

The impact of larval and juvenile fish on zooplankton and algal dynamics

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Abstract

The impact of young-of-the-year (YOY) fish predation on zooplankton dynamics and cascading effects down to phytoplankton were studied in lake enclosures using different densities of larval and juvenile European perch (*Perca fluviatilis*). Two experiments, one in June and one in August, were performed in Lake Dagstorpssjön, a slightly eutrophic lake in Scania, southern Sweden. In our experiments, we found that in August, there was a negative relation between YOY perch density and cladoceran biomass and between YOY perch density and cladoceran size. Moreover, in August, both rotifer and algal abundance increased with increasing YOY density, and species composition of algae was affected. At high YOY densities, there was also a negative effect on water transparency. In June, when growth of larval perch was slow and daphnid abundance low, larval perch was not the major structuring force on either zooplankton or algal communities. In early summer, the likelihood of YOY perch having an impact on cladoceran biomass is dependent on the timing of many factors. One factor is the timing between larval occurrence and the increase in large cladoceran biomass that will enhance larval growth. In late summer, however, a high enough predation pressure of juvenile fish will prevent recovery of large herbivores after the midsummer decline in zooplankton abundance and will drive the algal community toward a late summer species composition of small algal cells and blue-green algae.

Most YOY fishes are planktivorous and may reach high abundances in summer. Therefore, YOY fish are potentially important regulators of zooplankton communities (Whiteside et al. 1985; Cryer et al. 1986; Mills et al. 1987; De Vries and Stein 1992; Qin and Culver 1995), and their effects may cascade down to the phytoplankton (Mills et al. 1987; Kurmayer and Wanzenböck 1996). Bioenergetic models predict that in several species, including percids and cyprinids, YOY fish have a higher mass specific consumption rate than older fish (Post 1990; Hewett and Johnson 1992; Karås and Thoresson 1992) and that the mass specific consumption rate is at its highest in larval fish and then decreases during the first summer (Post 1990; Karjalainen et al. 1997). However, few and to a large extent contradicting data exist regarding the size and density at which YOY fish have an impact on zooplankton and if this effect cascades down to phytoplankton. Pond and enclosure experiments have shown that high densities of larval walleye (*Stizostedion vitreum*), juvenile gizzard shad (*Dorosoma cepedianum*), and European perch (*P. fluviatilis*) may affect daphnid zooplankters in early and midsummer (DeVries and Stein 1992; Qin and Culver 1995, 1996; Hülsmann and Mehner 1997). Long-term enclosure experiments have shown that YOY fish continue to affect daphnids throughout the summer (Post and McQueen 1987; Kurmayer and Wanzenböck 1996). In field studies, similar impacts of YOY fish on zooplankton have been observed in late summer (Cryer et al. 1986; Mills et al. 1987; but see Mehner et al. 1995) but not in early summer (Treasurer

1992; Mehner 1996; Mehner et al. 1997). Mills et al. (1987) and Kurmayer and Wanzenböck (1996) showed that the impact of juvenile fish on zooplankton had a cascading effect on phytoplankton biomass and community composition during mid- and late summer. Post and McQueen (1987), however, found this effect to be weak.

The drastic decline in zooplankton abundance that is associated with the abrupt ending of the clear-water phase of many eutrophic lakes (Lampert et al. 1986) has been attributed to YOY fish predation (Whiteside 1988; Gliwicz and Pijanowska 1989; but see Luecke et al. 1990; Rudstam et al. 1993). Hence, if YOY fish affect zooplankton and algal dynamics at the time of the clear-water phase, YOY predation may drive the zoo- and phytoplankton communities into the late summer stage, characterized by small-sized herbivores, small edible algae, and later blue-green algal blooms (Sommer et al. 1986) and reduced water transparency. There are few studies focusing on the impact of different ontogenetic stages of YOY fish at densities natural for northern temperate lakes. This issue is of utmost importance in situations when YOY fish are released from competition from adult planktivore fish, e.g., after large-scale fish removals, such as fish kills or biomanipulations. The abundance of YOY fish (e.g., European perch and roach (*Rutilus rutilus*)) generally increases considerably after biomanipulation (Meijer et al. 1994; Benndorf 1995; Romare and Bergman in press), and thus, the effects of YOY fish may become a major problem after a biomanipulation (Meijer et al. 1994; Benndorf 1995).

