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journal or publication title	Japanese Journal of Limnology
volume	57
number	1
page range	27-37
year	1996-03-01
URL	<a href="http://hdl.handle.net/2297/7315">http://hdl.handle.net/2297/7315</a>

## Grazing and Food Size Selection of Zooplankton Community in Lake Biwa during BITEX '93

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### Abstract

Community grazing rate of zooplankton larger than 98  $\mu\text{m}$  in body size were examined at the north and south basins of Lake Biwa in late summer, 1993. The lake seston labeled with  $^{14}\text{C}$  was divided into different size fractions (<2, 2-8, 8-20 and 20-70  $\mu\text{m}$ ), and the grazing rate for each size fraction was determined under ambient food condition. During the study period, *Eodiaptomus japonicus* dominated, followed by *Daphnia galeata* at both sites. In all experiments, the grazing rate was higher for middle size fractions (2-8 and 8-20  $\mu\text{m}$ ) than the smallest and largest size fractions, indicating that the zooplankton communities selectively remove seston in the size range of 2-20  $\mu\text{m}$ . Community ingestion rate estimated from the grazing rate and abundance of ambient seston revealed that seston in the middle size fractions was main food of zooplankton. When abundance of seston <20  $\mu\text{m}$  was low relative to those >20  $\mu\text{m}$ , however, the largest size fraction contributed 57% of the ingested carbon, suggesting that the food source of zooplankton is not necessarily restricted to the small sestonic particles, even if feeding efficiency was low for large sestonic particles. Based on grazing rate, 6 to 10% of total seston was estimated to be removed by the zooplankton community within a day.

**Key Words:** zooplankton, grazing, seston, Lake Biwa, BITEX '93, size selectivity.

### 1. Introduction

In pelagic systems, grazing by zooplankton can be important loss process in populations of resource organisms including planktonic algae, bacteria and protozoans (LAMPERT, 1988; HESSEN *et al.*, 1989; STERNER, 1989; MAZUMDER *et al.*, 1990; CARRICK *et al.*, 1991; GASOL and VAQUÉ, 1993; URABE, 1994; URABE *et al.*, 1995). However, zooplankton do not ingest these potential food organisms at equal rate. Due to physiological and physical constraints in feeding apparatus and behavior, there is a size dependence to zooplankton feeding (BURNS, 1968; GLIWICZ, 1969; HESSEN, 1985; VANDER-PLOEG, 1990; DEMOTT, 1990). In addition, some zooplankton taxa such as calanoid copepods, actively discriminate among food items based on chemical characteristics (BUTLER *et al.*, 1989; DEMOTT, 1990; VANDER-PLOEG, 1990). It is

thus easily expected that species of the resource organisms differ in the extent to which they suffer grazing. Other than grazing, zooplankton can also affect phytoplankton by modulating nutrient cycling (STERNER, 1989; URABE, 1993, 1995; URABE *et al.*, 1995). To understand the details of zooplankton impact on resource organisms and material flows in a given lake, however, quantitative data on grazing rate and diet selection are essential.

In Lake Biwa, the largest lake in Japan, several studies have examined the grazing rate and feeding selectivity of zooplankton species. URABE *et al.* (1995) showed that grazing by zooplankton can be a major loss process of sestonic particles in the epilimnion at the north basin of L. Biwa in some seasons. NAKANISHI *et al.* (1992) also reached the same conclusion based on primary production rate and literature data on feeding rate of the zooplankton species.

Using elaborate methods with ambient food particles labeled by  $^{14}\text{C}$ , OKAMOTO (1984a) indicated that two dominant zooplankton species, *Daphnia galeata\** and *Eodiaptomus japonicus*, selectively ingest smaller phytoplankton in L. Biwa. NAGATA (1985) and NAGATA and OKAMOTO (1988) examined the feeding rate of these zooplankton species for bacteria. According to them, *Daphnia* can ingest bacteria as efficiently as algae smaller than  $25\ \mu\text{m}$ , but *Eodiaptomus* not. Apart from these experimental studies, KAWABATA (1987) examined gut contents of *D. galeata* and *E. japonicus*, and found that large individuals of these species can ingest large algae such as *Closterium aciculare* and *Melosira solida*. However, these studies have examined feeding performance of zooplankton at species or population levels. There are no quantitative data about grazing impact of zooplankton community on food organisms in different size categories in L. Biwa.

