals were exposed.

The mean ratio of total egg volume to body weight (E/B) was highest at 8 m ($0.191 \pm 0.0081\text{SE}$), the next highest at 14 m ($0.179 \pm 0.0131\text{SE}$) and least at 26–27.5 m ($0.159 \pm 0.0074\text{SE}$). This suggests that the individuals at shallower depths allocated more energy to reproduction than the individuals at deeper depths.

4 Discussion

Although the present study was conducted for a short period (48h), we observed the same DVM pattern of *D. galeata* twice (between the noons of 29 and 30 July and between those of 30 and 31 July). The results indicate that *D. galeata* individuals of different size groups had different distribution patterns in Lake Kizaki, and that larger individuals were distributed at deeper layers. Juveniles, small adults (600–900 μm in CL) and medium adults (650–950 μm in CL) stayed the whole day at 4–8 m, 8 m and

14 m depths, respectively, and did not perform DVM, while large adults ($>850 \mu\text{m}$ in CL) showed DVM between 14 m and 26–27.5 m (near the lake bottom) (Fig. 6). These distributions may be explained by different predation pressures and different food environments at different water depths.

It is assumed that larger *Daphnia* individuals are more easily detected by light-oriented predator fish than smaller individuals (O'BRIEN, 1979), and that the predation pressure is higher at shallower than deeper depths (GLIWICZ and PIJANOWSKA, 1988). Thus, smaller individuals may be able to stay in the shallower layer where predation intensity was high, while larger individuals were forced to stay at deeper layer to escape from the predators. Lake Kizaki is inhabited by an abundant planktivorous fish, the pond smelt (*Hypomesus transpacificus*), which prefers feeding on *Daphnia* (SHIRAISHI, 1960). FURUTA and KIMURA (1969) analyzed the vertical distribution of fish in Lake Kizaki in the summer of 1968 with an echosounder. The abundance of fish, which was highest at the depths of 8 m or less, decreased with increasing depth from 8 to 20 m and that no fish was found at layers deeper than 20 m. Although the study was conducted nearly 30 years ago, the vertical distribution of the fish was probably similar between that time and present time because the vertical profiles of temperature and dissolved oxygen concentration in the summer of 1968 were similar in the two studies.

The food level might be highest in the near surface layer, and less at deeper depths. This was suggested by the facts that chlorophyll *a* concentration of particles $<40 \mu\text{m}$ (edible particles) decreased with increasing water depth (Fig. 1), and that the *Daphnia* individuals distributed at shallower depths (smaller individuals) tended to have a larger clutch size relative to body size than the individuals at deeper depths (larger individuals) (Fig. 5).

Although the predation pressure by fish on small adult individuals might be relatively low, they must be preyed on to some extent. However, they could compensate for this loss due to predation by producing offspring intensively under the environment with high food abundance and high temperature, as suggested by higher birth rate and higher energy allocation to egg production. When the small adults grew to medium-sized ones, the predation pressure on them increased, so that they moved to a deeper layer at about 14 m depth, resulting in their being exposed to a lower food environment. However, they persisted at that depth for the whole day. Larger daphnids can withstand lower food level than smaller ones because they have higher efficiency in collecting food, lower metabolic energy loss relative to the body size, lower threshold food concentration for population growth and larger range of food particles ingested (BROOKS and DODSON, 1965; HALL *et al.* 1976; THRELKELD, 1976; GERRITSEN, 1984; GLIWICZ, 1990). This may be the reason why the medium-sized adults could get along at a lower food level at 14 m depth.

When the medium-sized adults grew more, the predation pressure on the large individuals became larger. The large adults thus descended to near the bottom (26–27.5 m depth) to avoid fish predation. GLIWICZ (1985, 1986) assumed that the depth where fish could detect *Daphnia* is ten times deeper than the transparency. In Lake Kizaki, the transparency was 4.5 m at the present study period. According to the Gliwicz assumption, the maximum depth of the lake (29.5 m) is not enough for *Daphnia* to escape from fish. However, there was a low oxygen layer near the bottom, the concentration being less than $2 \text{ mg O}_2\text{l}^{-1}$ at 26 m or deeper. Most fish avoid such a low oxygen layer, so that this layer probably offered a refuge to *Daphnia* from fish predation. HANAZATO *et al.* (1989) reported that in Lake Yunoko *D. longispina*, which had hemoglobin to withstand oxygen deficiency, descended in daytime to the low oxygen layer near the bottom to escape from fish. This may be also the case for the large adults of *D. galeata* in Lake Kizaki. Hemoglobin synthesis of *D. galeata* distributed in the low oxygen layer was confirmed by AJISAWA (1996).

