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NOTE

Effects of hydrologically confined fishes on bacterioplankton and autotrophic picoplankton in a semiarid marsh

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ABSTRACT: An enclosure experiment was conducted to assess the separate effects of exotic benthivorous (*Cyprinus carpio* L.), planktivorous (*Gambusia holbrooki* Gir.), and omnivorous (*Lepomis gibbosus* L.) fish on the dynamics of bacterioplankton (BAC) and autotrophic picoplankton (APP) in a semiarid Spanish marsh. Special emphasis was put on simulating the effect of natural fish density situations occurring under periods of hydrological confinement in the wetland, i.e. during summer draw downs or artificial water-level reductions, when fish biomass can reach high levels. The resulting simulation of such a scenario (*C. carpio*, 5000 to 6000 kg ha^{-1}; *L. gibbosus*, 1300 to 1700 kg ha^{-1}, and *G. holbrooki*, 115 kg ha^{-1}) revealed that *C. carpio* and *L. gibbosus* significantly increased the trophic level in the enclosures. This resulted in a significant increase of BAC in the respective treatments. *G. holbrooki*, on the other hand, failed to fuel BAC growth. Considering APP, composed of phycocyanin-rich picocyanobacteria *Synechococcus* sp., no fish treatment effects were detected, suggesting that the fishes, independent of biomasses used, were not important in driving APP. Results indicate that microbial communities respond in different ways to changes in fish biomass in fluctuating wetlands.

KEY WORDS: Bacterioplankton · Autotrophic picoplankton · Fishes · Enclosures · Wetland

Bacterioplankton (BAC) and autotrophic picoplankton (APP) abundances in pelagic systems can be regulated by bottom-up (nutrients) and top-down (predator control) regulating forces (reviewed in e.g. Weisse 1993, Stockner et al. 2000). Fishes can play a significant role in regulating bottom-up and top-down structuring forces in aquatic ecosystems. Therefore, their presence may have indirect effects on the components of the microbial web. Fish activity can influence the food web either by recycling nutrients or by changing zooplankton community composition by predation (e.g. McQueen et al. 1986), which in turn can regulate the strength of top-down effects to the base of the microbial web (Jeppesen et al. 1997, Adrian & Schneider-Olt 1999).

Knowledge of bottom-up and top-down effects on BAC and APP in aquatic systems stems largely from studies of lakes and marine systems. However, studies of wetlands, especially in arid and semiarid climates, are scarce. This constitutes an important gap in the understanding of wetland dynamics because microbial processes play a significant role in wetland functions, e.g. decomposition and energy flux through detritus-based food webs (Mitsch & Gosselink 2000). Fishes can often reach high biomasses in wetland ecosystems, concentrated by either naturally occurring reductions of the inundated area (i.e. evapotranspiration losses during summer droughts) or artificial management of the inundated area (Angeler et al. 2002). Hence, we can expect them to affect wetland microbial food webs. However, the literature on the biota-mediated effects on wetland bacteria and APP is still scanty (see reviews in Weisse 1993, Stockner et al. 2000).

This study was undertaken to address this deficiency in the literature. Using enclosures we aimed at assessing the impacts of 3 exotic fish species on BAC and APP dynamics in a semiarid marsh. We were particularly interested in simulating the effects of natural fish density and biomass situations occurring under hydrological stress conditions in wetlands.

MATERIALS AND METHODS

Study site. Las Tablas de Daimiel National Park, a Ramsar site, is a hypertrophic, riverine wetland in

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central Spain. It covers around 20 km^2 and lies within a heavily used agricultural basin (watershed ca. 13 000 km^2). The hydrological parameters are highly variable as a result of the meteorological characteristics associated with the semiarid climate (Angeler et al. 2000). Such variability is reflected in water-level changes, which can show intra-annual fluctuations of up to 1 m. Wide parts of the wetland are infested with cut-sedge. Reed-grass *Phragmites australis* [Cav.] Trin. ex Steud. and, to a lesser extent, cattail *Typha domingensis* [Pers.] Steud. also form important stands in the wetland. The ichthyofauna actually comprises 3 exotics: common carp *Cyprinus carpio* L., sunfish pumpkinseed *Lepomis gibbosus* L., and mosquitofish *Gambusia holbrooki* Gir.

