Changes in Species Composition of Cladoceran Community in Lake Kasumigaura during 1986-1989: Occurrence of *Daphnia galeata* and Its Effect on Algal Biomass

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Abstract

Seasonal changes of cladoceran community in Takahamairi Bay and the center region of Lake Kasumigaura were investigated from 1986 to 1989. The species composition of the cladoceran community was stable in summer, when *Diaphanosoma brachyurum* and *Bosmina fatalis* predominated. In contrast, during late fall-spring, it differed greatly among the years. This might be related to the predation by mysids, whose density also differed from year to year. The most marked change in species composition was the occurrence of *Daphnia galeata*, which had never been found in the lake before 1986. The grazing by *D. galeata* seemed to greatly reduce the phytoplankton biomass in Lake Kasumigaura, since the chlorophyll *a* concentration declined to very low levels when the daphnids became abundant. The birth rates of cladocerans were highest in summer. They tended to be higher in the shallower region than in the deeper one, indicating that the former was more productive for zooplankton.

Key words: cladoceran community, species composition, *Daphnia*, mysid, algal biomass, Lake Kasumigaura

1. Introduction

Seasonal changes of zooplankton community in Lake Kasumigaura from 1976 to 1985 have been reported by YASUNO *et al.* (1977, 1981), MORISHITA and YASUNO (1979) and HANAZATO and YASUNO (1988). The standing crop of zooplankton reached its highest level in summer, when cladocerans became dominant. The population dynamics and production of cladocerans were studied by HANAZATO and YASUNO (1985a, 1987a), and the zooplankton community investigation has been continued thereafter. The present study demonstrates the changes in the cladoceran community from 1986 to 1989. During this study period, a new cladoceran species, *Daphnia galeata*, occurred and seemed to affect the algal biomass greatly.

2. Methods

Samplings were performed monthly at two

stations in Takahamairi Bay and the center region of Lake Kasumigaura (Stas. 3 and 9: Fig. 1) from January 1986 through December 1989.

Fig. 1. Map of Lake Kasumigaura showing sampling stations.

The water depth was about 4 m at Sta. 3 and was about 6 m at Sta. 9. Remarkable stratification of water temperature is not observed throughout a year in this shallow lake. Water samples were taken using an acrylic tube sampler (5 cm in diameter and 2 m in length) which isolated the water column from the surface to 2 m in depth. Cladoceran zooplankton were collected by filtering 10 liter of the sampled water through a 93 μm mesh net from January 1986 to April 1987, and a 40 μm mesh net from May 1987 to December 1989. They were then fixed with sugar formalin (HANEY and HALL, 1973), and were counted under a microscope in the laboratory. Sampling and counting of Cladocera were duplicated at each station. Eggs in their brood chambers were also counted. Body length (from the top of the head to the posterior of the carapace) of each cladoceran individual was measured and the individual dry weight was estimated using the equations of body length-weight relationships determined by HANAZATO and YASUNO (1985a) for *Bosmina fatalis*, *Bosmina longirostris*, *Daphanosoma brachyurum* and *Moina micrura*, and by DUMONT *et al.* (1975) for *Daphnia ambigua* and *Chydorus sphaericus*. The weights of *Ceriodaphnia cornuta* and *Daphnia galeata* were calculated using the equations for *Ceriodaphnia quadrangula* (DUMONT *et al.*, 1975) and for *Daphnia longispina* (HANAZATO, unpublished data), respectively.

For the populations of the main Cladocera (*D. brachyurum*, *B. fatalis*, *B. longirostris*, *D. galeata* and *C. sphaericus*) with the densities > 1 individual $\cdot \text{l}^{-1}$, the instantaneous birth rates (b) were determined according to PALOHEIMO (1974) as follows,

$$b = \ln[(E/N) + 1]/D$$

where, N is the number of individual per liter, E is the number of eggs per liter, and D is the egg development time in days. The egg development times of cladocerans at the sampling occasion were estimated from water temperature at that time using the equations determined by HANAZATO and YASUNO (1985b) for *B. fatalis*, *B. longirostris* and *D. brachyurum*. For esti-

mation of the egg development time of *C. sphaericus*, the equation by VIJVERBERG (1980) for the same species was used. Because there were no available data for estimating the egg development time of *D. galeata*, the equation for *Daphnia longispina* determined by HANAZATO and YASUNO (1985b) was used.