During the BITEX '93 (an international research program entitled "Biwako transport experiment": KUMAGAI *et al.*, 1995), we had an opportunity to examine intensively the grazing rate of zooplankton at the north and south basins of L. Biwa. Here, as a part of BITEX '93, we report the grazing rate of zooplankton community for food particles in different size categories.

## 2. Materials and methods

Grazing experiments were conducted under semi-*in-situ* conditions on 26 August and 3 September 1993. Zooplankton were collected at 1 m depth at Station S (3 m deep) in the south basin and 5 m depth at Station N (50 m) in the north basin of Lake Biwa. The sampling depth was decided based on the vertical profile of zooplankton abundance: the zooplankton was most abundant in 5 m layer at Station N, while apparent peak was not found in the vertical profile at Station S (KAWABATA and URABE, 1995). Community grazing rate was estimated

for zooplankton that were retained on  $98\ \mu\text{m}$  mesh net.

### 2-1. Sampling and enumeration

Two days before the grazing experiment, lake seston used as labeled food was collected at each station using a modified 10-L Van Dorn sampler at 9:30–11:00 hours. On each station and date when the grazing experiment was made, zooplankton with lake water was collected as mentioned above. Immediately after the sampling, the zooplankton were placed into 20-L tanks with lake water, mixed gently, and then transferred to 20 (26 Aug.) or 24 (3 Sept.) 1.1-L polycarbonate bottles without any concentration. These live zooplankton in the polycarbonate bottles were transported to a laboratory near the shore of the lake and used for the grazing experiments.

Simultaneous with the live zooplankton sampling, additional four 10-L zooplankton samples were collected to estimate biomass and composition. Among them, two were concentrated using a plankton net with  $40\text{-}\mu\text{m}$  mesh ( $>40\ \mu\text{m}$  fraction). The remaining samples were filtered once through a  $98\ \mu\text{m}$  mesh net and then concentrated with the  $40\ \mu\text{m}$  mesh net ( $40\text{-}98\ \mu\text{m}$  fraction). These samples were fixed with acid Lugol's solution. All individuals in the samples were counted for developmental stages in copepods and for size classes in cladocerans. There were few rotifers during the study period. Dry weight of each zooplankton was estimated according to length-weight relationships shown in Table 1. The composition and biomass of zooplankton  $>98\ \mu\text{m}$  was determined from the difference between the  $>40\ \mu\text{m}$  and  $40\text{-}98\ \mu\text{m}$  zooplankton fractions.

Water samples were also collected to determine abundance and size composition of seston. According to SIEBURTH *et al.* (1978), seston was divided into three size fractions, pico- ( $<2\ \mu\text{m}$ ), nano- ( $2\text{-}20\ \mu\text{m}$ ) and micro-fractions ( $>20\ \mu\text{m}$ ), using a  $2\ \mu\text{m}$  Nuclepore membrane filter and a  $20\ \mu\text{m}$  mesh net. Sestonic particles in each fraction were concentrated onto precombusted Whatman GF/F glass-fiber filters. These filters were enveloped with pieces of aluminum foil and stored at  $-20\ ^\circ\text{C}$ . Sestonic carbon onto the

\*This species had been reported as *D. longispina hyalina* (OKAMOTO, 1984a, b) or *D. longispina* (NAGATA, 1985; NAGATA and OKAMOTO, 1988; KAWABATA, 1987; 1989), but was identified as *D. galeata* (J. HRBACEK, pers. comm.).

Table 1. Dry weight (DW:  $\mu\text{g}$ ) of individual crustaceans used to estimate zooplankton biomass. The furcal ramus of *M. dissimilis* copepodid stages, and head of *D. galeata* and *B. longirostris* are not included in the length (L: mm). In *E. japonicus*, individual body weight directly estimated are used.

