The effect of herbivorous crustacean zooplankton on epilimnetic carbon and phosphorus cycling

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Abstract

Plastic limnocorrals (LCs; volume 70 m³) in oligo-mesotrophic Lake Lucerne, Switzerland were used to manipulate planktonic communities by (1) removing large zooplankton at the start of the experiment, and (2) adding phosphate during experiments of two weeks duration.

Primary production (¹⁴C-assimilation), chlorophyll, standing crops and sedimentation of particulate organic carbon (POC) and of particulate phosphorus, as well as plankton composition were assessed simultaneously in two to four differently treated LCs. Carbon and phosphorus mass balances were calculated from assimilation, temporal change in standing crop of particulate matter, and sedimentation.

A quick elimination of crustaceans by screening hardly increased primary production, but decreased sedimentation and mineralisation of particulate organic carbon, and thus significantly enhanced the standing crop of POC, but decreased POC turnover. The exclusion of crustaceans increased the mean residence time of total phosphorus by a reduced P loss by sedimentation.

Increased grazing pressure during the experiment showed little grazing induced effect on plankton composition and primary production except at the very end.

We conclude that in an oligo-mesotrophic lake, buffering mechanisms attenuate the impact of changing grazing pressures on primary production.

Introduction

In lakes primary production, mineralization, seston composition and sedimentation are closely linked (Bloesch *et al.*, 1977; Bloesch & Bürgi, 1989; Tilzer, 1984). The extent to which photo-assimilated carbon is recycled within the epilimnion, determines the flux of nutrients and energy to the hypolimnion and the sediment, and thus

affects the metabolism of the whole ecosystem. Several studies show that up to 50–90% of the organic matter synthesized by phytoplankton is mineralized within the epilimnion (Quay *et al.*, 1986; Tilzer, 1984; Stabel & Tilzer, 1981; Richey, 1979; Bloesch *et al.*, 1977; Lean & Charlton, 1976; Rigler, 1973, 1964; Wetzel *et al.*, 1972; Ohle, 1962; Pomeroy, 1960).

Herbivorous zooplankton may influence the

epilimnetic cycle of organic matter in different ways: it affects sedimentation directly by forming fecal pellets (Ferrante & Parker, 1977; Uehlinger & Bloesch, 1987b; Bloesch & Bürgi, 1989) or indirectly by reducing the seston concentration or modifying phytoplankton structure (Vanni, 1987; Mazumder *et al.*, 1990), and detritus. It may reduce phytoplankton concentration, and thus, primary productivity, by its grazing activity (Lampert *et al.*, 1986). On the other hand, zooplankton-mediated nutrient regeneration is thought to enhance primary productivity per unit algal biomass (Lehman, 1980). Experiments in eutrophic lakes showed that due to the grazing of herbivorous crustaceans concentrations of dissolved nutrients increased (Bürgi *et al.*, 1979; Elliot *et al.*, 1983; Mazumder *et al.*, 1988). Therefore, it can be expected that herbivorous zooplankton will increase the residence time of nutrients in the euphotic zone, since nutrients are mainly lost by sedimentation as particulate matter.

Plankton communities are controlled by the resources base ('bottom up'), or by the higher trophic levels ('top down') (Pace, 1984; Shapiro & Wright, 1984; Carpenter *et al.*, 1985; Reinertsen *et al.*, 1986; McQueen *et al.*, 1986; Vanni, 1987; Kitchell *et al.*, 1987; Scavia & Fahnenstiel, 1987; Elser *et al.*, 1988), and in an annual cycle, probably both mechanisms are effective. Periods of 'top down' regulation, as e.g. the clearwater phase in early summer, should be reflected by an enhanced turnover of organic matter and nutrients.

To study the role of herbivorous crustacean zooplankton in short-term changes of phytoplankton biomass and primary productivity, and in sedimentation of organic matter and nutrients, experiments in limnocorrals (LCs) were performed. To create different experimental situations the size of the herbivorous zooplankton population was manipulated by screening. The results are published in several papers (Uehlinger & Bloesch, 1987a, 1987b; Bloesch & Bürgi, 1989; this study). The objectives of the present study are (1) to quantify the influence of herbivorous crustacean plankton on the cycling of organic carbon, (2) to test how primary production,

seston concentration and carbon turnover are affected by 'bottom up' or 'top down' regulation, and (3) to test to which extent the residence time of phosphorus in the epilimnion may be affected by the activity of herbivorous crustacean plankton.