Because a mysid, *Neomysis intermedia*, has been considered an important predator for the cladoceran populations in Lake Kasumigaura (HANAZATO and YASUNO, 1988), the mysid density was estimated by collecting the individuals with vertical tows from the lake bottom to the surface using 40 cm-diameter and 194 μm -mesh plankton net at the same time as the zooplankton sampling. The sampling and counting of the mysids were performed in duplicate.

Chlorophyll a concentration in the sampled water was determined by the UNESCO-SCOR method (UNESCO/SCOR, 1966) and was used to represent the algal biomass in the lake water.

3. Results

Figure 2 shows the seasonal changes in the density of cladoceran species at Sta. 3 during 1986–1989. In 1986, no Cladocera was found until June except for the scant appearance of *Daphnia ambigua* and *Bosmina longirostris* (the density $< 6 \text{ l}^{-1}$) during January–March. *Daphnosoma brachyurum*, *Bosmina fatalis* and *Chydorus sphaericus* occurred abundantly during summer–fall, and their density peaks appeared in August, September and October, respectively. Their densities declined in late fall, when *Daphnia galeata* appeared with low densities ($< 10 \text{ l}^{-1}$) but maintained its population until April 1987. In 1987, *Moina micrura* built up a large population in June. *D. brachyurum* and *B. fatalis* became dominant in August and September as in 1986, but they decreased rapidly in October. *C. sphaericus*, however, did not appear in this year. In 1988 and 1989, *D. brachyurum*, *B. fatalis* and *C. sphaericus* dominated the cladoceran community and the pattern of their seasonal succession was similar to that in 1986. In both years, *B. longirostris* and *D. galeata* appeared in the late fall, and the latter maintained the large popula-

Fig. 2. Seasonal changes in the density of cladoceran species at Sta. 3 from 1986 through 1989. The shaded area in 1987 indicates the period of no observation.

tion throughout the winter and early spring.

HANAZATO and YASUNO (1989a, 1989b, 1990) reported the appearance of *Daphnia longispina* toothed form in experimental ponds into which the bottom mud from Lake Kasumigaura was introduced. The *Daphnia* which appeared in the experimental ponds and the *Daphnia* which has been found annually in Lake Kasumigaura since the fall of 1986 are one and the same species. HANAZATO and YASUNO identified the *Daphnia* according to CHRISTIE (1983), but his taxonomy has not been widely accepted. Recently, FLOSSNER and KRAUS (1986) described the taxonomy of the *Daphnia hyalina-galeata* complex. On the basis of their taxonomy, the present investigation decided that the *Daphnia* observed in Lake Kasumigaura should belong

to *D. galeata*.

At Sta. 9, *D. brachyurum*, *B. fatalis*, *C. sphaericus* and *D. galeata* appeared abundantly (Fig. 3). *D. brachyurum* and *B. fatalis* predominated every summer and fall as at Sta. 3, but their densities were lower than those at Sta. 3 except for *D. brachyurum* in 1986. *C. sphaericus* built up a large population in October 1986, but scarcely appeared thereafter. *D. galeata* showed three density peaks as at Sta. 3 (in December 1986, January 1989 and December of 1989). The peak density in December 1986 was markedly higher at Sta. 9 than at Sta. 3. In the other seasons, however, *D. galeata* was less abundant at Sta. 9. *M. micrura* and *B. longirostris* were found at Sta. 9. as well as at Sta. 3, but their densities were usually below 10

Fig. 3. Seasonal changes in the density of cladoceran species at Sta. 9 from 1986 through 1989. The shaded areas in 1986 and 1987 indicate periods of no observation.

l⁻¹.