Experimental design, fish stocking scheme, and sampling. The enclosure study, carried out during a 6 wk period (28 June to 2 August 1999), consisted of 3 treatments to assess separately the fish-mediated effects of *Cyprinus carpio*, *Lepomis gibbosus*, and *Gambusia holbrooki* on the dynamics of BAC and APP. Each treatment and the control were carried out in triplicate. The *L. gibbosus* experiment was terminated after the fourth sampling date because fish kills occurred in all enclosures before the fifth sampling date. A detailed description of the enclosure design, sampling procedures, and determination of limnological parameters is given in Angeler et al. (2002). Briefly, enclosures consisted of polyethylene hose tubing (1 m diameter). Both ends of the hose tubing were attached to plastic rings (3 cm diameter) to increase mechanical stability and maintain the cylindrical form of the enclosures. The bottom ring was driven to about 40 cm into the sediment and the top ring suspended ca. 50 cm above the water surface, hence allowing for natural sediment-water and water-air interactions. Field sampling at weekly intervals included water temperature, pH, conductivity, depth, and Secchi transparency, and in the laboratory we determined total nitrogen (TN), ammonia (NH_4^+), total phosphorus (TP), soluble reactive phosphorus (SRP), chlorophyll *a* (chl *a*), water colour (WC), total suspended solids (TSS), and total organic matter (TOM). For this study we calculated dissolved organic carbon (DOC) concentrations on the basis of WC data according to Rasmussen et al. (1989).

Zooplankton were collected at about 20 cm below the surface by filtering 10 l of water of each enclosure through a 45 µm Nytal net and then fixed with 4% formalin. Taxa identification to the lowest possible rank, quantification, and biomass calculations were carried out as described previously (Angeler et al. 2002).

The fish stocking scheme for each enclosure (Table 1) is based on natural density estimates by means of catchment per unit effort measurements carried out during a spring trial preceding our experiment. For a detailed explanation and justification of this stocking scheme we refer to our previously published paper (Angeler et al. 2002).

Determination of BAC and APP. A 50 ml water sample was taken and fixed with formalin (1 to 2% final concentration) for counting APP and BAC cells. The samples were kept refrigerated (4°C) in the dark until slide preparation. APP abundance was estimated following the recommendations of MacIsaac & Stockner (1993). Accordingly, an aliquot of each sample was concentrated on 0.2 µm black polycarbonate membrane (Millipore) filters. Samples were prefiltered through 15 µm Nytal mesh to eliminate filamentous cyanobacteria and other large algae. Samples for BAC counts were stained with acridine orange (Hobbie et al. 1977) and filtered onto filters as used for APP counts. Slides were examined at ×1000 magnification by epifluorescence microscopy in a dark room using a Leica photomicroscope equipped with an epifluorescence illuminator. Two sets of filters were used: 450BP 510RKP 520LP (blue light) for BAC and 515-560BP

Table 1. Fish stocking scheme of individual enclosures simulating natural biomasses of *Cyprinus carpio* (5000 to 6000 kg ha^{-1}), *Lepomis gibbosus* (1300 to 1700 kg ha^{-1}), and *Gambusia holbrooki* (115 kg ha^{-1}) found during a period of hydrological stress in the wetland. Fish size was chosen based on individuals readily caught in the wetland. Given the dimensions of enclosures, benthivorous juveniles were selected for the *C. carpio* treatment. For further details see Angeler et al. (2002). SD: standard deviation

Treatment and enclosure	Number of individuals	Total weight (g) per enclosure	Average individual weight (g) ± SD	Average individual fork length (cm) ± SD
C. carpio 1	2	650	325 ± 106	27 ± 4.2
C. carpio 2	2	550	275 ± 35.3	28.5 ± 4.9
C. carpio 3	2	575	287.5 ± 159.1	26.3 ± 7.4
L. gibbosus 1	6	146	24.33 ± 14.1	10.4 ± 1.9
L. gibbosus 2	7	179	25.57 ± 23.4	10.4 ± 2.3
L. gibbosus 3	6	137	22.83 ± 9.4	10.5 ± 1.6
G. holbrooki 1	38	11.35	0.30 ± 0.25	2.86 ± 0.7
G. holbrooki 2	38	11.64	0.31 ± 0.19	2.79 ± 0.7
G. holbrooki 3	38	11.70	0.31 ± 0.26	2.77 ± 0.7

Table 2. Limnological parameters (means of 3 enclosures ± standard error [SE]) of treatments and control. Significant differences between the respective treatments and the control as revealed by repeated measures (RM) ANOVA are highlighted: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. DOC: dissolved organic carbon; SRP: soluble reactive phosphorus; TN: total nitrogen; TP: total phosphorus; TSS: total suspended solids