Methods

Between 1982 and 1984 seven experiments, each of 12 days duration, were performed in oligomesotrophic Lake Lucerne, Switzerland. Experiments took place during the phytoplankton spring bloom (March/April), and during as well as shortly after the clear water phase (end of May to early July), when the biomass of the herbivorous zooplankton was high (Table 1). Only the latter experiments, which were particularly appropriate

Table 1. Mean biomasses [g wet weight m^{-2}] of herbivorous zooplankton (a), and net and nannoplankton (b) in the limnocorral experiments in Lake Lucerne.

(a) herbivorous zooplankton

No. of experiment and season	Control LC			95 μm filtered LC		
	Phylo-podes	Cope-podes	Rotifers	Phylo-podes	Cope-podes	Rotifers
82/1 March/April	0.51	0.81	0.24	0.02	0.02	0.27
82/1 March	4.02	2.58	0.06	0.05	0.24	0.08
83/2 May/June	56.63	1.20	0.72	0.09	0.00	0.57
84/A May/June	15.80	1.00	0.55	0.62	0.00	0.57
84/B May/June	10.27	0.38	0.43	0.94	0.61	0.94
82/2 June	12.9	0.37	18.52	0.79	0.01	12.10
83/3 June/July	19.30	0.24	0.00	0.07	0.00	0.00

(b) net- and nannoplankton

No. of experiment and season	Control LC			95 μm filtered LC		
	Net	Nanno	Total	Net	Nanno	Total
82/1 March/April	6.15	3.47	9.62	4.12	5.57	9.69
82/1 March	3.70	13.39	17.09	3.03	7.67	10.70
83/2 May/June	0.38	7.92	8.30	0.52	6.56	7.08
84/A May/June	0.34	0.63	0.97	0.80	0.83	1.73
84/B May/June	0.36	0.55	0.91	0.70	0.60	1.30
82/2 June	0.76	10.19	10.95	0.71	11.60	12.31
83/3 June/July	3.68	2.62	6.30	2.77	3.17	5.94

to study the influence of zooplankton on carbon and phosphorus turnover, are considered in this paper.

Two to four limnocorrals (LCs), three meters in diameter, eleven meters long and with a closed bottom, were simultaneously exposed nearshore the Lake Research Laboratory Kastanienbaum (Uehlinger *et al.*, 1984). At the beginning of each experiment most crustacean zooplankton was removed with a large Nybolt net of 95 μm mesh size in one of two (respectively two of four) LCs (for technical details see Uehlinger *et al.*, 1984). To prevent excess phosphorus depletion, NaH_2PO_4 was added periodically with a plastic hose (Goldman, 1962) as shown in Table 2.

Photosynthetically active radiation (PAR) was continuously recorded about 500 m from the experimental site at the Lake Research Laboratory using a quantum sensor (LI-190) and a printing integrator (LI-500). The vertical PAR distribution was measured in the center and at the north and south walls of the LCs with a scalar quantum sensor (LI-190B) and an integrating quantum meter (LI-188, all instruments manufactured by LI-COR Inc., Lincoln, Nebraska, USA).

Water samples were usually taken at 5, in experiments 83/2 and 83/3 at 12 different depths at the center of the LCs, using Friedinger bottles. Water analysis comprised total phosphorus (TP), soluble reactive phosphorus (SRP), particulate phosphorus (PP), particulate organic carbon (POC), total inorganic carbon (TIC) and chlorophyll as described by Uehlinger *et al.* (1984). PP

and POC did not include the larger crustacean zooplankton (Uehlinger & Bloesch, 1987b). Phosphorus removal by wall growth was measured according to Uehlinger *et al.* (1984). Phytoplankton and zooplankton was sampled and analyzed according to Bloesch & Bürgi (1989). In two experiments (83/2 and 83/3), water samples from the control LCs were filtered through 150 μm Nybolt nets and the POC of the fraction $> 150 \mu\text{m}$, which consisted exclusively of crustaceans, was determined. To estimate the 'crustacean' POC, crustacean wet weight was assumed to have a carbon content of 5% (Bürgi, unpublished). To obtain estimates of algal carbon algal fresh weights were multiplied by 0.1 (Nauwerck, 1963). Sediment trap samples were taken and analyzed according to Uehlinger *et al.* (1984).

Primary production was measured with the ^{14}C acid bubbling method (Gächter & Mares, 1979) during midday (10 a.m. to 2 p.m.) in 0, 0.5, 1.5, 3, 6, and 9 m depth at the center of an LC and at 0, 0.5, and 1.5 m at two sites close to the 'north' and 'south' wall of the LC. In experiment 82/2 measurements were performed in 0.5, 2, 4, 6, and 9 m depth at three to five sites (center, east, west, north, and south) to check for local differences. Integral (midday) production rates were obtained by numerical integration of the primary production rates as measured in the different depths. Daily production was calculated with a model, using vertical PAR attenuation, continuously recorded PAR data and photosynthesis irradiance relationships which were obtained from midday productivity measurements (Bührer unpublished). Consecutive measurements of the primary production (from sunrise to 10 a.m., from 10 a.m. to 2 p.m., and from 2 p.m. to sunset) showed that the model overestimated daily production by less than 5%.

