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Phosphorus uptake by *Microcystis* during passage through fish guts

Abstract—Herbivorous fish feed on cyanobacteria. Digestability differs, however, between cyanobacteria species without mucous cover and mucilaginous genera such as *Microcystis.* The latter can pass fish guts almost undamaged, and it has been hypothesized that they can take up nutrients during gut passage. Here we tested whether live *Microcystis,* as food for juvenile roach labeled with ^{33}P, indeed showed higher radioactivity after gut passage as compared to gut contents in control experiments with fish fed heated *Microcystis. Microcystis* showed high viability after passage through roach guts, and live colonies had a significantly higher radioactivity than dead ones. We conclude that *Microcystis* is protected against digestion in roach guts and can directly use the phosphorus supplied in the fish guts during passage.

Cyanobacteria (e.g., *Microcystis* spp. and *Aphanizomenon* spp.) are sometimes dominant planktonic primary producers in eutrophic lakes. While a combination of several biotic and abiotic factors (e.g., resistance against grazing, low light climate, high water temperature, low TN/TP ratios, or hydrodynamic effects) influence blooms of cyanobacteria, their function as food for other aquatic animals is less clear. Although some cyanobacteria species are directly consumed by the zooplankton (DeBernardi et al. 1981), others seem to be protected from grazing by producing toxins or 'bad taste' compounds (Carmichael 1992). Feeding on cyanobacteria has been reported from herbivorous and omnivorous fish species as well (Prejs 1984; Datta and Jana 1998). Omnivorous roach (*Rutilus rutilus*), an abundant cyprinid in many European lakes, include cyanobacteria in their food, especially during the midsummer decline of large zooplankton and increasing roach densities. In contrast to more specialized phytoplankton feeders (e.g., tilapia), roach, like other stomachless fish, lack pepsin- and acid-secreting cells in the intestine. While digestion is facilitated only through mechanical disruption by pharyngeal teeth, assimilation efficiency for cyanobacteria is low (Prejs 1984).

However, the energy gain for fish while they are feeding on cyanobacteria depends on biochemical properties of cyanobacterial colonies. Whereas species without mucous cover, such as *Aphanizomenon,* can be well digested, and thus, their nutrients can be assimilated by fish (Vörös et al. 1997; Kamjunke et al. 2002*a*,*b*), mucilaginous species like *Microcystis* seem to pass the fish gut rather unaffected (Vörös et al. 1997; Datta and Jana 1998), and only the nutrients from attached bacteria were definitely assimilated (Kamjunke and Mehner 2001).

On the other hand, cyanobacteria may even benefit by the gut passage through fish. Miura and Wang (1985) observed a doubling of the photosynthetic activity of cyanobacteria excreted by bighead (*Aristichthys nobilis*). From investigations of snails fed cyanobacteria, it had been supposed that undigested cyanobacterial cells can take up nutrients from the alimentary canal during passage (Cuker 1983). Phosphorus uptake was demonstrated by microautoradiography for the green algae *Sphaerocystis* after passage through *Daphnia* (Porter 1976) and by uptake of radiolabeled P for the green algae *Scenedesmus* in *Daphnia* (Boersma pers. comm.). A similar P-uptake of cyanobacteria during passage through fish guts has only been supposed so far (Miura and Wang 1985; Vörös et al. 1997). Therefore, we tested whether the mucous-possessing *Microcystis* can directly use the high phosphorus concentrations in guts without being digested if they are consumed by omnivorous fish. To do this, we adapted previous experimental procedures with radioactive tracers toward a protocol that labeled juvenile roach with ^{33}P, and we fed them with live and dead *Microcystis* colonies.

Methods—A natural cyanobacteria suspension (mainly *Microcystis aeruginosa*) was collected, using a 150-μm plankton net, from the surface layer of Lake Templin (80 km north of Berlin, Germany) during August 2002. The sample was subsequently resuspended in aerated tap water. Subsamples for analysis of species composition were preserved with Lugol's solution. Cells were counted by the sedimentation technique, after having disintegrated the colonies, using a high-speed blender (Ultra-Turrax, 20,000 $\times$ g). Attached bacteria were detached by homogenizing of subsamples with the blender. Biomass of attached bacteria was calculated as the difference between homogenized and natural samples (Kamjunke and Mehner 2001) and was estimated by staining with DAPI (4′6-diamidino-2-phenylindole) using an epifluorescence microscope (Axiovert, Zeiss).