Variable	*Cyprinus carpio*	*Lepomis gibbosus*	*Gambusia holbrooki*	Control
Temperature (°C)	25.7 ± 0.1	25.8 ± 0.2	25.6 ± 0.1	25.8 ± 0.1
Dissolved oxygen (mg l^{-1})	4.0 ± 1.3	4.2 ± 0.7	2.84 ± 0.6	2.6 ± 0.4
pH	7.8 ± 0.04	7.7 ± 0.03	7.6 ± 0.08	7.6 ± 0.02
Conductivity (mS cm^{1})	4.6 ± 0.1	4.7 ± 0.2	4.7 ± 0.1	4.7 ± 0.08
Water level (cm)	90 ± 2	92 ± 1	87.5 ± 1	82 ± 1
Secchi depth (cm)	47 ± 6	52 ± 6	76 ± 5***	54 ± 6
SRP (mg l^{-1})	0.04 ± 0.01	0.02 ± 0.02	0.02 ± 0.001	0.02 ± 0.01
TP (mg l^{-1})	0.72 ± 0.09***	0.46 ± 0.10*	0.34 ± 0.04	0.36 ± 0.04
NH_4 (mg l^{-1})	2.07 ± 0.38	0.79 ± 0.46	0.49 ± 0.32	1.37 ± 0.21
TN (mg l^{-1})	6.52 ± 0.41***	5.04 ± 0.81***	4.45 ± 0.34	4.47 ± 0.47
Chlorophyll *a* (µg l^{-1})	215 ± 24***	70 ± 14**	50 ± 18	33 ± 8
TSS (mg l^{-1})	31 ± 5***	22 ± 5**	14 ± 6	13 ± 2
DOC (mg l^{-1})	5.29 ± 0.20*	5.44 ± 0.36*	4.86 ± 0.11*	13.81 ± 1.52
Rotifers (µg l^{-1})	305 ± 138**	276 ± 479**	316 ± 131**	12 ± 6
Copepods (µg l^{-1})	57 ± 35	1064 ± 592*	2172 ± 135**	1294 ± 603
Cladocerans (µg l^{-1})	Not present	Not present	Not present	222 ± 93
Total zooplankton (µg l^{-1})	363 ± 139***	1340 ± 579	2489 ± 1468	1528 ± 575

580RKP 580LP (green light) for APP. At least 400 cells per sample were counted. When cell abundance was very low, 20 to 30 random microscope fields were counted. The cell dimensions were obtained from measurements of amplified photomicrographs. Cell volumes were calculated using formulae for geometric shapes (spheres and cylinders ending with hemispheric caps) approximating the shapes of the cells (rods and cocci for BAC and spherical cells for APP).

Statistical analyses and hypotheses testing. All data were log transformed to satisfy the assumptions of normality and homogeneity. A repeated measures (RM) ANOVA procedure was selected to evaluate treatment effects and any temporal effects on BAC and APP biovolume and abundance during the study period. Only data from sampling dates 1 to 4 were included in the analysis because of the limited data set of the *Lepomis gibbosus* treatment (see above). A Duncan test was carried out to compare significant differences between treatments post hoc. All statistical analyses were performed with the STATISTICA (StatSoft) software package.

RESULTS

The limnological environment (Table 2) as shaped by the different fish species has been discussed by Angeler et al. (2002). Briefly, total nutrient fractions, chl *a*, and turbidity levels were significantly higher in the *Cyprinus carpio* and the *Lepomis gibbosus* treatments. DOC concentrations were significantly lower in all fish treatments than in the control, but these data have to be regarded with caution because of the assay method used to calculate DOC. Secchi depth was significantly different in the *Gambusia holbrooki* treatment only. Zooplankton community composition and biomass were different between fish treatments and the control. Rotifers dominated in the *C. carpio* treatment. The *L. gibbosus* and *G. holbrooki* treatments were characterised by a mixture of rotifers and copepods. Cladocerans, rotifers, and copepods occurred in the fishless control (Table 2).