Net production of particulate organic carbon in the water column (NP_{POC}) was calculated as follows:

$$\text{NP}_{\text{POC}} = \text{S}_{\text{POC}}[t_0, t_1] + \text{POC}(t_1) - \text{POC}(t_0) \quad (1)$$

for S_{POC} being the measured sedimentation of

Table 2. Phosphorus fertilization in the limnocorral experiments in Lake Lucerne.

Experiment No. and date	$\text{PO}_4\text{-P}$ added
82/2 17–29 June 1982	32 mg m^{-2} daily except on 26 June
83/2 26 May–7 June 1983	4.8 mg m^{-2} on 30 May and 3 June
83/3 30 June–12 July 1983	4.8 mg m^{-2} daily from 30 June–8 July and on 10 July; uncontrolled phosphorus input by gulls from 8–12 July
84/A 24 May–5 June 1984	10.6 mg m^{-2} on 24, 26 and 28 May
84/B 24 May–5 June 1984	19.5 mg m^{-2} on 24 May; 21.1 mg m^{-2} on 26 and 28 May; 10.6 mg m^{-2} on 30 May and 9.6 mg m^{-2} on 1 June.

POC per m² during intervals of 12 days [t₁, t₀], and POC being the seston standing crop per m² at the beginning and the end of the interval [t₁, t₀]. The mean error of NP_{poc} (f_{NP}) was calculated as:

$$f_{NP} = \sqrt{f_{POC}^2 + f_S^2} \approx f_{POC}, \quad (2)$$

since $f_{POC} \gg f_S$

for:

$$\begin{aligned} f_{POC} &= \text{mean error of POC standing crop} \\ &= \text{POC}[t_2] - \text{POC}[t_1] \\ &\approx 0.36 \text{ g m}^{-2} \quad \text{and} \\ f_S &= \text{mean error of POC sedimentation} \\ &= 0.1 \sqrt{SS_i^2} \end{aligned}$$

Mass balances of particulate organic carbon during intervals of 12 days [t₀, t₁] were calculated using equation (3):

$$\begin{aligned} \text{POC}(t_1) - \text{POC}(t_0) &= C_{ASS}[t_0, t_1] \\ &- S_{POC}[t_0, t_1] - R_{POC}[t_0, t_1] \end{aligned} \quad (3)$$

where C_{ASS}[t₀, t₁] is the cumulated primary production, and R_{POC}[t₀, t₁] the carbon mineralisation during the time interval [t₀, t₁].

The mean error of C_{ASS} (f_C) was calculated according to

$$f_C = 0.13 \sqrt{SP_i^2} \quad (4)$$

for P = daily C assimilation per m² (primary production).

Mass balances for phosphorus were calculated according to equation (5):

$$\begin{aligned} \text{TP}(t_1) - \text{TP}(t_0) &= F[t_0, t_1] - S_{PP}[t_0, t_1] \\ &- W[t_0, t_1] \end{aligned} \quad (5)$$

TP is the total phosphorus at the beginning and the end of the 12 day interval. F[t₀, t₁] represents phosphorus fertilization, S_{PP}[t₀, t₁] is sedimentation of PP, and W[t₀, t₁] is phosphorus retained by the 'Aufwuchs' community of the LC wall. The assessment of P-uptake is difficult because of methodological problems (Lean & White, 1983). P-uptake calculated as Q * carbon assimilation,

where Q is the average P:C ratio of algae, does not consider dark uptake and yields only rough uptake estimates, which, depending on the assumptions for Q, may vary by one order of magnitude (Uehlinger & Bloesch, 1987a). Since we had no reliable method at hand for estimating P-uptake, we did not address the question to which extent herbivorous crustaceans affected phosphorus turnover, however the mean residence time of phosphorus (τ_P) was calculated as

$$\tau_P = \frac{\text{TP}_{\text{mean}} * (t_1 - t_0)}{S_{PP}[t_0, t_1] + W[t_0, t_1]}$$

TP_{mean} is the mean total phosphorus concentration during an experiment.

Results

Zooplankton

Screening with a 95 μm net reduced the biomass of the herbivorous zooplankton at least tenfold, except for experiment 82/2, when most of the herbivorous microzooplankton (ciliates and rotifers), which dominated the zooplankton at that time, passed the nets. The rotifer *Asplanchna* sp. formed large populations in both LCs with maxima on day 5 (95 μm filtered LC) and day 9 (control LC) of that particular experiment. Usually crustaceans in the control LC were dominated by herbivorous phyllopods (*Daphnia galeata* and *D. hyalina*), which were, however, restricted in their vertical migration by the closed bottom of the LC, compared to a truly pelagic situation. Detailed information on the temporal changes of zooplankton are given by Bloesch & Bürgi (1989).