Species	Specific weight	Reference
<i>Eodiaptomus japonicus</i>		
naupliar stage	$\text{DW} = 3.47 \times \text{L}^{2.26}$	McCAULY (1984)
copepodid stage		
I	$0.82 \mu\text{g} \cdot \text{ind}^{-1}$	KAWABATA and URABE
II	1.35	(unpubl.)
III	2.57	
IV	3.84	
V male	5.14	
V female	5.64	
VI male	5.88	
VI female	7.81	
<i>Mesocyclops dissimilis</i> *		
naupliar stage	$\text{DW} = 7.83 \times \text{L}^{2.55}$	McCAULY (1984)
copepodid stage	$\text{DW} = 3.56 \times \text{L}^{2.26}$	McCAULY (1984)
<i>Daphnia galeata</i>	$\text{DW} = 9.85 \times \text{L}^{2.71}$	URABE and WATANABE (1990b)
<i>Diaphanosoma brachyurum</i>	$\text{DW} = 5.07 \times \text{L}^{3.05}$	McCAULY (1984)
<i>Bosmina longirostris</i>	$\text{DW} = 32.2 \times \text{L}^{2.60}$	URABE and WATANABE (1990b)

\* This species had been identified formerly as *M. leuckarti* or *M. thermocyclopoides* (DEFAYE and KAWABATA, 1993)

glass-fiber filter was analyzed with a CHN analyzer (Yanaco, model MT-3).

## 2-2. Grazing experiments

Grazing rate of zooplankton community was examined for food particles in four size fractions (<2, 2-8, 8-20 and 20-70  $\mu\text{m}$ ). In the present study, grazing rate ( $G$ ) is defined as water volume (liter) cleared per unit time (day) by zooplankton assemblage in unit water volume (liter).

Two days before the grazing measurements, the lake water collected at each station was filtered by 70  $\mu\text{m}$  nylon mesh screen and seston in the filtrate was labeled in 500 ml aliquots with 200-250  $\mu\text{Ci}$   $\text{NaH}^{14}\text{CO}_3$  for 48 hr at constant light condition by cool-white fluorescent bulbs. Grazing experiments were performed under dim light condition at 26°C which was almost the same to the water temperature where the zooplankton samples were collected (25~27°C). To initiate the grazing experiments, the labeled seston was filtered through either Nuclepore filters (2 or 8  $\mu\text{m}$ ) or nylon screen mesh (20 or

70  $\mu\text{m}$ ). Then, 30-55 ml from one of these filtrates was added to the 1.1-L Polycarbonate bottles containing the zooplankton. Thus, the amount of labeled seston was less than 5% of total seston in the bottle. For each fraction, four (26 Aug.) or three bottles (3 Sept.) were used for feeding trial and remaining two bottles were used for 0-time measurement (see below).

During the feeding trial, two 1-ml aliquots of feeding suspension was sampled and filtered onto 0.2  $\mu\text{m}$  Sartorius filters to determine the radioactivity of the food. Animals were allowed to feed for 15 min according to OKAMOTO (1984a).

At the end of feeding trial, the contents of the bottle were filtered through 98  $\mu\text{m}$  nylon mesh disk (45 mm in diameter). Zooplankton retained on the mesh disk were rinsed with 0.001 N HCl and then several times with distilled water. Immediately after rinsing, the mesh disk with zooplankton was placed in a scintillation vial without any fixation to prevent loss of isotope. Liquid scintillation fluor (10 ml

of Aquasol-2) was added to each vial within 2 hr after the feeding trial, and radioactivity was measured with a liquid scintillation counter. Quenching correction was made by the external standard method.

To correct for errors due to labeled food retained on the mesh disk but not ingested by zooplankton, the contents of bottles for 0-time measurement were filtered onto the mesh disk immediately after the labeled food was injected. The radioactivity at 0-time was usually less than 10% of that at the end of feeding trial. Quenching by the nylon mesh disk was also checked by putting a known amount of radioisotope into the scintillation vials containing 10 ml of the fluor, but no significant difference was detected in counting efficiency between vials with and without the mesh disk.

The grazing rate on each size fraction was calculated according to equations by MAZUMDER *et al.* (1990). The grazing rate on food smaller than  $i \mu\text{m}$  ( $G_i: \text{d}^{-1}$ ) was calculated as follows,

$$G_i = (Z_i - Z_i^*) \times (24\text{hr} \times 60 \text{ min}) / (F_i \times t) \quad (1)$$

where,  $Z_i$  and  $Z_i^*$  are radioactivity on the mesh disk ( $\text{dpm} \cdot \text{l}^{-1}$ ) at  $t$  and 0,  $F_i$  = radioactivity in food ( $\text{dpm} \cdot \text{l}^{-1}$ ); and  $t$  = feeding time (min). Then the community grazing rate for a size fraction ( $G_{ij}: i < j$ ) was estimated by