Morphotypes of BAC were mainly rods and cocci. Filamentous bacteria occurred in a negligible number and were hence not quantified, so results on BAC refer to single-cell bacteria only. BAC abundance (cells ml^{-1}) ranged from 4.7×10^6 to 21×10^6 in the *Cyprinus carpio* treatment, from 5.0×10^6 to 22×10^6 in the *Lepomis gibbosus* treatment, from 4.0×10^6 to 13×10^6 in the *Gambusia holbrooki* treatment, and from 1.1×10^6 to 13×10^6 in the fishless control. In terms of biovolume (mm^3 l^{-1}), BAC ranged from 0.6 to 4.2 in the *C. carpio* treatment, from 0.6 to 7.8 in the *L. gibbosus* treatment, from 0.5 to 2.0 in the *G. holbrooki* treatment, and from 0.1 to 1.6 in the control.

The overall effects of the 3 fish treatments are summarised in Table 3. RM-ANOVA revealed that the mean BAC abundance and volumes were significantly different between treatments. Post hoc comparisons indicated that the *Cyprinus carpio* and the *Lepomis gibbosus* treatment had significantly higher BAC abundances and volumes than the control. On the other hand, the *Gambusia holbrooki* treatment did not

Table 3. Results of RM-ANOVA examining fish treatment effects on log-transformed bacterioplankton and autotrophic picoplankton (APP) data. *Significant differences. Ti: time; Tr: treatment

	df effect	MS effect	df error	MS error	*F*	p
Bacteria density						
Tr	3	0.09	6	0.02	5.12	0.04*
Ti	3	0.12	18	0.03	3.89	0.03*
Tr × Ti interaction	9	0.08	18	0.03	2.79	0.03*
Bacteria volume						
Tr	3	0.51	6	0.1	5.15	0.04*
Ti	3	0.14	18	0.04	3.99	0.02*
Tr × Ti interaction	9	0.07	18	0.04	1.93	1.11
APP density/volume						
Tr	3	0.67	5	1.34	1.34	0.36
Ti	3	4.03	15	0.74	5.42	0.01*
Tr × Ti interaction	9	0.31	15	0.74	0.42	0.9

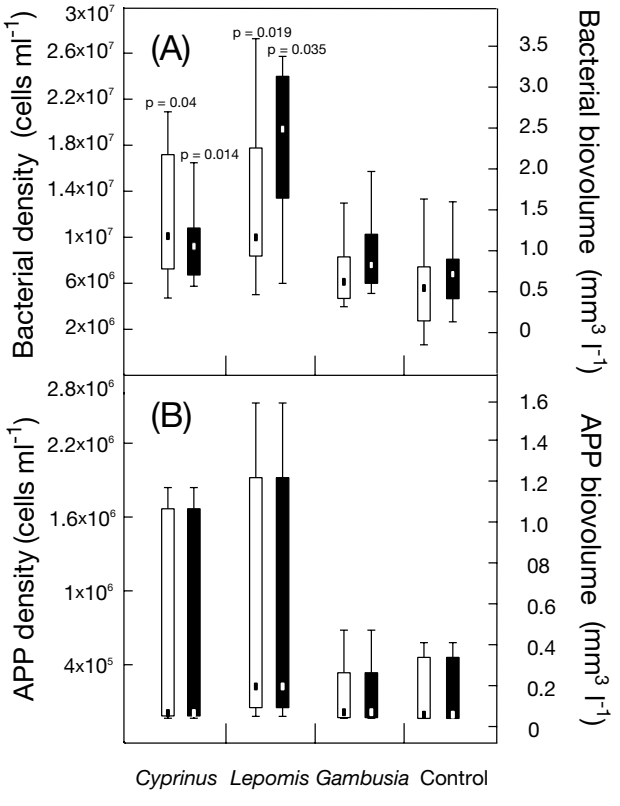

Fig. 1. Box-whisker plots for comparison of abundance (white boxes) and biovolume (black boxes) of (A) bacterioplankton and (B) autotrophic picoplankton (APP) in the respective treatments. Plots include all data from the 3 replicate enclosures per treatment obtained during the whole experiment (6 sampling dates: *Cyprinus carpio* treatment, *Gambusia holbrooki* treatment, control; 4 sampling dates: *Lepomis gibbosus* treatment). Those that differed significantly from the control are highlighted by presenting p-levels obtained form post hoc comparisons (Duncan test). Whiskers represent the maxima and minima of data, boxes the data in the 25 to 75% range, and dots the median

differ significantly form the control (Fig. 1). Both volume and abundance fluctuated during the experiment, resulting in significant temporal effects in the RM-ANOVA (Table 3). The *C. carpio* and *G. holbrooki* treatments and the control peaked on the third sampling date, while the *L. gibbosus* treatment increased until the end (Fig. 2). The different patterns of time trajectories and influences of fish are reflected in a significant treatment × time interaction (Table 3).