^{33}P uptake by and adsorption on live versus dead cyanobacteria were compared. To kill cyanobacteria, 400 ml of the suspension was heated to 75°C for 45 min. Most of the cyanobacteria remained in colonies after heating. Two hundred milliliters of both live and heated cyanobacteria suspension were incubated with 1 μl $^{33}PO_4$ (110 TBq mmol^{-1}, Amersham) at 22°C for 3 h during daylight. To remove bacteria attached to colonies, 1-ml subsamples were homogenized by an Ultra-turrax (T 25, 10,000 $\times$ g) and filtered onto 0.85-μm cellulose nitrate filters (Sartorius). Filters were dried and placed in scintillation vials. After adding 15 ml Filtercount (Packard) to each vial, radioactivity on the filters was measured using a Liquid Scintillation Analyzer (TRICARB 1900; Packard). The external standard ratio method was used to correct for quenching.

Viability of cyanobacterial cells was inspected separately

after heating, filtration, homogenizing, and gut passage through roach. The two-color fluorescence assay LIVE/DEAD BacLight (Molecular Probes) was used. One milliliter of cyanobacteria suspension was mixed with 1 ml dye solution containing 6 μmol L^{-1} SYTO 9 and 30 μmol L^{-1} propidium iodide and incubated at 22°C in the dark for 20 min. Two microliters of the stained cyanobacterial solution was trapped between glass slides, and viability of cells was analyzed using a fluorescence microscope. Viable cells show a green and dead cells a red fluorescence.

Algae (*Scenedesmus obliquus*, culture, Institute of Freshwater Ecology and Inland Fisheries) for labeling the zooplankton (food for fish) were cultivated in Bourrelly medium in aerated 1.5-liter Erlenmeyer flasks and labeled by adding 5 μl $^{33}PO_4$ (110 TBq $mmol^{-1}$, Amersham) each day over a period of 11 d. Zooplankton (mainly *Daphnia cucullata*) was collected with a 150-μm plankton net from small ponds.

Samples were cultured over a period of 7 d in aerated tap water and were fed with 50 ml of labeled *Scenedesmus* twice a day. Juvenile 1^+ roach of 2.58 ± 0.52 g wet mass (mean ± SD) were caught using a dip net during July and August 2002 in Lake Großer Müggelsee (Berlin, Germany) and were acclimatized in basins for 2 weeks. Thereafter, 10 roach each were kept in two 15-liter aquaria in 1-d-old tap water with artificial aeration at 20°C at a natural day–night rhythm. The roach were fed with labeled zooplankton twice a day over a period of 4 d. The daily rations were generally completely ingested after 30–45 min. Before the experiments started, all roach were starved for the next 48 h to ensure that no labeled food remained in their alimentary canals. Ten fish each were placed by chance in two new aquaria with similar design, as described above. The treatment group of roach was fed with a suspension of live cyanobacteria (500 ml). The other group was used as control and was fed with the same amount of heated cyanobacteria. Water circulation caused by aeration kept cyanobacteria in suspension. Roach were allowed to feed on cyanobacteria for 24 h.

The next day, roach were anesthetized with carbon dioxide–rich water, rinsed with distilled water, killed, and weighed to the nearest 0.0001 g. Roach were gutted without damaging the gut. The distal half of the gut was placed on a glass slide and emptied by gentle squeezing and rinsing with sterile filtrated water. Only fish with filled guts were used for analyses. Gut contents were resuspended in sterile filtered water, homogenized as described above, and filtered onto 0.85-μm cellulose nitrate filters (Sartorius). The filters were weighed to the nearest 0.0001 g and placed into scintillation vials. After adding 15 ml Filtercount (Packard) to each vial, radioactivity of gut contents was measured as described above. To determine radioactivity of fish tissue, roach carcasses were placed in scintillation vials and homogenized by using an ultraturrax. Two milliliters of tissue solubilizer (Soluene, Packard) was added to each vial. Vials were heated to 50°C until tissue was dissolved. After adding 12 ml Hionic Fluor (Packard) to each vial, radioactivity was measured as described above. The phosphorus transfer to cyanobacteria was calculated from the ratio of ^{33}P uptake (pg ^{33}P (g gut content)$^{-1}$) to ^{33}P in the fish (pg ^{33}P (g fish tissue)$^{-1}$) multiplied by the phosphorus concentration of the fish (0.5% of wet mass, *see* Mehner et al. 1998).

