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Feeding Behavior of One-year-old Silver Carp, *Hypophthalmichthys molitrix*, on Dominant Phytoplankton During a Summer in the Enclosure of Shallow-hypertrophic Lake

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여름철에 우점하는 식물플랑크톤에 대한 1년생 백연의 먹이습성. 김백호*・최민규・Takamura Noriko (원광대, [1]일본국립환경연구소)

수심이 얕은 부영양호수에서 우점하는 식물플랑크톤에 대한 1년생 백련어의 섭식특성을 조사하고자, 1997년 5월 23일부터 9월 18일까지 호수의 연안에 4개의 enclosure를 설치하고, 어류투입 이후의 각 enclosure 수중과 어류의 장 내용물 중의 식물플랑크톤 군집의 변화를 비교하였다. 조사기간동안 각 enclosure의 수온, 플랑크톤의 총생물량, 어류 아가미의 여과공 등은 시간에 따라 큰 변화가 없었으며, 어류성장은 주로 투입된 어류의 밀도에 의존되었다. 어류의 내용물에 의하면, 저밀도 투입 enclosure에서 수중과 어류 전장간의 플랑크톤군집의 유사도가 높게 나타났으며 ($p < 0.05$), 전체적으로 모든 enclosure에서 크기가 큰 ($> 100{,}000 \mu m^3$) 식물플랑크톤-*Oscillatoria*, *Anabaena*, *Melosira* 등은 어류투입이후 크게 감소되지 않았다. 어류의 먹이선택지수(α)와 플랑크톤의 크기 (Ingestion unit)사이에도 매우 낮은 상관성을 보였다 ($r = 0.001$, $p > 0.5$). 식물플랑크톤의 분석결과, 백연은 남조나 녹조에 비해 규조를 더 선호하였는데, 이는 규조의 세포벽이 다른 조류에 비해 소화과정동안 쉽게 파괴되지 않고, 저배율의 현미경적시야에서도 간단히 확인된다는 점 등, 선택지수를 과대평가하게 되는 단점이 있기 때문에 백련어의 먹이습성에 대한 방법론적 개선이 필요하다고 판단된다.

Key words : Feeding selectivity, Similarity index, Silver carp, Phytoplankton, Ingestion unit, Enclosure

INTRODUCTION

Silver carp, *Hypophthalmichthys molitrix* (Val.), is a phytoplanktivorous filter-feeder, feed algae of various sizes (Cremer and Smitherman, 1980; Smith, 1989). The usage of silver carp to improve water quality in eutrophic lakes has been investigated since the 1970s (Sirenko *et al*., 1976; Kajak *et al*., 1977; Smith, 1985; Laws and Weisburd, 1990; Starling, 1993; Lieberman, 1996). Silver carp feeds moving and unmoving targets through a mechanical filtration. Food items are passed through the gill matrix with numerous pores, and towards the esophagus by the sucking and pumping actions of the suprabranchial organ (Wilamovski, 1972; Lazzaro, 1987), and masticated by the pharyngeal teeth (Xie, 1999).

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Studies of silver carp demonstrated that filter-pore sizes (FPS) ranged between 12 and 41 μm (Wilamovski, 1972; Liu, 1981; Hampl *et al*., 1983; Spataru *et al*., 1983), but silver carp could filter up to 4.5 μm (Xie, 1999), perhaps because of secretion of digestive mucus (Lazzaro, 1987) or progressive clogging of prey in the gill matrix (Durbin and Durbin, 1975). These studies also found that the FPS generally does not change as the fish grows, but they were unable to precisely determine the actions of the gill rakers or the digestive acids and/or enzymes in the intestine on specific prey (Bitterlich, 1985a, b, c). Therefore, the size of the prey filtered, the mechanism by which the fish breaks down algal cells and the process of digestion of algae as they are move along the digestive tract are still unclear.