$$G_{ij} = (G_j \times F_j - G_i \times F_i) / (F_j - F_i) \quad (2).$$

Ingestion rate for a size fraction ( $I_{ij}: i < j$ ) was calculated by

$$I_{ij} = S_{ij} \times G_{ij} \quad (3),$$

where  $S_{ij}$  is seston abundance in size fraction  $i-j$ . Total ingestion rate ( $TI: \mu\text{g C} \cdot \text{l}^{-1} \cdot \text{d}^{-1}$ ) and total grazing rate ( $TG: \text{d}^{-1}$ ) were estimated as follows,

$$TI = \Sigma (S_{ij} \times G_{ij}) \quad (4),$$

$$TG = \Sigma (S_{ij} \times G_{ij}) / \Sigma S_{ij} \quad (5).$$

Significant differences between grazing rates on different size fractions were examined by one-way ANOVA and post hoc Fisher's PLSD comparison test with the aid of a computer program package (Stat View SE+Graphics: FELDMAN *et al.*, 1988).

### 3. Results

On 26 August, composition of zooplankton  $>98 \mu\text{m}$  was similar between Stations N and S, and more than 59% of the zooplankton biomass was composed of copepodid stages of *Eodiaptomus japonicus* (Table 2). *Daphnia galeata* was also abundant and shared about 25% of the biomass at both stations. On 3 September, although 40% of the biomass was composed of *E. japonicus* at both stations, the zooplankton composition differed between the stations. On this date, *D. galeata* increased and made up 44% of the zooplankton biomass at Station N, while density of this species was low

Table 2. Biomass (B:  $\mu\text{g DW} \cdot \text{l}^{-1}$ ) and its percentage composition (%) of zooplankton.

Taxon	26 Aug.				3 Sept.			
	Station N		Station S		Station N		Station S	
	B	%	B	%	B	%	B	%
<i>Eodiaptomus japonicus</i>								
nauplii	0.5	0.2	2.0	1.2	1.4	0.5	1.6	1.0
copepodids	123.3	59.1	107.7	65.0	121.7	40.5	73.2	47.6
<i>Mesocyclops dissimilis</i>								
nauplii	8.5	4.1	1.2	0.7	6.9	2.3	0.9	0.6
copepodids	10.9	5.2	9.5	5.7	22.7	7.6	42.9	27.9
<i>Daphnia galeata</i>	54.7	26.2	39.8	24.0	132.5	44.1	12.6	8.2
<i>Diaphanosoma brachyurum</i>	10.8	5.2	5.5	3.3	15.2	5.1	22.5	14.6
Total	208.7		165.7		300.4		153.7	

and *Mesocyclops dissimilis* made up 28% of biomass at Station S. The zooplankton biomass was higher at Station N than Station S on both dates. Biomass of metazoan zooplankton  $<98 \mu\text{m}$  was less than 1% of the zooplankton  $>98 \mu\text{m}$  during the study period (KAWABATA and URABE, 1995).

Although seston abundance was similar

between the dates and stations, large difference was found in its size composition (Table 3). On 26 August, the abundance of seston in the 2-20  $\mu\text{m}$  fraction was higher than those in other fractions at Station N. At Station S, however, the middle fraction (2-20  $\mu\text{m}$ ) was less abundant compared to other size fractions. On 3 September, 70% of seston was composed of the

Table 3. Abundance of seston ( $\mu\text{gC}\cdot\text{l}^{-1}$ ) in different size fractions.

Size fraction	26 Aug.		3 Sep.	
	Station N	Station S	Station N	Station S
$<2 \mu\text{m}$	131	180	97	179
2-20 $\mu\text{m}$	185	133	86	273
$>20 \mu\text{m}$	150	180	412	117
total	466	493	595	569