Based on fluorescence spectra, APP was composed of more than 95% of phycocyanin (PC)-containing picocyanobacteria *Synechococcus* sp. APP patterns were different from those observed for bacteria. All fish treatments and the control experienced the highest abundances and volumes on the first sampling date (*Cyprinus carpio* treatment: 5.6×10^6 cells ml^{-1} in abundance, 2.9 mm^3 l^{-1} in volume; *Lepomis gibbosus* treatment: 8.26×10^6 cells ml^{-1}, 4.2 mm^3 l^{-1}; *Gambusia holbrooki* treatment: 2.0×10^6 cells ml^{-1}, 1.04 mm^3 l^{-1}; control: 4.1×10^6 cells ml^{-1}, 2.2 mm^3 l^{-1}). A drastic decline was observed in all treatments and the control between the first and the second sampling date. Abundance and volume minima were generally reached on the last sampling date. Observed minima were 3.5×10^3 cells ml^{-1} and 0.002 mm^3 l^{-1}, respectively, in the *C. carpio* treatment, 1.8×10^5 cells ml^{-1} and 0.09 mm^3 l^{-1} in the *L. gibbosus* treatment (note that sampling spanned only 4 sampling dates in this treatment), 1.9×10^3 cells ml^{-1} and 0.002 mm^3 l^{-1} in the *G. holbrooki* treatment, and 8.5×10^2 cells ml^{-1} and 0.0002 mm^3 l^{-1} in the control. These temporal patterns (Fig. 2) are reflected in a significant time effect in the RM-ANOVA analysis ($p < 0.05$; Table 3).

The overall effects of the 3 fish treatments on APP are summarised in Table 3. Even though APP abundance and volume were slightly higher in the *Cyprinus carpio* and the *Lepomis gibbosus* treatments than in the *Gambusia holbrooki* treatment and the control,

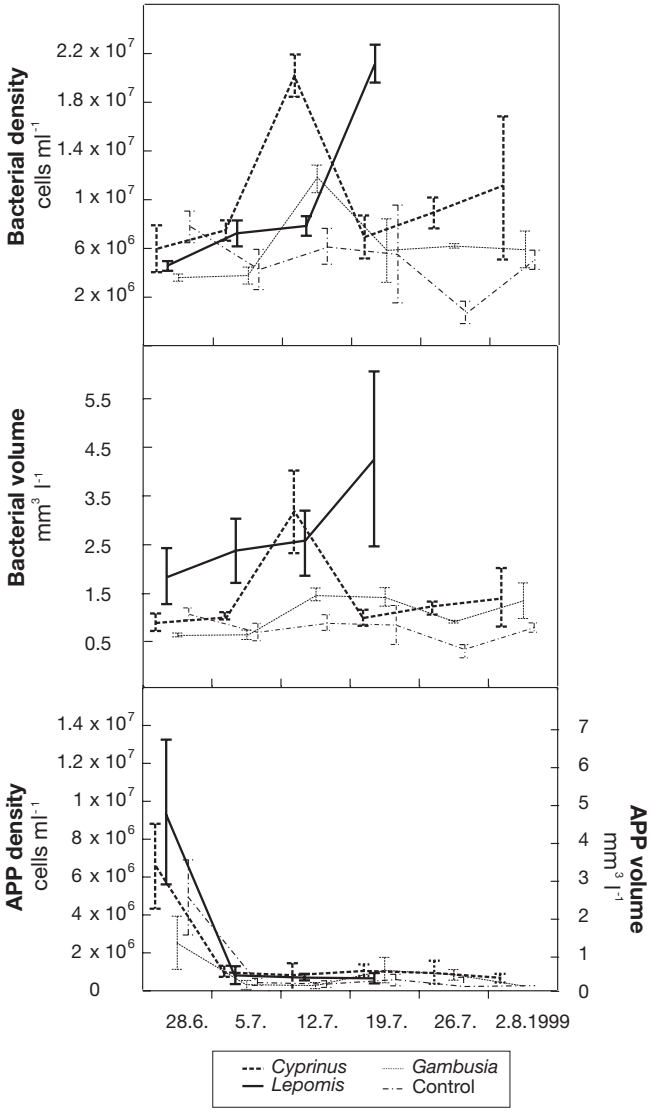

Fig. 2. Time trajectories of densities and biovolumes of bacterioplankton and autotrophic picoplankton during the enclosure experiment. Shown are the means of 3 enclosures ± 1 SE

RM-ANOVA revealed no significant treatment effects (Table 3, Fig. 1). Likewise, the interaction between treatment and temporal effects was not significant, suggesting that APP dynamics followed similar patterns in all treatments and the control in the course of the experiment.