Silver carp unselectively consumes cyanobacteria, and unavoidably feed algae only when abundant (Vovk, 1974; Xie, 1996), although they much prefer diatoms to green algae, euglenoids and cyanobacteria (Prowse, 1964; Xie and Takamura, 1996). Bitterlich (1985a, b, c) reported that the digestive enzymes in the intestine of stomachless fish did not completely digest cells, because of the neutral pH; large populations of cyanobacteria have been observed in the hindgut of fish (Malyarevskaya *et al*., 1972; Kajak *et al*., 1977), and these cells did not display morphological changes during a digestion (Moriarty *et al*., 1973). However, feeding experiments have shown that the fish could very well assimilate isotope-labeled algae such as *Microcystis* and *Euglena* (Zhu and Deng, 1983), *Anabaena* (Herodek *et al*., 1989) and green algae (Iwata, 1976). Our previous study (Fukushima *et al*., 2000), has shown that the presence of silver carp significantly suppressed the chlorophyll-*a* concentration of phytoplankton >40 μm, and induced the outbreak of phytoplankton <2 μm. Nevertheless, the microscopic examination revealed that the fish rarely remove larger algae such as *Oscillatoria*, *Anabaena* and *Melosira*, which were abundant in a hypertrophic lake during the summer.

Therefore, the silver carp's feeding selectivity and its ability to digest various algae, particularly in hypertrophic lakes, are still not clear. The objectives of the study were to determine: 1) the major characteristics of the prey of silver carp; 2) the quantities and types of algae ingested and remained in the fish intestine; and 3) any difference between the phytoplankton communities in the water and the intestine of silver carp with different fish stocking densities and culture times.

MATERIALS AND METHODS

This lake is the second largest in Japan (16,800 ha), shallow (mean depth 4 m, maximum depth 7 m) and hypertrophic. The annual means of total phosphorus and total nitrogen are 0.095 and 1.150 mg/L, respectively (Takamura *et al*., 1996). The water residence time is 0.55 y, and there is virtually no vertical stratification. The lake is the main local source of water for drinking, irrigation and industrial use, but it has been affected by heavy blooms of cyanobacteria since the 1970s (Takamura *et al*., 1992)

We set up to 4 enclosures (each 5×5 m $\times 2.5$ m deep) near the shore of Lake Kasumigaura (140° 02′N, 36° 00′E), after the method of Fukushima *et al*. (2000). Two enclosures (1A and 2A) allocated for fish stocking from 22 May to 23 July, 1997 (Stock A), and other two enclosures (1B and 2B) from July 23 to 18 September, 1997 (Stock B) (Table 1). Fish were reared in enclosures 1A and 2A during early summer at low and high densities, respectively. Enclosures 1B and 2B were free of silver carp during early summer but were stocked on 23 July at low and high densities, respectively. The water temperature in the enclosures ranged from 17～29°C during the experiments. The mean (±SD) fork length and body weight of the silver carp in 1A and 2A were 139 ±10 mm and 39±9 g, respectively, when stocked on 22 May, while those in 1B and 2B were 182± 14 mm and 87±20 g, respectively, when stocked on 23 July. At the end of each stocking period, we collected the fish from the enclosures, measured their size and weight and calculated their percent growth. Fish growth was calculated as (final biomass-initial biomass)/(initial biomass) $\times 100$. Dead or lost silver carp were replaced with individuals of similar size throughout the experiment.

To observe the gill apparatus and the suprabranchial organ, the FPS and the gut contents of silver carp, 10 fish were sampled from each enclosure on the final day of each stocking period, with the exception of enclosure 1A, from which only 7 were sampled, totally 37 fish. First of all the head of fish was removed with a scissor, fixed with ethanol and placed in a glass bottle. To measure the FPS the gill arch and the supra-

Table 1. Number, biomass, percent growth and filter pore size (FPS) of silver carp stocked in the 4 enclosures.

Enclosure	No. fish	Initial biomass (g/m^3)	Final biomass (g/m^3)	Fish growth (%)	FPS (μm) Mean ± SD (range)	No. fish for FPS measurement
1A	15	9.1	31.2	242	18.4 ± 1.3 (16.4 ~ 20.2)	7
2A	57	37.4	76.5	105	18.9 ± 1.4 (16.9 ~ 21.5)	10
1B	15	20.9	42.5	103	20.0 ± 1.0 (18.8 ~ 21.8)	10
2B	57	78.8	93.9	19	19.6 ± 1.1 (18.2 ~ 21.3)	10

branchial organs were removed and observed under a Nikon dissecting microscope. The analysis of the gut content was made after dissecting 1−cm pieces of foregut and hindgut from the fish with scissors. Each gut fragment was squeezed with fine forceps to remove the gut juice, which was then preserved in formalin (final concentration 3 ~ 5%).