At Sta. 3, the instantaneous birth rates of *D. brachyurum* and *B. fatalis* became highest in July–September but declined rapidly in fall (Fig. 4). The annual highest values ranged between 0.2 and 0.3 in *D. brachyurum*, while the highest values of *B. fatalis* were above 0.4 except in 1988. Thus, the *B. fatalis* population was more productive than the *D. brachyurum* population in summer. A similar tendency was observed at Sta. 9, but the instantaneous birth rates of cladocerans were usually lower at Sta. 9 than at Sta. 3. From fall to spring, the rates were usually small. However, *D. galeata* sometimes showed high rates (about 0.2) even in those seasons (e.g., in November 1988 and May 1989 at Sta. 3, and February 1987 at Sta. 9).

The highest cladoceran biomass was found in September or October of 1986, 1987 and 1989. It is mainly composed of *B. fatalis* (Fig. 5). At Sta. 9, on the other hand, the biomass usually became highest in August, when *D. brachyurum* was dominant. In 1988, however, the highest biomass peak appeared in December at Sta. 3

and *D. galeata* mainly established this peak. This species also elevated the cladoceran biomass greatly at Sta. 9 in the same season, but the appearance of its peak was delayed for one month, and occurred in January 1989. The abundant occurrence of *D. galeata* was again observed in December 1989 both at Stas. 3 and 9. The biomass reached a considerably high level (840 g dry wt·m⁻³) at Sta. 3.

A mysid, *Neomysis intermedia*, established large density peaks in spring and early summer (Fig. 6). They often appeared in fall but never became abundant (the density < 10 individuals·m⁻³) except in the fall of 1988 at Sta. 9. The density reached 136 individuals·m⁻³ at that time. At Sta. 3 in 1988 and at Stas. 3 and 9 in 1989, no mysid was caught by vertical tows in the fall.

Figure 7 shows the seasonal changes in chlorophyll *a* concentration at Stas. 3 and 9 during 1986–1989. The concentrations were minimum in January–March. At Sta. 3, the minimum concentration was 20–30 µg·l⁻¹ in 1986–1988, but fell to 0.7 µg·l⁻¹ in January 1989. At Sta. 9,

Fig. 4. Seasonal changes in the instantaneous birth rate (b) of the main cladoceran species at Stas. 3 and 9 from 1986 through 1989. The shaded areas in 1986 and 1987 indicate periods of no observation.

the minimum concentration was below $6 \mu\text{g}\cdot\text{l}^{-1}$ in 1986, 1987 and 1989, while it became markedly higher ($21.7 \mu\text{g}\cdot\text{l}^{-1}$) in 1988. From spring to fall, the concentration was maintained at a high level (around $100 \mu\text{g}\cdot\text{l}^{-1}$ at Sta. 3 and around $50 \mu\text{g}\cdot\text{l}^{-1}$ at Sta. 9). In 1986, the chlorophyll a concentration fluctuated at around $150 \mu\text{g}\cdot\text{l}^{-1}$ at Sta. 3, which was apparently higher than in the other years. Blue-green algae bloomed from July to October; *Anabaena* dominated in July and *Microcystis* in August–October (TAKAMURA and YASUNO, in prep.). From late fall to spring, *Cyclotella*, *Synedra* and *Coscinodiscus* were abundant.

The relationships between chlorophyll a concentration and total cladoceran biomass are presented in Fig. 8. No correlation is noted

between their patterns in Fig. 8a, in which the data for all seasons (January–December) were plotted. The data were then classified into two groups in terms of the season: blooming season of blue-green algae (July–October) and the remaining seasons (non-blooming season for blue-green algae; November–June). They were plotted in Figs. 8b and 8c. The chlorophyll a concentration tended to become low when the cladoceran biomass was high during November–June (Fig. 8c), a relationship not recognized in the blooming season of blue-green algae (Fig. 8b).

4. Discussion

Previous studies on the zooplankton community in Lake Kasumigaura (YASUNO *et al.*, 1977;

Fig. 5. Seasonal changes in the biomass of the total cladoceran species at Stas. 3 and 9 from 1986 through 1989. The shaded areas in 1986 and 1987 indicate periods of no observation. Abbreviations in the figure show the dominant species when the biomass peak appeared. Bf = *Bosmina fatalis*; Db = *Diaphanosoma brachyurum*; Mm = *Moina micrura*; Dg = *Daphnia galeata*.