Results—Cyanobacteria suspensions (average colony size 1,427 ± 653 cells, mean ± SD) were a mixture of *Microcystis aeruginosa* (95.2–96.3% of biomass in subsamples) and some *Aphanizomenon.* Other phytoplankton species were found only in single individuals. Cyanobacteria biomass in the food suspension ranged between 928 and 1,198 mg L^{-1}. Biomass of attached bacteria ranged between 1.7 and 2.8 mg L^{-1}, comprising on average 0.2% of total cyanobacteria biomass. Bacteria attached to colonies passed the filter after homogenization, and thus, any potential radioactivity included in attached bacteria was included in the filtrate and was not retained by the filter.

Homogenizing and filtration did not damage cyanobacterial cells, since after both treatments *Microcystis* cells showed bright green fluorescence. In addition, more than 60% of *M. aeruginosa* cells (61.7 ± 13.6%, mean ± SD; $n = 3$ fishes) were viable after passage through roach guts. Heating inactivated the cyanobacterial ^{33}P uptake. On average, 99.4% of the added ^{33}P was retained on filters from live suspensions, whereas only 13.2% of added ^{33}P was found on the filters from heated suspensions (Mann-Whitney *U*-test, $U = 0$, df = 11, $P = 0.002$).

The majority of roach fed upon the cyanobacteria suspension during the experiments. However, in total, one roach from the treatment group and three fish from the control group showed empty guts, such that no further analyses could be made. Therefore, from a total of 20 roach used during the experiment, data were obtained from nine roach fed with live cyanobacteria and from seven roach fed with heated cyanobacteria.

Roach wet mass did not differ between treatment and control groups (*t*-test: $t = -0.545$, df = 14, $P = 0.594$). Similarly, neither gut contents of roach (wet mass) nor ^{33}P content of roach tissue (pg g^{-1} wet mass) differed significantly between treatment and control (gut content: $t = -0.728$, df = 14, $P = 0.479$; ^{33}P content of tissue: $t = 0.584$, df = 14, $P = 0.568$). In contrast, the estimated phosphorus transfer from fish to cyanobacteria differed significantly between live (10.81 ± 1.84 mg P (g gut content)$^{-1}$) and heated (5.44 ± 1.39 mg P (g gut content)$^{-1}$) phytoplankton (Fig. 1; *t*-test: $t = -2.208$, df = 14, P (one-tailed) = 0.022).

Discussion—The data obtained during the experiments provide evidence that live *Microcystis* can use the fish-internal phosphorus supplied during their passage through roach guts. Despite strong variability between individual samples, there was a clear tendency toward higher phosphorus transfer to *Microcystis* if fish were fed with live cyanobacteria as opposed to those that were fed with heated *Microcystis.*

Fish release phosphorus by excretion via gills and by egestion via the gut (Nakashima and Leggett 1980). Therefore, P-uptake from the gut is possible if cyanobacteria cells remain alive. Our results show that *Microcystis* cells can pass the guts without being damaged. In previous experiments, exponential growth of *Microcystis* after cultivation of feces was observed (Kamjunke et al. 2002*a*). In addition, roach that were fed with *Microcystis* showed lower growth rates in contrast to those fed with *Aphanizomenon,* a fact that was mainly attributed to poor digestability because of