Qualitative and quantitative analyses of phytoplankton were carried out with integrated water samples. These samples were collected by lowering a column sampler (diameter 5 cm, capacity 4.7 L) close to the sediment at the center of the enclosure on 20 and 23 July for 1A and 2A, and on 15 and 18 September for 1B and 2B. A 100 mL subsample from each water sample was preserved with 1% Lügol's iodine solution. We counted the number of each type of phytoplankton in the water samples and fish intestines under a Nikon inverted light microscope. Nineteen dominant phytoplankton were identified to the species level, and others to the generic level. The cell length and width of the dominant phytoplankton species were measured, and the average volume of the cells was calculated according to Wetzel and Likens (1991).

To measure the function of algae as a food for silver carp, namely, ingested unit (IU) is newly defined as a measurement of mean size and shape of phytoplankton occurred in the water. The size calculation included the usual number of phytoplankton forming a colony; we used data from over 100 cells of each solitary species. We also ignored the change in the structure and dimensional ornamentation of each phytoplankton in water. Because the lived cell is commonly bigger than that of fixed cell, as 1.33 times in case of 2% Lügol's iodine solution (Strathmann, 1967), and 1.28 times in and 0.5% glutaraldehyde solution (Verity *et al.*, 1992). In conclusion, our IU values were slightly over− and under−estimated compared to the lived phytoplankton in enclosures. The IU value included non−chlorophyllous parts, cytoplasmic connections between many branches (*Westella* and *Dictyosphaerium*), mucilagenous sheaths (*Phormidium*) and hyaline layers between the cell wall and the nucleoplasm (*Kirchneriella, Sphaerocystis* and *Oocystis*), apart from the flagella and spines of *Microspora, Tetraspora, Volvox* and *Scenedesmus*. To examine whether or not ingested algae remained alive, chloroplasts or chromatophores were observed in the cells in the fish's intestine by the method of Takamura and Yasuno (1983).

We calculated Shoener's (1970) index to assess similarities in phytoplankton between the foregut and the water, and the hindgut and the water. For the former similarity, we sampled the water from each enclosure at the same time that fish were collected. For the latter similarity, we compared the contents of water samples obtained 3 d before fish sampling with the hindgut contents, because we had estimated the gut−passage time in fish of this size at this water temperature to be 66 h (Liu, 1990). To evaluate the selective preference of silver carp for individual phytoplankton species, we calculated the α index of Chesson (1983) for each dominant phytoplankton species by comparing the phytoplankton biomass in the foregut with that in water sampled on the same day as the fish samples were taken.

To evaluate the statistical significance in the difference of similarity in phytoplankton community between the foregut and the water, the hindgut and the water, and the foregut and the hindgut, the Mann−Whitney test for nonparametric testing was applied. Simple correlation analyses between the IU values and total biomass of each phytoplankton species, and selectivity of silver carp on phytoplankton species were conducted.

RESULTS

The growth of the silver carp (expressed as %) was affected by a density of fish stocked: the bio-

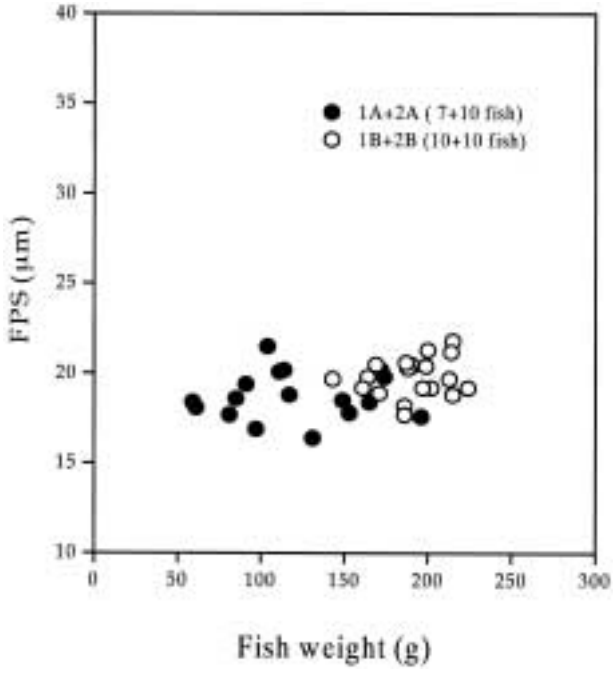

Fig. 1. Relationship between filter pore size (FPS) and weight of silver carp in the four enclosures. Ten fish were examined from each enclosure, except for 1A, where only 7 were examined.