MORISHITA and YASUNO, 1979; YASUNO *et al.*, 1981; HANAZATO and YASUNO, 1985a, 1987a, 1988) reported the dominance of *D. brachyurum* and *B. fatalis* every summer. This was observed also in the present study. Thus, it may be concluded that the species composition in the cladoceran community is stable in summer. In contrast, the species composition during late fall-spring changed from year to year. Thus, at Stas. 3 and 9, *B. fatalis* and *D. galeata* were abundant in 1986, while cladocerans were scarcely found in 1987. In 1988 and 1989, *C. sphaericus*, *B. longirostris* and *D. galeata* predominated at Sta. 3, while only *D. galeata* became abundant at Sta. 9.

The occurrence of *D. galeata* is given special mention as the first record of the species in

Lake Kasumigaura. Species of the genus *Daphnia* had never been found in the lake before 1983. The first colonization of *Daphnia* was performed by *D. ambigua* in the spring of 1984 (HANAZATO and YASUNO, 1985c, 1988). The occurrence of *Daphnia* in Lake Kasumigaura seemed to be related to mysid predation, because the seasons when *Daphnia* appeared accorded well with the seasons when the mysids were absent. Before 1983, the mysids established large populations twice a year, in spring and fall, while no Cladocera were found from fall through spring (HANAZATO and YASUNO, 1988). Since 1983, however, the mysids have often failed to establish populations. Their absence certainly encouraged the colonization of the daphnids.

Fig. 6. Seasonal changes in the density of *Neomysis intermedia* at Stas. 3 and 9 from 1986 through 1989.

Fig. 7. Seasonal changes in chlorophyll *a* concentration in the water column (from surface to 2 m deep) at Stas. 3 and 9 from 1986 through 1989.

Fig. 8. Relationships between chlorophyll *a* concentration and total cladoceran biomass during all seasons (a), blooming season of blue-green algae (July-October; b), and no blooming season of the blue-green algae (November-June; c) in 1986-1989.

The mysid predation might also suppress other cladoceran populations, since *B. fatalis*, *C. sphaericus* and *B. longirostris* built up large populations in the fall of 1986, 1988 and 1989 at Sta. 3 and the fall of 1986 and 1989 at Sta. 9, when mysids scarcely appeared, whereas few cladocerans occurred in autumn of the other years, when mysids were usually abundant. Mysids have a strong predation impact on cladoceran populations and often eliminate various cladoceran species from lakes (RICHARDS *et al.*, 1975; GOLDMAN *et al.*, 1979; RIEMAN and FALTER, 1981; LANGE LAND, 1988). In Lake Stugusjoen (Norway), Cladocera was scarce when the biomass of mysids (*Mysis relicta*) was reportedly high (50–300 mg dry wt·m⁻²) (LANGE LAND, 1988). The biomass of *Neomysis* in Lake Kasumigaura was much higher: the density peaks of mysids at Stas. 3 and 9 during the present study period were 800–3,000 individuals·m⁻², which approximately equal 500–2,000 mg dry wt·m⁻² (TODA, personal communication). HANAZATO and YASUNO (1988) suggested that in Lake Kasumigaura from 1980 to 1985, the cladoceran densities during fall to spring were mainly controlled by mysid predation. This may well be true of the cladoceran community during 1986–1989.

Cladocerans are important grazers on phytoplankton and suppress the phytoplankton biomass in many lakes. Therefore, a negative correlation between cladoceran abundance and phytoplankton biomass has often been observed in various water bodies (OLRIK *et al.*, 1984; LAMPERT, 1988). In Lake Kasumigaura, the negative correlation between them was not detected if the data during all seasons (January–December) or during blooming season of blue-green algae (July–October) were plotted (Fig. 8). However, when the data during November–June were plotted, a marked negative correlation appeared both at Stas. 3 and 9. These results may suggest that the biomass of the blue-green algae was not affected by the grazing of cladoceran zooplankton probably because the algae were inedible for cladocerans. In contrast, during November–June, the algal biomass decreased