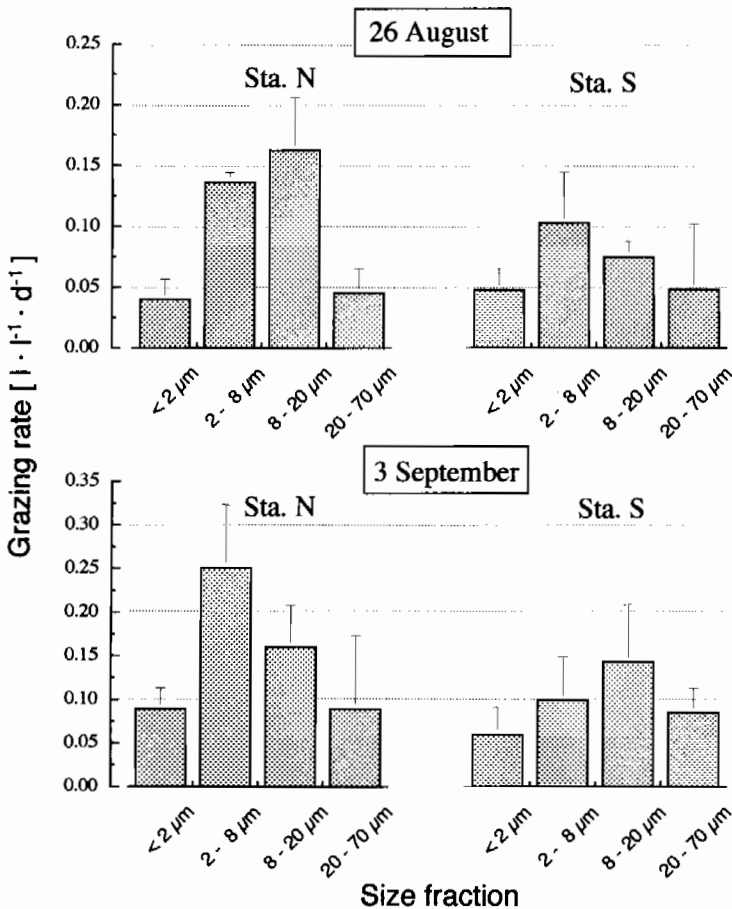


Fig. 1. Grazing rate of zooplankton community for food in different size fractions. Vertical bars are 3 SE on the mean.

largest fraction ( $>20 \mu\text{m}$ ) at Station N, while the middle fraction contributed 50% of seston at Station S. Throughout the study period, dominant species of phytoplankton at Station N was *Gomphosphaeria lacustris* (Cyanophyceae), while at Station S, it was *Melosira granulata* (Bacillariophyceae) (KUMAGAI *et al.*, 1955). Further information on abundance and composition of phytoplankton during the study period will be given in elsewhere (NAKANO *et al.*, in prep).

The grazing rate differed significantly between food particles in different size fractions (Fig. 1). In all experiments, post hoc comparison test revealed that the grazing rate was significantly higher for middle fractions (2-8  $\mu\text{m}$  and 8-20  $\mu\text{m}$ ) than the smallest size fractions (Table 4). The grazing rate did not significantly differ between food particles in 2-8  $\mu\text{m}$  and 8-20  $\mu\text{m}$  except for 3 September at

Station N where it was highest for 2-8  $\mu\text{m}$  fraction. The grazing rate for the largest size fraction was significantly lower than those in either (Station S) or both (Station N) of the middle size fractions. On both dates, the grazing rate for food particles  $<2 \mu\text{m}$  was one half of that for 2-8  $\mu\text{m}$  at Station S, while one third at Station N. This result implies that food size preference of the zooplankton community was less marked at Station S compared to Station N.

From the grazing rate and seston abundance in each size fraction, ingested carbon from each fraction was calculated (Fig. 2). Since we did not separate seston into 2-8 and 8-20  $\mu\text{m}$  fractions, grazing rate for 2-20  $\mu\text{m}$  fraction was estimated by applying  $G_2$  and  $G_{20}$  to eq. 2 and then ingestion rate for that fraction was calculated using eq. 3. The carbon ingested by the zooplankton community was mainly from the middle size fractions except for 3 September at

Table 4. Results of statistical analyses for grazing rates on different size fractions.