mass of fish was greater in the low-density enclosure than that of the high-density, and Stock A than for Stock B, respectively (Table 1). The filtering apparatus of the silver carp used in the study generally appeared to be similar to that described by Wilamovski (1972). The distance between adjacent ribs or rakers re-measured averaged 82.3 μm (n = 37, SD = 3.5) in this study. The average FPS of the fish (59～272 g) was 19.3 μm (range 16.4～21.8 μm), and there was a weak relationship (r = 0.38, p = 0.019, n = 37) between the FPS and the fish weight (Fig. 1 and Table 1).

Totally 201 taxa occurred in this study, but only 19 dominant phytoplankton contributed >95% of the total algal biomass (Table 2). Only in enclosure 1A were all of these phytoplankton species present; the number of dominant phytoplankton species in the Stock B enclosures dropped. The IU values of the phytoplankton species ranged from about 1,100 to 777,000 μm^3. Cyanobacteria, *Merismopedia tenuissima* was the most abundant (10^{10}～10^{12} μm^3) in each of the 4 enclosures over the experimental periods. The phytoplankton biomass tended to decrease significantly (r = 0.58, p < 0.01 for all enclosures; Fig. 2)

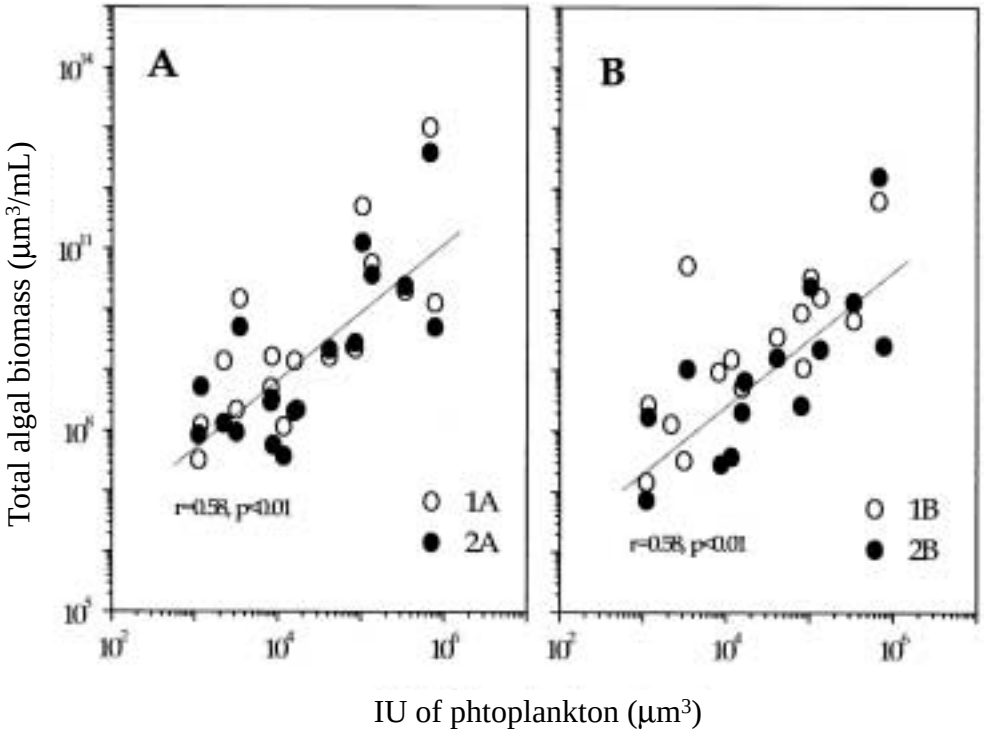

Fig. 2. Total biomass and ingested unit (IU) values of phytoplankton species in the four enclosures. Algal biomass below 10^6 μm^3 was counted as zero. The IU value of each phytoplankton species is listed in Table 2.