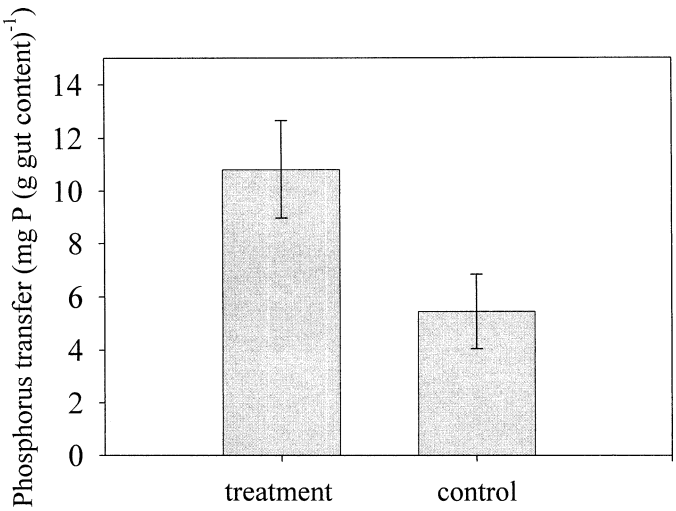

Fig. 1. Phosphorus transfer (mean ± SE) in gut contents of roach (mg P (g gut content)$^{-1}$) fed either live (treatment, $n = 9$) or heated (control, $n = 7$) *Microcystis.*

the mucous cover that protects *Microcystis* cells (Kamjunke et al. 2002*a*). A comparably weak digestability of *Microcystis* colonies with viable cyanobacteria cells found in fecal pellets after egestion was documented for both cyprinids and tilapia with low intestinal pH values (Datta and Jana 1998). Although uptake and incorporation of phosphorus by cyanobacteria is stimulated by light, it is generally also possible in the dark (Healey 1982). Furthermore, phosphorus uptake is possible in the range of intestinal pH values of 6.12–7.72 reported for cyprinids (*see* Prejs 1984). Therefore, it had been assumed, but never tested, that mucilaginous cyanobacteria are able to take up nutrients during passage through fish guts (Vörös et al. 1997). Vanderploeg et al. (2001) suggested that zebra mussels (*Dreissena polymorpha*) promote blooms of *M. aeruginosa* by repelling viable cells in pseudofeces. Cuker (1983) observed viable algae and cyanobacteria cells in feces of snails (*Lymnaea*) and assumed nutrient recycling within the animals. Porter (1976) reported enhancement of algal (*Sphaerocystis schroeteri*) growth due to ^{33}P-uptake in *Daphnia magna* intestines.

Some methodological uncertainties may have influenced the reliability of our results. A potential complication that may affect radioactivity measured in gut contents are residues of labeled zooplankton dating back to the zooplankton feeding phase of the experiment. In pretests, however, roach always displayed empty guts after 48 h starvation at 20°C water temperature. Persson (1982) reported an evacuation time for juvenile roach of 12 h at 20.2°C. Therefore, it can be assumed that the measured gut contents consisted only of cyanobacteria colonies. A second source of error may be found in attachment or adsorption of ^{33}P at the surface of *Microcystis.* Feces of roach are often covered with mucous (Prejs 1984). Despite homogenizing and rinsing of gut contents, attachment or adsorption of ^{33}P to cyanobacteria cells, mucilage, or filters may lead to an overestimation of ^{33}P uptake. However, attachment of phosphorus at the surface may nevertheless support P-uptake by cyanobacteria, even if uptake rate is delayed. Another effect may come from the bacteria that normally colonize the mucilaginous *Microcystis* colonies (Worm and Søndergaard 1998). Bacterial biomass in our samples was lower, as compared with other aquatic ecosystems (Worm and Søndergaard 1998). In addition, roach can digest attached bacteria (Kamjunke and Mehner 2001). Therefore, the number of attached bacteria that may have remained on the filters should have been too small to be responsible for a large proportion of ^{33}P uptake. Finally, there is evidence of different kinds of bacteria in the alimentary tract of roach (Prejs 1984). Therefore, it is possible that intestine bacteria took up ^{33}P and remained on filters, thus increasing the radioactivity measured. Overall, however, we would point out that gut contents of both treatment and control groups were treated in the same way, such that the sources of error listed may have had a comparable impact on both groups. The measured differences in radioactivity therefore more likely reflect real differences in ^{33}P uptake between live and heated cyanobacteria.