In this study, we examined the effect of early and late stages of YOY European perch on zoo- and phytoplankton dynamics. To do this, we used natural densities of perch in two enclosure experiments. The first experiment was carried out between late May and early July (“the June experiment”), and the second experiment was carried out in the same lake during early August to early September (“the August experiment”). Our results were not compared with the impact of YOY fish in the lake, since we had no lake data

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Table 1. Experimental design of the enclosure studies in Lake Dagstorpssjön in the June and August 1996 experiments, showing the stocking, final and average daily abundance (No. m⁻³) of YOY perch (*P. fluviatilis*), average daily biomass (g m⁻³), and average daily mean size and final mean size (mm ± SE). Perch larvae were 7.8 ± 0.1 mm long at the start of the June experiment, and 45.5 ± 0.3 mm at the start of the August experiment.

June						August					
Stocking abund.	Final abund.	Average daily abund.	Average daily biomass	Average daily size	Final size	Stocking abund.	Final abund.	Average daily abund.	Average daily biomass	Average daily size	Final size
(No. m ⁻³)		(g m ⁻³)		(mm)		(No. m ⁻³)		(g m ⁻³)		(mm)	
0	0	0	—	—	—	0*	0	0	—	—	—
1.4	0.6	0.9	0.06	16	29 ± 1	0.4	0.2	0.3	0.7	63	75
1.4	0.6	0.9	0.06	17	31 ± 1	0.4	0.2	0.3	0.6	59	67
1.6	0.8	1.1	0.06	16	27 ± 2	0.4	0.4	0.4	1.0	62	73 ± 3
2	1	1.4	0.06	16	26 ± 2	0.4	0.4	0.4	1.0	62	73 ± 4
2.2	1.2	1.6	0.10	16	28 ± 1	1	0.4	0.6	1.4	61	71 ± 0
2.4	1.2	1.7	0.13	18	32 ± 1	1	0.4	0.6	1.3	60	69 ± 0
3	1.4	2.1	0.12	17	30 ± 2	1	0.6	0.8	1.7	60	69 ± 3
4	2.2	3.0	0.16	16	28 ± 2	1	0.8	0.9	1.3	54	60 ± 1
5	2.2	3.4	0.12	14	23 ± 2	2	1.4	1.7	2.3	52	57 ± 1
7	3.4	4.9	0.08	12	17 ± 0.5	2	1.6	1.8	2.3	51	55 ± 2
20	10.4	14.5	0.42	14	20 ± 0.4	2	1.6	1.8	2.0	51	55 ± 2
						2	1.6	1.8	2.4	52	55 ± 2

* In August, four fishless enclosures were used.

on YOY fish densities. The main aim of the study was to compare the impact of YOY perch on plankton dynamics along a gradient of fish densities and between early and late summer conditions. We also tested the hypothesis that YOY perch should have a lower impact in late than in early summer because of the lower mass specific consumption rate of later stages of YOY perch. The maximum consumption rate at 18°C is 3–10 times lower for YOY perch weighing 1–3 g (WW) than for larval perch weighing 0.01–0.1 g, i.e., 0.2–0.25 g g⁻¹ d⁻¹ in August compared to 0.75–2 g g⁻¹ d⁻¹ in June (Post 1990; Karjalainen et al. 1997).

Study area

Dagstorpssjön is a slightly eutrophic and humic lake situated in the middle of Scania, southern Sweden. The lake area is 0.48 km², maximum depth is 5 m, and mean depth is 2.8 m. Sparsely rooted vegetation grows in the shallow parts of small bays, but most of the shorelines are stony and steep. The fish community is dominated by roach (*R. rutilus*), white bream (*Blicca bjoerkna*), bream (*Abramis brama*), and perch (*P. fluviatilis*). The zooplankton community is characterized by relatively high numbers of rotifers in the spring and has a summer community consisting of cladocerans (mainly *Bosmina coregoni* and *Daphnia cucullata*) and copepods (mainly cyclopoid copepods) (Gelin et al. 1981).

Materials and methods

In the June experiment, we suspended 12 plastic bags (1.6 m in diameter, 2.5 m deep, 5-m³ volume, with a sealed bottom) from floating wooden frames in a small, 3–4-m-deep bay of Lake Dagstorpssjön. Enclosures were filled with lake water on 29 May 1996. Lake water was filtered through a

0.5-mm mesh to prevent fish larvae from entering the enclosures. Most lake zooplankton, including *Daphnia*, was small sized at that time and thus not hindered by the mesh. We randomly assigned enclosures to different fish densities. YOY fish were added to the enclosures on 30 May 1996 in densities ranging from low (0 YOY m⁻³) to high (20 YOY m⁻³), with emphasis on densities around one to three YOY m⁻³ (Table 1). We used perch larvae that were hatched in the laboratory from field-obtained roe and reared them in aquaria for 3 weeks at ambient lake water temperatures. Due to very low spring water temperatures, perch larvae had only reached a mean total length (TL) of 7.8 mm ± 0.1 (SE) at the start of the experiment, and the mean initial weight was calculated to be 0.003 g using length/weight regression (Mooij et al. 1994). To test for handling mortality, which we expected to be high, larval fish were transported and handled the same way as the fish that were added to the enclosures, only these fish were added to aquaria. Directly after transport, the mortality was 20%, and after 24 h in the aquaria, the total mortality was around 75%.