Date	Station	ANOVA			Multiple comparison*
		df	F	P	
26 August	N	3, 8	53	0.001	<u>&lt;2</u> , <u>20-70</u> , <u>2-8</u> , <u>8-20</u> $\mu\text{m}$
	S	3, 8	4.5	0.038	<u>&lt;2</u> , <u>20-70</u> , <u>8-20</u> , <u>2-8</u> $\mu\text{m}$
3 September	N	3, 12	13.6	0.001	<u>&lt;2</u> , <u>20-70</u> , <u>8-20</u> , <u>2-8</u> $\mu\text{m}$
	S	3, 12	5.1	0.017	<u>&lt;2</u> , <u>20-70</u> , <u>2-8</u> , <u>8-20</u> $\mu\text{m}$

\*Significant difference at 5% level is denoted by different underlines

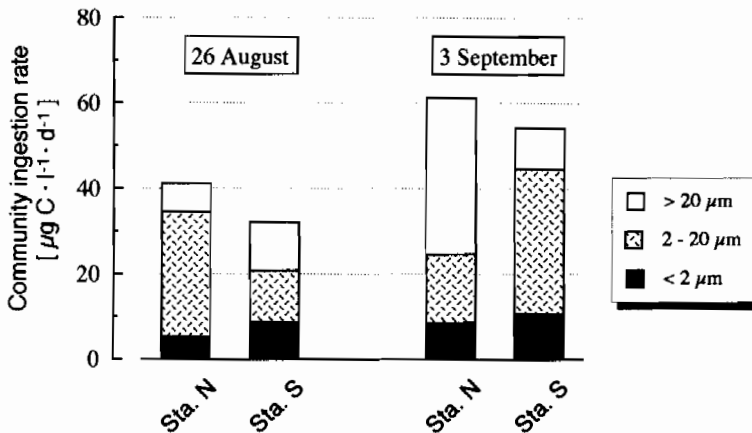


Fig. 2. Community ingestion rate of zooplankton and contribution of each food size fraction to the ingestion rate.

Station N where 57% of the ingested carbon was from the largest size fraction. The contribution of the smallest size fraction to the ingested carbon was lowest in all dates and stations.

Total ingestion and total grazing rates are shown in Table 5. A two-fold difference was found in the total ingestion rate among the experiments. The total ingestion rate was lowest on 26 August at Station S and highest on 3 September at Station N. Weight-specific ingestion rate (normalized by zooplankton biomass) also varied with the highest value on 3 September at Station S. The total grazing rate was in the range from 0.065 to 0.103 liter  $\cdot$  l<sup>-1</sup>  $\cdot$  d<sup>-1</sup>, implying that the zooplankton community removed 6.5 to 10.3% of seston within a day. The weight-specific grazing rate was relatively stable among the experiment and in the range from 0.4 to 0.6 liter  $\cdot$  mg DW<sup>-1</sup>  $\cdot$  d<sup>-1</sup>.

#### 4. Discussion

OKAMOTO (1984a) indicated that *E. Japonicus* and *D. galeata* individuals ingest preferentially smaller algae in the warm water season. However, since he used algae smaller than 10  $\mu$ m as the smallest food size category, vulnerability of picoplankton to the zooplankton grazing has been unclear. In the present study, the grazing rate for the smallest fraction (<2  $\mu$ m) was always lower than that for the middle fractions (nanoplankton: 2–8  $\mu$ m and 8–20  $\mu$ m). The result implies that picoplankton are less vulnerable to the zooplankton grazing compared to nanoplankton both at the north and south basins. The lower grazing rate for picoplankton

was probably due to predominance of *E. japonicus*, because calanoid copepods in general do not ingest preferentially picoplankton (see review in STERNER, 1989; VANDERFLOEG, 1990). NAGATA and OKAMOTO (1988) demonstrated that *E. japonicus* cannot ingest bacteria efficiently.

A number of studies have examined bacterial ingestion of daphnid species (TEZUKA, 1971; NAGATA and OKAMOTO, 1988; HESSEN *et al.* 1989, URABE and WATANABE 1990a, 1991, and literatures therein). Among them, NAGATA and OKAMOTO (1988) suggested that, contrasting with *E. japonicus*, *Daphnia galeata* in L. Biwa is an efficient bacterial feeder. The present study, however, does not coincide with their conclusion. It should be noted that picoplankton include organisms larger than bacteria, such as solitary cyanobacteria. Thus, if *D. galeata* is an efficient bacterial feeder, we can expect an increase in the grazing rate for picoplankton relative to that for nanoplankton with increasing the proportion of this species. At the north basin, *D. galeata* increased and made up about one half of the zooplankton biomass on 3 September. Nonetheless, the grazing ratio of pico- to nanoplankton on 3 September at the north basin was 0.35, being similar to or smaller than those in other date and sites (0.29–0.60). The results suggest that *D. galeata* is not necessarily more efficient at bacterial feeding than other zooplankton species in L. Biwa. From the feeding response to changes in bacterial and algal densities, URABE and WATANABE (1991) indicated that *D. galeata* does not rely on bacteria as

Table 5. Total and weight specific ingestion and grazing rates.