Together with previous work on roach feeding on cyanobacteria (Kamjunke and Mehner 2001; Kamjunke et al. 2002*a*,*b*), our results illuminate a surprising ecological interaction between primary producers and omnivorous fish. The large colony size of *Microcystis* minimizes not only mortality, through grazing by zooplankton, but is also a main precondition that the particulate-feeding roach can see the colonies and feed upon this species. The enhanced consumption of cyanobacteria during periods of low zooplankton biomass is thought to be one reason for the competitive superiority of roach in eutrophic lakes (Persson and Greenberg 1990). However, roach can obtain sufficient energy for growth only if fed with *Aphanizomenon,* whereas most *Microcystis* cells are not digested, such that only some carbohydrates from mucous can be used (Kamjunke et al. 2002*a*,*b*). Fecal nutrients are usually not immediately available to phytoplankton. Depending on the digestibility of food items, 50% of phosphorus can be released via egestion (Lamarra 1975). According to our results, the ability to pass fish guts almost undamaged while directly using the high phosphorus concentrations in the guts gives *Microcystis* a competitive advantage, as compared to, for example, *Aphanizomenon. Microcystis* has a high affinity for phosphorus at low concentrations, is able to store phosphorus in polyphosphate granula (Jacobson and Halmann 1982), and can rapidly use it if lake-wide phosphorus concentrations become low. Phosphorus limited *Microcystis* might have shown even higher phosphorus uptake. The potential sedimentation within the fish feces to nutrient-rich bottom water could be a further advantage. *Microcystis* can overwinter on sediments for long periods, and these dormant stages then form a source for a new growth circle (Fallon and Brock 1981).

In general, fishes can influence phytoplankton assemblages via ''top-down'' effects on zooplankton and nutrient recycling (Vanni and Layne 1997). Several factors (e.g., trophic state of lakes and food web structure) influence the ecological importance of nutrient release by fish. During summer months with low external phosphorus load and high water temperatures, phosphorus release by roach has been proved to support algal nutrient demands (Braband et al. 1990; Persson 1997). Several field studies have shown a maximum proportion of cyanobacteria in the gut content of between 40% and 73%

for juvenile roach (Weatherley 1987; Mehner et al. 1998) and of 85–90% for older roach (Persson 1983, 1987). The percentage of *Microcystis* that might benefit from gut passage varies with cyanobacterial biomass and roach abundance. A rough calculation was made based on data of Lake Müggelsee, a shallow eutrophic lake in eastern Germany (*see* Driescher et al. 1993), from which the fish for our experiments were caught. In summer 2001, the mean biomass of *Microcystis* was 0.32 g wet mass m^{-3} (Köhler pers. comm.). Roach dominated the juvenile fish community, with a mean biomass of 0.6 g m^{-3} in the littoral. Seventy percent of roach consumed cyanobacteria (Lewin unpubl. data). Previous experiments with juvenile roach have shown that the daily consumption of *Microcystis* can reach 20% of roach wet mass (Kamjunke et al. 2002*b*). Assuming a *Microcystis* survival of 60% in the guts, in total 0.05 g cyanobacteria m^{-3} d^{-1} (=16% of available *Microcystis* biomass in littoral areas) might have benefitted from passage through the gut of juvenile roach. In summer, SRP concentration in Müggelsee normally decreases to very low levels (<3 μg L^{-1}). Assuming a carbon content of 10% of wet mass in *Microcystis* and a C : P ratio of 50 : 1, which results in a phosphorus content of 2 mg P g wet $mass^{-1}$, a phosphorus transfer of 10 mg P g wet $mass^{-1}$, as measured in our experiments, would supply five times the biomass phosphorus. In other eutrophic European lakes, roach biomasses were given with 122–300 kg ha^{-1} (Brabrand et al. 1990; Horppila and Peltonen 1997; Persson 1997). Therefore, phosphorus uptake during gut passage might be important in shallow eutrophic lakes with extended littoral areas and high roach abundances during periods of high phosphorus demand of phytoplankton.

In summary, it can be concluded that the protection of *Microcystis* colonies against digestion and the resulting ability for phosphorus uptake from the fish contribute to the competition strength of *Microcystis* during periods of low in-lake phosphorus concentration, which often occur simultaneously with periods with low zooplankton biomass, and the subsequent enhanced herbivory in roach.

Wolf-Christian Lewin

Institute of Freshwater Ecology and Inland Fisheries
Department of Biology and Ecology of Fishes
P.O. Box 850 119 D-12561 Berlin, Germany

Norbert Kamjunke

Institute of Biochemistry and Biology
University of Potsdam
Maulbeerallee 2 D-14469 Potsdam, Germany

Thomas Mehner[1]

Institute of Freshwater Ecology and Inland Fisheries
Department of Biology and Ecology of Fishes
P.O. Box 850 119, D-12561 Berlin, Germany

[1] Corresponding author.

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