DISCUSSION

This study shows that the fish species examined had a differential impact on BAC and APP. In the case of BAC, it seems that trophic conditions in the enclosures were responsible for the observed BAC patterns. The *Cyprinus carpio* and the *Lepomis gibbosus* treatment had significantly higher levels of trophy, reflected in nutrients and chl *a* levels, than the *Gambusia holbrooki* treatment and the control. Because BAC biomass is known to increase with increasing trophic state, owing to their high affinity for inorganic (Caron et al. 1988) and organic nutrients (Cole 1982), it is concluded that *C. carpio* and *L. gibbosus* may have fuelled the BAC standing crop. The effective nutrient regeneration of both species may be due to the higher fish biomasses used in these treatments and because of their benthic activity that adds sediment bound nutrients to the water column (Brabrand et al. 1990). *G. holbrooki*, which were stocked in much lower biomasses and which is known to be exclusively planktivorous, failed to increase trophy, thereby limiting BAC growth.

On the basis of this apparent bottom-up control of BAC via nutrients, we believe that zooplankton grazing on BAC was less important during our study. First, the impact of rotifers and copepods, which dominated in all fish treatments, is generally considered to be much less significant than that of large cladocerans (Arndt 1993). Even if they were capable of exerting a top-down control on BAC during our study, it was not sufficient to counterbalance the bottom-up effects of nutrients in the *Cyprinus carpio* and *Lepomis gibbosus* treatments (Pedrós-Alió & Brock 1982). Second, mid-sized cladocerans *Ceriodaphnia reticulata* Jurine developed in the fishless control (Angeler et al. 2002) but BAC levels were in the same range as in the *Gambusia holbrooki* treatment, where cladocerans were lacking. This suggests a low *C. reticulata* grazing impact on BAC. Bogdan & Gilbert (1984) determined experimentally that *C. reticulata* is generally an ineffective grazer in the picoplankton size spectrum.

The APP community, which prevailed during our study, was typical for hypertrophic environments (Vörös et al. 1998). The initial abundances in the enclosures were high but they were well within the naturally occurring abundance range (Rodrigo unpubl.). In contrast to BAC, however, APP levels did not differ significantly between treatments and the control. Even though the abundance of APP is known to increase with trophic state across aquatic systems (e.g. Stockner & Antia 1986, Wehr 1989)—with a simultaneous decrease of their relative contribution to total phytoplankton biomass and production—such a pattern was not found in our enclosures. Fishes were obviously unable to promote APP growth by their nutrient regeneration activity. In contrast, other mesocosm studies found an increase of APP abundance in the presence of fish and attributed this increase to fish nutrient recycling and reduction of herbivore grazing (Rhew et al. 1999, Tzaras et al. 1999).

Interestingly, APP levels decreased by ca. 1 order of magnitude until the end of the study. The patterns of decline were similar in all treatments and the control. Because of this similarity in dynamics, we do not consider zooplankton grazing to be important for the APP mortality. The existing differences in zooplankton community composition and biomass between treatments imply that copepods, rotifers, and cladocerans selectively consumed APP, accounting for similar loss rates independently in the respective enclosures, but this is ecologically unrealistic. Temperature, which is also known to influence APP dynamics (e.g. Rhew et al. 1999), can be ruled out because of insignificant variation during our study period. Viral lysis and light characteristics, which are also known to affect APP (Weisse 1993, Vörös et al. 1998), were not assessed in the present study. We are unable to accurately interpret the APP dynamics during our experiment based on the present data set. Further study is necessary to distinguish between the influence of biotic and that of abiotic forces on wetland APP dynamics.

In concluding, it is important to highlight that the marked differences of fish biomass in the respective treatments simulate natural biomass situations of the 3 species during periods of hydrological stress. Wetland ecosystem contraction during drought or artificial water-level reductions can lead to concentrated fish populations, which, in turn, influence biological processes, including the microbial food web.

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