The large adults therefore stayed near the bottom to reduce mortality due to predation. However, the layer was not a favorable place for *Daphnia*, because of the low food and oxygen concentrations, both of which reduce rates of growth and reproduction in *Daphnia* (HANAZATO, 1996 ; HANAZATO and DODSON, 1995). Hence, the

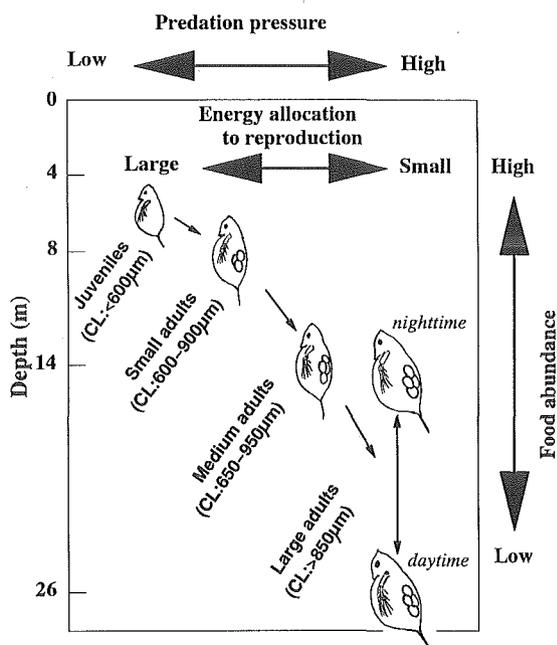


Fig. 6 Scheme showing the changes in vertical distribution of *D. galeata* with growth. It is assumed that the predation pressure by fish is larger for larger individuals than smaller ones.

large adults had to move upwards to 14 m depth in the evening to get food and more oxygen.

Although the large adults migrated to the upper layer, their reproductivity was still low in comparison with that of the smaller adult individuals, as indicated by their lower birth rate. This might be because that they were exposed to the harsh environment in the near bottom layer (deficiencies of food and oxygen) for nearly half the day. Thus, large adults performed DVM at the cost of reduced reproductivity.

The difference in the strategy between small- and large-sized adults shown here is similar to that between the smaller *D. galeata* and the larger *D. hyalina* in Lake Constance. That is, *D. galeata*, which stayed whole day in epilimnion, had higher values in birth rate, population growth rate and mortality than *D. hyalina*, which performed DVM (LAMPERT and SOMMER, 1997).

It may be concluded that the different sized (=different life stage) *D. galeata* in Lake Kizaki showed different patterns of distribution at noon and midnight under the balance of predation pressure and amount of food resource (Fig. 6).

We explained the difference in the DVM pattern among different sized *D. galeata* in Lake Kizaki as a result of changing the pattern with the daphnid's growth (a result of phenotypic plasticity in a population). However, DE MEESTER *et al.* (1995) have demonstrated that clones differing in body size of a *D. hyalina* x *galeata* hybrid population differ in DVM pattern, with the largest clone showing the greater DVM. Genetic variation as well as phenotypic plasticity in a population may concern the daphnid's DVM patterns in Lake Kizaki, as shown in DVM of *D. pulicaria* (LAIBOLD *et al.* 1994) and the copepod *Diaptomus kenai* (NEILL, 1990, 1992) although LAIBOLD *et al.* (1994) have mentioned that the phenotypic plasticity is more important than the genetic variation.

References

- AJISAWA, S. (1996). Population dynamics of *Daphnia galeata* and their mechanisms to reduce predation pressure in Lake Kizaki. Thesis of master of science, Fac. Sci., Shinshu Univ., 1995.
- BOTTRELL, H. H., A. DUNCAN, Z.M. GLIWICZ, E. GRYGIEREK, A. HERZIG, A. HILLBRICHT-ILKOWSKA, H. KURASAWA, P. LARSSON and T. WEGLENSKA (1976). A review of some problems in zooplankton production studies. *Norw. J. Zool.*, **24**, 419-456.
- BROOKS J. L. and S.I. DODSON (1965). Predation, body size, and composition of plankton. *Science*, **150**, 28-35.
- DE MEESTER, L., L.J. WEIDER and R. TOLLRIAN (1995). Adaptive antipredator defenses and genetic polymorphism in a pelagic predator-prey system. *Nature*, **378**, 483-485.
- DODSON, S.I. (1988). The ecological role of chemical stimuli for the zooplankton: predator avoidance behavior in *Daphnia*. *Limnol. Oceanogr.* **33**, 1431-1439.
- DUMONT, H. J., I. VAN DE VELDE and S. DUMONT (1975). The dry weight estimate of biomass