Seston

At the beginning of the experiments phytoplankton mainly consisted of cryptophyceae (*Cryptomonas* sp., *Rhodomonas* sp.), which usually dominate the phytoplankton of Lake Lucerne at that time of year (Bürgi *et al.*, 1985). During the course of most experiments, however, the phytoplankton in the LCs changed to diatoms, dinoflagellates or green algae, regardless whether the LC was

Fig. 1. Chlorophyll (chl *a*) standing crops in the control and the 95 μ m filtered LCs of experiments 82/2 to 84/B

Legend: $\square$: Control LC $\blacksquare$: 95 μ m filtered LC

screened or not. The ratio netplankton: nanoplankton increased during most experiments; this trend was slightly enhanced in the presence of crustaceans. Algal biomasses were lower in the controls than in the 95 μ m filtered LCs, but in experiments 83/2 and 83/3 these differences were surprisingly small. In most experiments, area values of chlorophyll decreased after an initial growth phase (Fig. 1). This trend was less pronounced in the 95 μ m filtered units. In the control LCs, where zooplankton grazed the phytoplankton, area values of chlorophyll were on average 15 to 37% lower than in the 95 μ m filtered LCs. Relative differences between controls and 95 μ m filtered LCs usually increased towards the end of the experiments. In the 82/2 experiment the chlorophyll standing crop rose with duration of the ex-

Fig. 2. Vertical distribution of chlorophyll concentrations at the end of experiments 82/2 to 84/B (day 13)

Legend: $\square$: Control LC $\blacksquare$: 95 μ m filtered LC

periment, reflecting the high P fertilization. In addition, the initially low population of herbivorous zooplankton in the control LC increased rapidly during the last four days of the experiment and presumably caused a decrease in chlorophyll (Fig. 1) at the very end of the experiment. The final increase of chlorophyll in experiment 83/3 is connected with an invasion of black-headed gulls causing massive phosphorus input by faeces. POC concentrations (zooplankton not included) were distinctly lower in the control LCs than in the 95 μ m filtered LCs, particularly towards the end of the experiments (Fig. 3). This trend was less pronounced for PP and algal carbon. A comparison of crustacean C with algal and detritus C showed that in the control LCs the trophic biomass pyramids (phytoplankton-zooplankton) were steep or even inverted, and that suspended

Fig. 3. Particulate organic carbon (POC) standing crops in the control and the 95 μm filtered LCs of experiments 82/2 to 84/B

Legend: $\square$: Control LC
 $\blacksquare$: 95 μm filtered LC
 $\circ$: POC in zooplankton of control LC

seston consisted to a major part of detritus carbon (Fig. 4).

Sedimentation

In the presence of herbivorous zooplankton the sedimentation of POC and PP was distinctly higher than in the 95 μm filtered LCs, although POC and PP standing crops were lower in the control LCs (Tables 4a and 6a). A more detailed description of the influence of phytoplankton and zooplankton on sedimentation fluxes is given by Bloesch and Bürgi (1989).

Primary production

Daily production was not correlated with chlorophyll, except for experiment 83/2. Daily changes

Fig. 4. Trophic biomass pyramids (phyto- and zooplankton) in the control LCs of experiments 82/2 to 84/B

Fig. 5. Integral midday primary production (C assimilation) in the control and the 95 μm filtered LCs of experiments 82/2 to 84/B

Legend: $\square$: control LC $\blacksquare$: 95 μm filtered LC

took place simultaneously in both filtered and control LCs. Temporal patterns of integral midday primary production rates show that herbivorous zooplankton reduced to some extent primary production towards the end of an experiment (Fig. 5). Only in two experiments was in-

Table 3. Primary production:

- (a) Integral midday primary production rates per chlorophyll averaged over the duration of the experiments: [mg C (mg chl)⁻¹ h⁻¹].

Experiment	95 μ m filt. LC	Control LC	Difference*
82/2	1.77 $\pm$ 0.76	1.51 $\pm$ 0.67	significant
83/2	1.78 $\pm$ 0.74	1.95 $\pm$ 0.46	not significant
83/3	3.29 $\pm$ 1.95	2.70 $\pm$ 0.96	not significant
84/A	2.93 $\pm$ 0.50	3.76 $\pm$ 0.88	significant
84/B	3.53 $\pm$ 0.85	3.49 $\pm$ 1.11	not significant

* Significance of differences between 95 μ m filtered and control LC calculated by analysis of variance (ANOVA) for $P < 0.05$.