when cladocerans became abundant. In particular, chlorophyll *a* concentration became very low when *D. galeata* established large populations (in December 1988–January 1989 and December 1989 at Sta. 3; in December 1986, February 1987 and January 1989 at Sta. 9: see Figs. 5 and 7). *D. galeata* certainly reduced the algal abundance. *Daphnia* is the most efficient grazer on phytoplankton, and often leads to a dramatic reduction in phytoplankton biomass in lakes (SHAPIRO, 1980). The spring clear phase in lakes is a well known phenomenon that *Daphnia* reduced the phytoplankton biomass (LAMPERT *et al.*, 1986). HANEY (1973) and JARVIS (1986) measured *in situ* community grazing rate of zooplankton and reported that *Daphnia* was the most important grazer and the community grazing rate exceeded 100% when the density of *Daphnia* reached to about 50–100 individuals·l⁻¹. Such high daphnid density was often attained by *D. galeata* in Lake Kasumigaura. Thus, *D. galeata* certainly exerted a great influence on phytoplankton community in the lake.

The biomass and instantaneous birth rates of cladocerans were usually highest in summer, reflecting its peak production. The previous studies (HANAZATO and YASUNO, 1985a, 1987a) also reported that the highest biomass and production of cladocerans occurred in summer in Lake Kasumigaura. These results indicate the large food supply available to zooplankton in this season. Summer was the season when blue-green algae, mostly *Microcystis* spp., bloomed heavily. *Microcystis* has been considered to be inedible for cladoceran zooplankton (SIRENKO *et al.*, 1976; LAMPERT, 1981, 1982; HANAZATO and YASUNO, 1984, 1987b; NIZAN *et al.*, 1986). However, HANAZATO and YASUNO (1987b, 1987c) demonstrated that *Microcystis* becomes available as cladoceran food when it is decomposed. This decomposition in summer may assure the food supply for the cladocerans in Lake Kasumigaura, as earlier suggested by HANAZATO and YASUNO (1987a, 1987b). Thus, the detritus food-chain seemed to be the main energy channel from phytoplankton to zooplankton in summer. Recently, HANAZATO and

WATANABE (in prep.) emphasized the importance of bacteria in the decomposition of *Microcystis* as food for zooplankton.

HANAZATO and YASUNO (1987a) showed that the productivity of cladocerans was higher in the shallower regions than in the deeper regions of Lake Kasumigaura. They hypothesized that the resuspension of detritus from the bottom, which could be utilized by zooplankton as their food, would be correlated with the water depth, and consequently the shallower regions could be more productive for zooplankton than the deeper regions. In the present study, the biomass and instantaneous birth rates of cladocerans also tended to be higher at the shallower Sta. 3 than at the deeper Sta. 9. The present results support HANAZATO and YASUNO (1987a) hypothesis.

Acknowledgments

We are indebted to the members of the Lake Kasumigaura research group in the National Institute for Environmental Studies for their assistance in the field work. Thanks are also due to Dr. J. URABE for his valuable comments on the taxonomy of *Daphnia*, and to Dr. H. TODA for his helpful suggestions.

摘 要

霞ヶ浦における枝角類動物プランクトン群集の変動(1986-1989): *Daphnia galeata* の出現とそれが植物プランクトン量に及ぼす影響

1986-1989の4年間にわたり霞ヶ浦における枝角類動物プランクトン群集の変動を調べた。枝角類群集の種組成は夏には安定しており、*Daphanosoma brachyurum* と *Bosmina fatalis* が優占した。一方、秋から春にかけては変動が大きく、これにはイサザアミの捕食が大きく関与しているように思われた。最も顕著な種組成の変化は *Daphnia galeata* の出現である。この種は1986年以前には霞ヶ浦では観察されていなかった。*D. galeata* の現存量が高くなったときにはクロロフィル量がかなり低くなった。*Daphnia* が摂食活動によって植物プランクトン量を大きく減少させたものと考えられる。霞ヶ浦の枝角類の増殖速度は夏に高く、また水深の浅い地点で深い地点よりも高くなる傾向があり、浅い地点では動物プランクトンの生産

量が高いことが推察された。

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Received: 18 April 1990

Accepted: 15 October 1990