- in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia*, **19**, 75-97.
- FURUTA, Y. and S. KIMURA (1969). On the vertical distribution of fishes and limnological conditions in Lake Kizaki and Lake Nakatsuna in summer. *Bull. Freshwat. Fish. Res. Lab.*, **19**, 103-110 (in Japanese).
- GERRITSEN, J. (1984). Size efficiency reconsidered: A general foraging model for free-swimming aquatic animals. *Am. Nat.*, **123**, 450-467.
- GLIWICZ, Z. M. (1985). Predation or food limitation: an ultimate reason for extinction of planktonic cladoceran species. *Ergeb. Limnol.*, **21**, 419-430.
- GLIWICZ, Z. M. (1986). A lunar cycle in zooplankton. *Ecology*, **67**, 883-897.
- GLIWICZ, Z. M. (1990). Food thresholds and body size in cladocerans. *Nature*, **343**, 638-640.
- GLIWICZ, Z. M. and J. PIJANOWSKA (1988). Effect of predation and resource depth distribution on vertical migration of zooplankton. *Bull. Mar. Sci.*, **43**, 695-709.
- HALL, D. J., S.T. THRELKELD, C.W. BURNS and P.H. CROWLEY (1976). The size- efficiency hypothesis and the size structure of zooplankton communities. *Ann. Rev. Ecol. Syst.*, **7**, 177-208.
- HANAZATO, T. (1996) Combined effects of food shortage and oxygen deficiency on life history characteristics and filter screens of *Daphnia*. *J. Plankton Res.*, **18**, 757-765.
- HANAZATO, T. and S.I. DODSON (1995). Synergistic effects of low oxygen concentration, predator kairomone, and a pesticide on the cladoceran *Daphnia*. *Limnol. Oceanogr.*, **40**, 700-709.
- HANAZATO, T., M. YASUNO and M. HOSOMI. (1989). Significance of a low oxygen layer for a *Daphnia* population in Lake Yunoko, Japan. *Hydrobiologia*, **185**, 19-27.
- HANEY, J. F. and D.J. HALL (1973). Sugar-coated *Daphnia*: a preservation technique for Cladocera. *Limnol. Oceanogr.*, **18**, 331-333.
- JOHNSEN, G. H. and P.J. JACOBSEN (1987). The effect of food limitation on the vertical migration in *Daphnia longispina*. *Limnol. Oceanogr.*, **32**, 873-880.
- LAMPERT, W. (1989). The adaptive significance of diel vertical migration of zooplankton. *Func. Ecol.*, **3**, 21-27.
- LAMPERT, W. (1991). The dynamics of *Daphnia magna* in a shallow lake. *Verh. Internat. Verein Limnol.*, **24**, 795-798.
- LAMPERT, W. (1993) Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator-avoidance hypothesis. *Ergeb. Limnol.*, **39**, 79-88.
- LAMPERT, W. and U. SOMMER (1997). *Limnoecology*. Oxford University Press, New York.
- LEIBOLD, M. A., A.J. TESSIER and C.T. WEST (1994). Genetic, acclimatization, and ontogenetic effects on habitat selection behavior in *Daphnia pulicaria*. *Evolution*, **48**, 1324-1332.
- LOOSE, C. J. and P. DAWIDOWICZ (1994). Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. *Ecology*, **75**, 2255-2263.
- MARKER, A. F., E.A. NUSCH, H. RAI and B. RIEMANN (1980). The measurement of photosynthetic pigments in freshwaters and standardization of methods: Conclusion and recommendations. *Ergeb. Limnol.*, **14**, 91-106.
- NEILL, W. E. (1990) Induced vertical migration in copepods as a defense against invertebrate

- predation. *Nature*, **345**, 524-526.
- NEILL, W. E. (1992). Population variation in the ontogeny of predator-induced vertical migration of copepods. *Nature*, **356**, 54-57.
- O'BRIEN, W. J. (1979). The predator-prey interaction of planktivorous fish on zooplankton. *Am. Sci.*, **67**, 572-581.
- PALOHEIMO, J. E. (1974). Calculation of instantaneous birth rate. *Limnol. Oceanogr.*, **19**, 692-694.
- SEKINO, T. and T. YOSHIOKA (1995). The relationship between nutritional condition and diel vertical migration of *Daphnia galeata*. *Jpn. J. Limnol.*, **56**, 145-150.
- SHIRAISHI, Y. (1960). The fisheries biology and population dynamics of pond-smelt, *Hypomesus olidus* (Pallas). *Bull. Freshwat. Fish. Res. Lab.* **10**, 1-263 (in Japanese).
- STICH, H-B. and W. LAMPERT (1981). Predator evasion as an explanation of diurnal vertical migration by zooplankton. *Nature*, **293**, 396-398.
- THRELKELD, S. T. (1976). Starvation and the size structure of zooplankton communities. *Freshwat. Biol.*, **6**, 489-496.
- ZARET, T. M. and J.S. SUFFERN (1976). Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol. Oceanogr.*, **21**, 804-813