Table 2. Feeding selectivity (Chesson's α index) of silver carp for each dominant phytoplankton species, and their ingested unit (IU) values, in the 4 enclosures. The IU values include cytoplasmic connections and mucilagenous sheaths, but exclude flagella and spines.

Dominant species	Selectivity index				IU values (μm^3)
	1A	2A	1B	2B	
Nitzschia acicularis	0.00	0.10	0.24	0.24	1108.4
Chlamydomonas sp. (>15 μm)	0.00	0.00	0.03	0.01	1169.0
Coelosphaerium sphaericum	0.00	0.00	0.00	0.13	2208.0
Aulacoseira granulata	0.06	0.14	0.00	0.00	3126.8
Lyngbya limnetica	0.00	0.01	0.03	0.01	3427.1
Monoraphidium contortum	0.01	0.00	0.00	0.17	8146.0
Dictyosphaerium pulchellum	0.02	0.03	0.00	0.00	8377.6
Chodatella wratislaviensis	0.02	0.07	0.00	0.00	8722.3
Ankistrodesmus falcatus	0.09	0.06	0.03	0.02	11641.5
Cyclotella meneghiniana	0.70	0.31	0.20	0.16	15598.5
Westella botryodies	0.00	0.00	0.12	0.00	16755.2
Scenedesmus protuberans	0.01	0.03	0.00	0.04	41147.6
Synedra unla	0.00	0.00	0.04	0.00	79892.4
Melosira distans	0.02	0.02	0.00	0.00	84496.2
Oscillatoria agardhii	0.01	0.02	0.01	0.10	103118.2
Actinastrum Hantzschia	0.04	0.08	0.13	0.00	134481.0
Kirchneriella obesa	0.00	0.00	0.08	0.00	337789.5
Merismopedia tenuissima	0.00	0.00	0.00	0.05	678348.8
Anabaena flos-aquae	0.00	0.11	0.08	0.03	777014.7

with decreasing volume of individual cells or colonies.

The similarity index between the phytoplankton community in the fish intestine and the water in each enclosure varied in close relation to the average weight of the fish, or inversely to the stocking density (Fig. 3). The similarity index was higher in enclosures with smaller fish but lower fish density, both for the foregut and hindgut, than in enclosures with large fish and higher fish density, respectively ($p < 0.05$, except for similarity indices of the foregut between 1B and 2B, *U*-test).

The α index of Chesson (1983) showed that silver carp greatly preferred 5 diatoms, namely *Nitzschia, Aulacoseira, Cyclotella, Melosira* and *Synedra* despite the fact that cyanobacteria occurred abundantly in each enclosure. Of these, *Cyclotella meneghiniana* (13~17 μm) was most preferred by fish, with a selectivity index of 0.2~0.7 (Table 2). This diatom was preferred in other enclosures as well. Two other diatoms, *Aulacoseira granulata* ($\alpha = 0.14$ for 2A) and *Nitzschia acicularis* ($\alpha = 0.24$ for Stock-B) were also selectively ingested. In contrast, the selectivity indices for *Lyngbya limnetica, Melosira distans* and *Chlamydomonas* (>15 μm) were consistently low across all the enclosures ($\alpha = 0.03$). There was no relationship between the selectivity indices and