- (b) cumulated total of primary production (C_{ASS}) within 13 days: [g C m⁻²]

Experiment	95 μ m filt. LC	Control LC	Difference**
82/2	20.6 $\pm$ 0.87*)	20.2 $\pm$ 0.84*)	not distinct
83/2	9.9 $\pm$ 0.44	8.9 $\pm$ 0.38	distinct
83/3	9.6 $\pm$ 0.41	8.1 $\pm$ 0.33	distinct
84/A	10.4 $\pm$ 0.39	9.9 $\pm$ 0.38	not distinct
84/B	12.1 $\pm$ 0.45	9.8 $\pm$ 0.36	distinct

* Mean error of cumulated primary production according to equation (4).

** The difference between the 95 μ m filt. LC and the control LC is considered to be distinct, if $\Delta C_{ASS} > (f_c \text{ of control LC} + f_c \text{ of 95 } \mu\text{m filt. LC})$.

- (c) net production $NP_{POC} = \text{POC sedimentation} + \text{difference in POC seston from day 1 to 13}$: [g C m⁻²]

Experiment	95 μ m filt. LC	Control LC	Difference**
82/2	6.7 $\pm$ 0.36*)	6.3 $\pm$ 0.36*)	not distinct
83/2	2.6 $\pm$ 0.36	1.0 $\pm$ 0.36	distinct
83/3	4.6 $\pm$ 0.36	2.4 $\pm$ 0.36	distinct
84/A	4.8 $\pm$ 0.36	3.2 $\pm$ 0.36	distinct
84/B	4.6 $\pm$ 0.36	3.7 $\pm$ 0.36	distinct

* Mean error of net production according to equation (2).

** The difference between the 95 μ m filt. LC and the control LC is considered to be distinct, if $\Delta NP_{POC} > (f_{NP} \text{ of control LC} + f_{NP} \text{ of 95 } \mu\text{m filt. LC})$.

tegral midday production rate per chlorophyll significantly higher in the control than in the 95 μ m filtered LC (Table 3). In most experiments net phytoplankton production of particulate organic carbon (NP_{POC}) was substantially lower in the control than in the 95 μ m filtered LC. The cumulated total of primary production in 13 days, as integrated from daily production (¹⁴C-assimilation), was affected only by about 10% (Table 3). Differences between the control and the 95 μ m filtered LC were distinctly smaller than day to day differences within one LC.

Carbon cycling

The influence of herbivorous crustaceans on the epilimnetic carbon cycle is given by the carbon mass balance (equation 1). An average of all experiments indicates that the elimination of crustaceans decreased mineralisation by 15% and sedimentation by 25% (Table 4); POC turnover time decreased by approximately 10%. In some experiments crustacean grazing hardly influenced one or several of these variables: experiment 82/2, where a considerable rotifer concentration in both LCs (Table 1) blurred the crustacean effect, and no difference was observed in any of these factors, – experiments 84/A and B, where mineralization was not influenced by crustacean elimination, whereas sedimentation decreased.

Phosphorus

Concentrations of soluble reactive phosphorus (SRP) were similar in the 95 μ m filtered and in the control LC (Table 5) with differences close to the detection limit, except for when herbivorous phytoplankton reached high biomasses as in experiment 82/2 (control LC during the last few days) and in experiments 83/3 (control LC). The massive phosphate addition in experiment 82/2 caused a distinct increase of SRP during the course of the experiment. The phosphorus input by black-headed gulls during the last few days of experiment 83/3 raised the SRP concentration distinctly. However, moderate fertilization (experiments 83/2, 82/3, 84/A/B) hardly raised SRP concentrations during the course of the experiments. Area values of total phosphorus (TP) were

Table 4a. Mass balance of organic carbon in the time interval from the 1st to the 12th day.

Experiment	95 μm filtered LC				Control LC			
	C_{ASS}	S_{POC}	ΔPOC	R_{POC}	C_{ASS}	S_{POC}	ΔPOC	R_{POC}
83/2 $\text{g}\cdot\text{m}^{-2}$	9.92	1.46	1.11	7.31	8.90	1.98	0.96	7.88
%	100	14.8	11.2	73.7	100	22.3	10.8	88.5
84/A $\text{g}\cdot\text{m}^{-2}$	10.45	2.30	2.46	5.68	9.92	3.52	0.32	6.72
%	100	22.1	23.6	54.4	100	35.5	3.24	67.8
84/B $\text{g}\cdot\text{m}^{-2}$	12.06	2.11	2.52	7.42	9.79	3.14	0.31	6.13
%	100	17.5	20.9	61.6	100	32.0	3.21	62.6
82/2 $\text{g}\cdot\text{m}^{-2}$	20.65	2.53	4.17	13.95	20.3	2.94	3.39	13.97
%	100	12.3	20.2	67.5	100	14.5	16.7	68.8
83/3 $\text{g}\cdot\text{m}^{-2}$	9.59	2.85	1.80	4.94	8.06	3.32	0.90	5.64
%	100	29.7	18.8	51.5	100	41.2	11.2	70.0
average %		19.3		61.7		29.1		71.5
standard deviation %		6.16		8.19		9.55		8.87
coeff. of variation %		32.0		13.3		32.8		12.4

* $\Delta\text{POC} = \text{POC}(t_1) - \text{POC}(t_0)$.