	26 Aug.		3 Sept.	
	St. N	St. S	St. N	St. S
Total ingestion rate ( $\mu$ gC $\cdot$ l <sup>-1</sup> $\cdot$ d <sup>-1</sup> )	41.2	32.1	61.3	54.2
Specific ingestion rate ( $\mu$ gC $\cdot$ mgDW <sup>-1</sup> $\cdot$ d <sup>-1</sup> )	197.5	193.6	204.1	352.5
Total grazing rate (l $\cdot$ l <sup>-1</sup> $\cdot$ d <sup>-1</sup> )	0.088	0.065	0.103	0.095
Specific grazing rate (l $\cdot$ mgDW <sup>-1</sup> $\cdot$ d <sup>-1</sup> )	0.424	0.393	0.343	0.620



diet. Using labeled natural seston, MAZUMDER *et al.* (1990) demonstrated that the grazing rate in *Daphnia*-dominated community for sestonic particles  $<3 \mu\text{m}$  was far lower than that for 3–8  $\mu\text{m}$  particles. On the other hand, HESSEN *et al.* (1989) showed that *D. longispina* ingested bacteria as efficiently as algae in a dystrophic humic lake. Feeding ability and efficiency of *Daphnia* to picoplankton may differ not only between species but also clones and localities with different nutritional conditions.

Higher grazing rate for a particular size fraction seems to suggest that the zooplankton ingest mainly food particles in that size category. However, such an image is incorrect. On 3 September at Station N when seston  $>20 \mu\text{m}$  was much abundant relative to seston  $<20 \mu\text{m}$  (Table 3), the largest size fraction (microplankton) contributed 57% of carbon ingested by the zooplankton (Fig. 2). OKAMOTO (1984b) also indicated that about 50% of carbon ingested by *E. japonicus* and *D. galeata* was from seston larger than 25  $\mu\text{m}$  when large algal species dominated phytoplankton biomass. KAWABATA (1987) found a large number of algal cells  $>30 \mu\text{m}$ , such as *Closterium* and *Melosira*, in the gut of *E. japonicus* and *D. galeata* when these algae were abundant in L. Biwa. Unfortunately, we do not have information on dominant phytoplankton species in the largest size fraction on 3 September at Station N. However, the results obtained here and previous studies suggest that the high ingestion rate for microplankton is not unusual in L. Biwa especially when large algae dominate phytoplankton biomass. This implies that the zooplankton grazing on the microplankton can not be negligible in material flows of this lake.

It should be noted, however, that the high ingestion rate for the largest fraction on 3 September at Station N simply results from a decrease in the amount of pico- and nanoplankton and increase in the microplankton available, but not due to changes in food size preference by the zooplankton assemblage. A food item with lower grazing rate implies less preferable food because of nutrient inadequacy or difficulty in detection, capture, handling or swal-

lowing. Thus, material transfer efficiency from microplankton to zooplankton is expected to be low compared to that from nanoplankton even when zooplankton ingest microplankton more abundantly than nanoplankton.

In the present study, all individuals larger than 98  $\mu\text{m}$  in body size were treated as suspension feeders, although late stages of *Mesocyclops dissimilis* prey on zooplankton (KAWABATA, 1991). However, this species feeds also on phytoplankton (KAWABATA personal observation) and was limited in the density during the study period. Thus, although we included *M. dissimilis* in estimating the weight-specific grazing rate, such a treatment would not bring about serious error in our conclusion.

The weight-specific total ingestion rate estimated here, 198–356  $\mu\text{gC}\cdot\text{mg DW}^{-1}\cdot\text{d}^{-1}$ , is within the range of previous studies. On the basis of individual feeding rate, OKAMOTO (1984b) calculated daily carbon rations of *D. galeata* and *E. japonicus*, being 16–77% of body carbon depending on body size in summer. Assuming 0.44 carbon: dry weight ratio (KAWABATA and URABE, unpubl.), these values correspond to the weight-specific ingestion rate of 70–339  $\mu\text{gC}\cdot\text{mg DW}^{-1}\cdot\text{d}^{-1}$ . URABE *et al.* (1995) estimated particle elimination rate of the zooplankton community in L. Biwa, being 290  $\mu\text{gC}\cdot\text{mg DW}^{-1}\cdot\text{d}^{-1}$  in average from June to November. Considering the difference in methodology, food condition and zooplankton composition among the studies, the total ingestion rate estimated here seems to coincide well with the previous results.