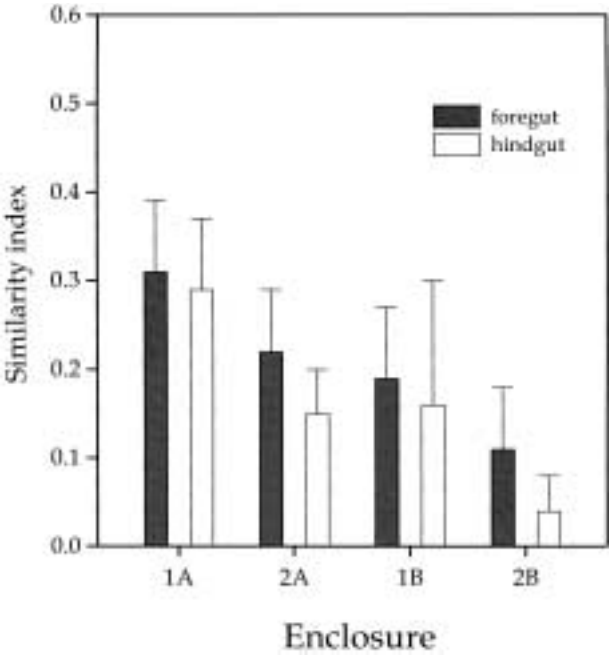

Fig. 3. Similarities between phytoplankton communities in the fish intestine and water in the four enclosures. The index was calculated by the method of Shoener (1970), and was used to compare the composition of phytoplankton species in the foregut and the water, and in the hindgut and the water. For analysis of gut contents, 10 fish were collected from each enclosure, except for enclosure 1A, where only 7 were collected.

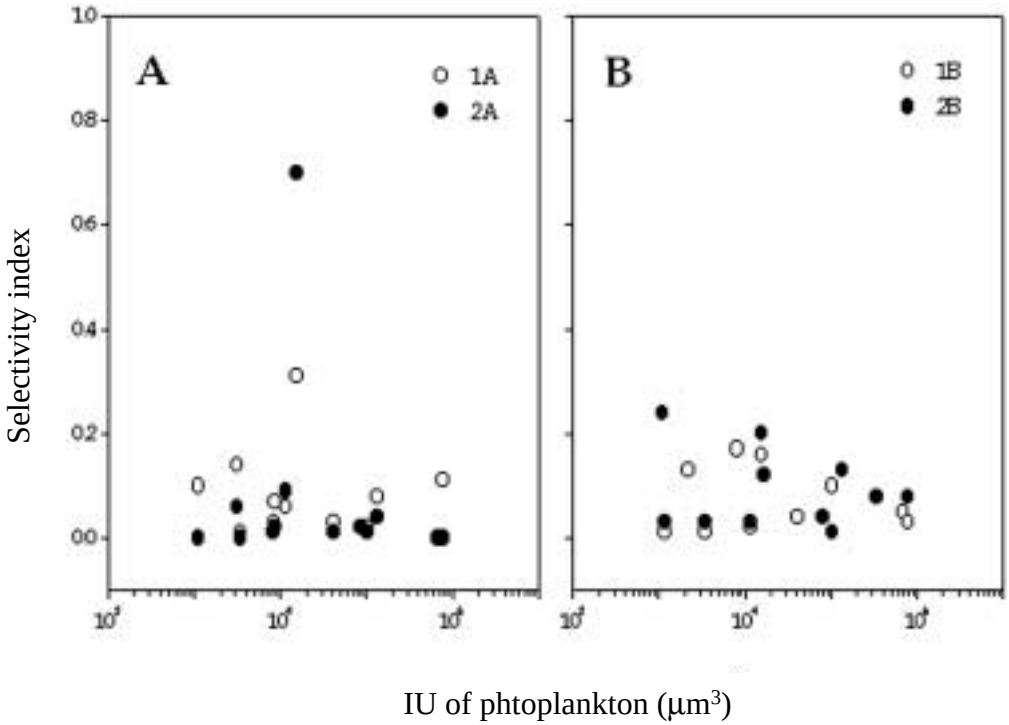

Fig. 4. Feeding selectivity (Chesson's α index) of silver carp and ingested unit (IU) values of phytoplankton. We calculated the selectivity index for each major phytoplankton by the method of Chesson (1983), based on the relative algal abundance in the foregut of fish and water. For analysis of the gut content 10 fish were collected from each enclosure, except for enclosure 1A, where only 7 were collected.

IU values of phytoplankton in any of the enclosures ($r = 0.001$, $p > 0.05$, Fig. 4).

DISCUSSION

The feeding behavior of most filter feeders is greatly influenced by various factors, such as visibility, size and density of prey, acclimation (Adamek and Spittler, 1984; Lazzaro, 1987), temperature (Reynolds, 1984; Szumiec, 1997) and cyanobacterial toxins (Tidwell *et al*., 1992; Fukushima *et al*., 2000). In our feeding experiments with 1-y-old silver carp during five summer months, the stocking density remarkably influenced its feeding habit; in particular, fish growth was remarkably retarded in enclosure 2B with a high density of stocked fish. But, there were no major changes in FPS of silver carp (16.4～21.8 μm) with fish size (59～272 g) and water temperature (23～26°C) in each enclosure during the study period. Despite the fact that the present work is based on fish of small or limited size, our results unequivocally suggest that the stocking density controls the feeding behavior of silver carp during summer in the eutrophic lake.