Table 4b. Mean turnover time of POC (without crustaceans).

Experiment:	82/2		83/2		83/3		84/A		84/B		
LC:	95 μm	Control	95 μm	Control	95 μm	Control	95 μm	Control	95 μm	Control	
POC:											
Mean standing crop [g m ⁻²]	6.09	5.42	5.09	3.43	4.93	3.87	6.80	4.92	6.27	5.28	
Sedimentation [g m ⁻² ·day]	0.21	0.24	0.12	0.17	0.24	0.28	0.19	0.29	0.18	0.26	
Mineralisation [g m ⁻² ·day]	1.16	1.16	0.61	0.66	0.41	0.47	0.47	0.56	0.62	0.51	
Turnover time [days]	4.43	4.32	8.33	7.41	9.38	8.16	9.16	7.14	7.67	7.88	

Table 5. Mean concentrations of soluble reactive phosphorus (SRP) during the experiments [mg m^{-3}].

Experiment	95 μm filtered LC	Control LC
82/2	7.4 ± 8.6 11*	8.4 ± 9.4 15*
83/2	0.8 ± 0.1	2.5 ± 0.6
83/3	0.9 ± 1.2	0.7 ± 0.9
84/A	0.9 ± 0.3	1.0 ± 0.4
84/B	1.2 ± 0.4	1.9 ± 1.1

* Concentration at the last day of experiment 82/2.

about equal in the filtered and control LCs. The mean residence time of total phosphorus (τ_P) varied between 7.5 and 74 days (Table 6b). In three of five experiments the presence of crustacean zooplankton decreased P by at least 30%, while in two experiments (83/3, 84/A) differences in P were minor. Phosphorus mass balances, calculated according to equation 5, were often imbalanced (Table 6a). The phosphorus excess found in experiment 83/3 can be explained by a massive invasion of black-headed gulls (P-containing ex-

Table 6a. Mass balance of total phosphorus [mg P m^{-2}] in the time interval from the 1st to the 12th day.
95 μm filtered LC

Experiment	Fertilization F	Sedimentation S_{PP}	ΔTP	P retained by Aufwuchs	Net imbalance of TP
83/2	10	17	- 9	2	0
84/A	32	34	+ 45	29	+ 76
84/B	82	35	+ 61	11	+ 25
82/2	350	64	+ 233	7	- 46
83/3	38	31	+ 85	38	+ 106

Control LC

Experiment	Fertilization F	Sedimentation S_{PP}	ΔTP	P retained by Aufwuchs	Net imbalance of TP
83/2	10	38	- 37	7	+ 6
84/A	32	53	- 2	5	+ 24
84/B	83	57	+ 45	4	+ 13
82/2	350	85	+ 196	10	- 59
83/3	48	43	+ 15	20	+ 30

Table 6b. Mean residence time of total phosphorus in the limnocorrals.

Experiment:	82/2		83/2		83/3		84/A		84/B	
LC:	95 μm	Control	95 μm	Control	95 μm	Control	95 μm	Control	95 μm	Control
Phosphorus:										
Mean total P [$\text{mg}\cdot\text{m}^{-2}$]	290	282	117	128	43.4	43.8	136	121	152	152
Sedimentation (S_{PP}) [$\text{mg}\cdot\text{m}^{-2}\cdot\text{d}$]	5.33	7.08	1.42	3.17	2.58	3.58	2.83	4.42	2.92	4.75
Aufwuchs (W) [$\text{mg}\cdot\text{m}^{-2}\cdot\text{d}$]	0.58	0.83	0.17	0.58	3.17	1.67	2.42	0.42	0.92	0.33
Total loss [$\text{mg}\cdot\text{m}^{-2}\cdot\text{d}$]	5.92	7.92	1.58	3.75	5.75	5.25	5.25	4.83	3.83	5.08
Mean residence time [d]	49.1	35.7	74.1	34.2	7.5	8.3	25.8	25.0	39.5	29.8

crements), but no events could be associated with the excesses in the experiments 84/A and B and with the deficits in experiment 82/2. It is noticeable that both LCs of one experiment showed either P deficits or excesses, whereas the observed quantities were different. Mazumder *et al.* (1989) also observed net imbalances in the P-budget of their enclosure experiments, they could not precisely account for.