The community grazing rate of the zooplankton on total seston was less than 11% in all experiments. One may suspect that this grazing rate is too low to affect the seston abundance. However, since primary production is vertically limited to the shallow euphotic layer, but the zooplankton are not, the amount of carbon ingested by the zooplankton per unit area may be comparable to areal primary production rate even when grazing rate per unit volume is low. In other words, the magnitude of grazing impact on phytoplankton community depends not only on the community grazing rate but also primary

production rate. Indeed, URABE *et al.* (1995) revealed that, on an areal basis, the amount of sestonic carbon ingested or removed by the zooplankton community is comparable to primary production rate in some seasons in the north basin of L. Biwa. Furthermore, even slight difference in food selectivity causes large changes in species composition of resource community (STERNER, 1989). Thus, the higher grazing rate for nanoplankton relative to pico- and microplankton may play an important role in determining phytoplankton composition in L. Biwa. Compared to the north basin, the south basin is eutrophic and more productive. Thus, although the community grazing rate was similar between the two basin, the grazing impact of zooplankton on phytoplankton community would be less conspicuous in the south basin.

In the present study, the grazing experiments were conducted in limited season and site. The grazing impact on algal and bacterial populations is expected to change according to various factors including abundance and composition of zooplankton. In the south basin of L. Biwa, rotifers are usually abundant (MATSUBARA, 1993), although few rotifer individuals were found in the present study. To clarify the details of grazing impact on algal and bacterial populations in L. Biwa, therefore, further studies are needed on the feeding performance of zooplankton in different seasons and sites.

#### Acknowledgments

We are grateful to Michio KUMAGAI for his organization of BITEX '93. Without his effort and cooperation, we could not perform this study. We also wish to express our gratitude to Setsuo OKUDA who arranged use of a radioisotope laboratory, and to Masaru NISHIMURA and Toshiharu SUGIHARA, Toyobo Co., LTD, who provide us their lab space and facilities. Thanks are also due to Takaaki UEDA, Toshihiro MIYAJIMA, Shin-ichi NAKANO, Tatsuki SEKINO and Tadashi KOITABASHI for their help in field and lab works, to crews of R/V Hakken-go for assistance on shipboard, and to Toshi NAGATA for his valuable discussion and assistance in lab works. Comments by Bob STERNER

and anonymous reviewers improved the manuscript.

#### 摘 要

#### BITEX '93 期間中における琵琶湖動物プランクトン群集のグレージングと餌サイズ選択性

1993年8月から9月にかけて行われたBiteX '93の一環として、琵琶湖南湖及び北湖における動物プランクトン群集のグレージング速度と餌サイズ選択性を調べた。摂餌実験にあたっては、採集したセストンの一部を $^{14}\text{C}$ でラベルし、サイズにより4分画(<2, 2~8, 8~20及び20~70  $\mu\text{m}$ )した後、各サイズ分画に対するグレージング速度を現場と同じ餌環境下で測定した。実験時には*Eodiaptomus japonicus*と*Daphnia galeata*が動物プランクトンとして卓越していた。

摂餌実験の結果、南湖・北湖ともに動物プランクトン群集は2~20  $\mu\text{m}$ のセストンを選択的に食べ、2  $\mu\text{m}$ 以下及び20  $\mu\text{m}$ 以上のセストンに対する摂食率は相対的に低いことが明らかとなった。ただし、摂食量として見た場合、動物プランクトンの餌は主に2~20  $\mu\text{m}$ のセストンに限られるというわけではなく、20  $\mu\text{m}$ 以上のセストンに比べて20  $\mu\text{m}$ 以下のセストンが相対的に少ない場合には、動物プランクトンは20  $\mu\text{m}$ 以上の大型藻類を量的に多く摂食することが示唆された。実験期間中における動物プランクトン群集の1日あたり摂食量は、琵琶湖セストン量の6~10%になると見積もられた。

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Received : 5 July 1995

Accepted : 15 November 1995