Over the experiment periods, *Anabaena*, *Merismopedia* and *Oscillatoria*, showing high IU values (100,000 μm³), occurred abundantly in water even in the presence of silver carp. The results showed a highly significant relationship between the abundance and IU values of each phytoplankton in all the enclosures, without regard to the presence or density of fish (Fig. 2). In general, cyanobacteria may be ingested unselectively when occurring abundantly (Kajak *et al*., 1977; Tidwell *et al*., 1992), but they are not at all preferred and are even avoided by silver carp (Sirenko *et al*., 1976). The feeding behavior of silver carp in cyanobacteria-rich lake is not fully understood due to complex relationships among algal growth, mortality and feeding preferences of fish (Siegel, 1998), and also because the fish find it difficult to digest cyanobacteria (Payne, 1978; Bold and Wynne, 1985; Starling and Rocha, 1990). The morphological characteristics of phytoplankton and their abundance may be important in de-

termining the relevant prey of 1-y-old silver carp in highly mixed waters.

Our result that silver carp more preferred diatoms than cyanobacteria and green algae, is in accordance with previous observations (Prowse, 1964; Xie, 1999) and seems to be due mainly to the ease with which diatoms can be distinguished from the mixed debris in fish intestine. Low selectivity for cyanobacteria and green algae may be due to difficulties in distinguishing the dissociated cells from colonies or filaments. Appropriate techniques need to be developed to clearly understand and generalize the feeding behavior of stomachless fish such as silver carp.

Our findings indicate that the composition and relative abundance of phytoplankton in the water was more similar to that in fish fore-gut at low density than at high density. The density effect was significant in both the Stock A and Stock B experiments (Fig. 3, $p<0.05$, *U*-test). Because of the low grazing pressure, algae in the low-density enclosures, may more easily form aggregates or colonies in the water column than those in high-density enclosures. The results from an analysis of foregut content of fish may also confirm that fish ingest unselectively algal aggregates or colony as bulk or mass from water. Although the feeding selectivity of silver carp is still controversial and unclear if it really does occur (Kajak *et al*., 1972; Sirenko *et al*., 1973), it may be one of the expectations that there were weak relationship between the selectivity indices and the IU values of phytoplankton ($r<0.1$ for two low-density enclosures). In addition, although introduction of silver carp strongly induced the outbreak of small cryptomonads (<40 μm) such as *Cryptomonas* and *Plagioselmis* (Fukushima 2000), they were hardly found in fish gut, and then they had a low selectivity or no selectivity through the computation.

The present work revealed that the manipulation of silver carp did not effectively suppress the large filamentous phytoplankton with high IU values. However, the fish were able to maintain growth by using diatoms and other algae, rather than cyanobacteria and green algae.

ABSTRACT

The feeding behavior of 1-year-old silver carp, *Hypophthalmichthys molitrix* (Val.) on phytoplankton species in a shallow hypertrophic lake was studied from 22 May to 18 September, 1997. Over the experimental period, the filter-pore sizes of the fish, the total biomass of the phytoplankton and the water temperature in each enclosure changed little with time. The fish biomass in each enclosure increased with time, while their percentage of weight gain correlated negatively to the stocking density, due perhaps to competition for prey. An analysis of gut contents of silver carp showed a strong similarity between the algal communities in the foregut and the water, and was significant for the fish enclosure with a low density ($p<0.05$). The presence of silver carp rarely suppressed the abundance of phytoplankton such as *Oscillatoria, Anabaena* and *Melosira* even at high ingestion levels. There were weak relationships between the IU values of each phytoplankton and the selectivity of fish on them ($r = 0.001$, $p>0.5$). There was no doubt that the silver carp fed unselectively when cyanobacteria populations were high, even though the selectivity index for diatoms was slightly higher than those for cyanobacteria, green algae and cryptomonads. Improvements in methodologies are needed to clearly understand and generalize the feeding behavior of silver carp.

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