Discussion

The experimental setup created a specific ecological situation. At moderate latitudes planktonic communities never reach balanced situations, due to quickly changing climatic conditions and nutrient availabilities across a year. Our investigations were limited to a specific situation, namely the time span during or shortly after the clearwa-

Table 7. Summary of observed effects in the control and the 95 μm filtered LC.

Event	Experiment:				
	82/2	83/2	83/3	84/A	84/B
A) Starting conditions:					
– high zoo-/phytoplankton biomass ratio in control LC	x	x	x	x	x
– zooplankton dominated by <i>Daphnia</i> in control LC		x	x	x	x
– zooplankton dominated by rotifers in both LCs	x				
– good zooplankt. reduction effect by screening in 95 μm filtered LC		x	x	x	x
B) Phosphate mass balance:					
– total P addition during experiment in mg P/m^2	350	10	48	32	82
– uncontrolled P addition			x		
– distinct increase of SRP	x		(x)		
– distinct P loss by wall growth			x	x	
– observed P deficit (eq. 2)	x				
– observed P excess (eq. 2)			x	x	(x)
C) Developments during experiment: (+ increase, – decrease, o no change)					
– chlorophyll in control LC	+	–	–	–	–
– in 95 μm filt. LC	+	–	–	o	o
– sedimentation in both LCs	+	+	+	+	+
– primary production in both LCs		–	+		
D) Effects of zooplankton grazing (+ positive, – negative, o null, margin 15%) on:					
– Chlorophyll standing crop	–	–	–		–
– POC sedimentation	+	+	+	+	+
– net production	o	–	–	–	–
– cumulated total primary prod.	o	o	–	o	–
– integral midday primary prod.	o	–	–	+	–
– integral midday prim. prod. per chlorophyll	o	o	–	+	–
– POC mineralisation	o	+	+	+	o
– POC turnover time	o	o	–	–	o
– mean residence time of P	–	–	o	o	–
Experiments performed under 'ideal' conditions:		x			x

ter phase, when zooplankton biomass was high and phytoplankton biomass relatively low. We further modified the ecological system by cutting off horizontal water transport and either eliminating crustaceans larger than 95 μm or restricting their vertical migration. The differences in the vertical distribution of chlorophyll between the

control and the 95 μm filtered LC, which we observed during the last few days of several experiments (Fig. 2), probably reflect the influence of continuous grazing in the limnocostracans, because crustaceans were restricted in their diurnal vertical migration by the closed LC bottoms. In addition, we reduced the number of trophic levels by excluding fish and most carnivorous crustaceans. Our results are thus to be interpreted on a different scale than those of whole ecosystem studies. Although every ecosystem has to cope with changing environmental conditions, such changes do not occur as abruptly as in our investigation. The sudden biomanipulations forced the system to adjust its structure to a new situation, (Leffler, 1980).

Experimental setups were also influenced by changes in zooplankton biomass in the control LCs by natural influences, such as crustacean biomass increase during experiment 83/3. In exp. 82/2 and 84/A this increase took place at the very end, while in exp. 83/2 and 84/B random ups and downs occurred. Some of these situations, and especially that in exp. 83/3, enabled separate observations on the effects of a growing grazing pressure with time.

Assessing the impact of crustaceans on C- and P-cycling by elimination of crustaceans is an indirect approach, which assumes a certain reversibility of processes influenced by zooplankton. However, predator – prey interactions between zooplankton and algae show a tendency to hysteresis (Bürge *et al.*, 1979) and thus, generalisation of obtained results may be biased. Such restrictions are inherent to all ecological field experiments, which perturbate an ecosystem in one way or another, and make repeated observations necessary. Our investigations illustrate that different experiments in (apparently) similar situations do not always produce consistent quantitative results, even if utmost caution is applied in sampling and analysis. All this severely impedes mathematical modelling or statistical analysis and we are forced to stick to qualitative and semi-quantitative interpretations.

Seasonal records of mesotrophic Lake Lucerne show that during the clearwater phase max-

imum transparency in the water column occurs between mid-May to mid-June (Bürge *et al.*, 1985). We hypothesized that during this period phytoplankton standing stock should be controlled by herbivorous zooplankton (the 'top down' concept mentioned by McQueen *et al.*, 1986). In less than half of the experiments primary production appeared to be stimulated by the grazing activity of herbivorous zooplankton. The elimination of herbivorous zooplankton increased net phytoplankton production (NP_{POC}) as well as sestonic POC and PP concentrations significantly, whereas in most experiments the impact on phytoplankton standing stock (wet weight and chlorophyll) was rather modest. Only during experiments 84/A,B differences in phytoplankton standing stock between the 95 μm filtered and control LCs increased distinctly with time. These experiments took place exactly during the clear water phase, when the ratios of herbivorous zooplankton versus nanoplankton were particularly high in the control LC. There was a distinct difference in chlorophyll and primary production on the last day of all experiments, in favour of the 95 μm filtered LC.

Our results are complementary to observations by Lampert *et al.* (1986), who provided evidence that grazing causes the clearwater phase in mesoeutrophic Schöhsee by reducing phytoplankton biomass. Our experiments show that a complete and sudden elimination of herbivorous crustaceans does not necessarily induce a phytoplankton bloom, at least not within two weeks, even if phosphate is abundant (experiment 82/2). In the clearwater phase (exp. 84/A,B) the removal of crustaceans prevented the algal standing crop from decreasing, and in the post-clearwater phase (experiments 83/2 and 83/3) phytoplankton decreased less after crustacean removal.

These results are in favour of top down control, but only during the rather short clearwater phase, when crustacean biomass is increasing. Before and after herbivorous crustaceans have a surprisingly small effect on phytoplankton biomass. During most of the year, phytoplankton dynamics are therefore controlled by nutrients and climatic factors (bottom up theory). Differences in

grazing pressure were usually overridden by weather-induced ups and downs of the light regime and thus of primary production and standing crop (Figs. 1 and 5).

The assessment of carbon cycling in field experiments is difficult, since only primary production and sedimentation of particulate matter can be directly measured as fluxes, whereby daily primary production has to be calculated from short time incubations, and cumulative sedimentation measurements need an incubation of sediment traps for several days in order to collect enough material for analysis. Since carbon mineralisation was not directly measured, it had to be calculated according to equation (1).

The sudden elimination of crustaceans, which outweighed phytoplankton biomass 3–10 times, had a surprisingly small effect on the cumulated C-assimilation of 13 days, although nanoplankton, the preferred food of *Daphnia*, was a substantial part of phytoplankton at the beginning of all experiments. The rise in primary production after crustacean elimination was significant only in some experiments and averaged ca. 10% (Table 3). The results of those experiments with significant differences are in accordance with enclosure experiments in oligo-mesotrophic Castle Lake (Redfield, 1979), but were much less accentuated. The sudden release in grazing pressure enhanced primary production, decreased POC sedimentation and mineralization (see Table 4) and thus, enhanced the POC concentration, but epilimnetic carbon cycling responded only moderately. Turnover times of POC increased on average by about 10% when herbivorous crustaceans were excluded from the LCs (Table 4).

The exclusion of herbivorous crustacean plankton reduced P removal by sedimentation and thus, generally increased the mean residence time of TP (τ_P). In two experiments (83/3 both LCs; 84/A filtered LC) loss by wall growth contributed more than 30% to the total P loss. This partly explains the small differences in P between filtered and control LCs in these experiments. Herbivorous crustacean plankton enhance epilimnetic phosphorus depletion by ingesting small particles and egesting large and fast sinking fecal aggregates

(Uehlinger & Bloesch, 1987b; Bloesch & Bürgi, 1989). Generally the sedimentation rate increased during the experiments which may be explained by the relative increase of the netplankton observed in all experiments (Bloesch & Bürgi, 1989). This is in accordance with the results of Taylor (1984), who observed that large zooplankton tend to pass on their incorporated nutrients to the hypolimnion more readily than small zooplankton. Our experiments did not yield any indications which support the hypothesis that zooplankton grazing enhances the regeneration of phosphorus, and thus gross primary production in the epilimnion as a compensatory indirect effect in the sense of the mutualism-cybernetics theory (Vadas, 1989).

Contrary to a sudden arbitrarial elimination, zooplankton populations in natural environments decrease and grow slowly, giving phytoplankton growth room for adaptation. Experiment 83/3, where grazing pressure was growing with time, showed hardly any grazing-induced effect on phytoplankton composition and primary production, except for the very end of the experiment, because other factors were stronger. Not even nanoplankton, the preferred food source for *Daphnia*, was greatly affected by grazing. This experiment suggests, together with the majority of limnocorral experiments performed in this project, that zooplankton grazing is but a marginal factor in the control of primary production and phytoplankton successions of oligo-mesotrophic Lake Lucerne, except for extreme situations such as a clearwater phase. This is at variance with McQueen *et al.* (1986), whose model predicts that in oligotrophic lakes top-down effects are not well buffered, so that zooplankton-phytoplankton interactions should become significant. Our experiments indicate that also in oligo-mesotrophic ecosystems buffering mechanisms can attenuate the direct impact of changing grazing pressures on primary production.

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