The June experiment lasted 5 weeks; we first sampled on 29 May, before fish were added, and then every fifth day until 3 July, a total of eight samplings. At each sampling date, we measured Secchi depth and collected water samples to estimate Crustacean zooplankton abundance in both enclosures and the lake. Rotifers and phytoplankton were sampled at the start, middle, and end of the experiment. Water from each enclosure and from the lake was sampled with a 2-m-long tube sampler, with a diameter of 48 mm. A total of 10 liters of water was filtered through a 45-μm mesh net, and zooplankton were preserved in 4% formalin. A subsample (100 ml) was taken and preserved in Lugol's solution for phytoplankton analysis. At the end of the experiment, enclosures were drained, the water sieved through a 0.5-mm

mesh, and all fish collected. Lake water temperature was recorded continuously using a temperature logger suspended from one of the wooden frames at 0.5-m depth.

In the laboratory, fish were counted, and TL and WW were measured to the nearest millimeter and 0.01 g, respectively. Because YOY fish were stored in alcohol before being weighed in June, biomass values were corrected for loss of fat using a conversion factor estimated from weighing the August samples before and after preservation. Zooplankton were counted at $\times 40$ magnification, and at least 20 individuals were measured to the nearest 0.02 mm. Zooplankton biomass was estimated from length/weight regressions obtained from Bottrell et al. (1976). For phytoplankton analysis, permanent slides were made using HPMA (2-hydroxypropyl-metacrylate with the catalyst azo-bis-iso-butronitrile; Crumpton 1987). Algae were counted at $\times 250$ magnification, and at least 200 individuals were counted from each sample.

In the August experiment, we used 16 enclosures (of the same size and situated at the same site as in June). The enclosures were filled with lake water sieved through a 2-mm mesh on 2 August 1996, and YOY fish, caught with a dip net in Lake Ringsjön, a nearby lake, were added 4 d later. Fish were added at four densities: 0, 0.4, 1, and 2 fish m^{-3} (Table 1). Each treatment was replicated four times. We used juvenile perch with a mean length of $45.5 \text{ mm} \pm 0.3$ (SE) and a mean weight of $0.8 \text{ g} \pm 0.02$ (SE). The August experiment lasted 4 weeks; we first sampled on 6 August (before fish were added) and then once a week, for a total of five samplings. Sampling and analysis were performed as in the June experiment.

Because of high YOY mortality, treatments are hereafter labeled after average daily densities (per cubic meter) (Table 1). Average daily density of YOY perch was calculated from initial and final density in each enclosure using an exponential decay function ($N_t = N_0 e^{-mt}$), where m is mortality. To make Figs. 1 and 2 and the discussion of results easier to grasp, enclosures with similar densities (per cubic meter) of YOY perch were pooled into groups. The groups were expressed as the mean of the densities. In June, there were five groups: 0 YOY m^{-3} ($n = 1$), 1.0 YOY m^{-3} ($n = 3$), 1.6 YOY m^{-3} ($n = 3$), 2.8 YOY m^{-3} ($n = 3$), and 9.7 YOY m^{-3} ($n = 2$). In August, there were four groups: 0 YOY m^{-3} ($n = 4$), 0.3 YOY m^{-3} ($n = 4$), 0.7 YOY m^{-3} ($n = 4$), and 1.8 YOY m^{-3} ($n = 4$). Average daily size of YOY perch was calculated from initial mean size, and final size for each individual fish using an exponential function ($N_t = N_0 e^{gt}$), where g is growth in millimeters. Since we did not have reliable weight data for all sizes of fish, we did not use length/weight regressions to calculate average individual daily biomass of YOY perch. This was instead calculated from initial mean weight and final weight for each individual fish using the same exponential function as for size, where g is growth in grams (WW). The total average biomass (grams per cubic meter) for each enclosure was then calculated based on the sum of the individual weights plus additional mean weights to compensate for the mortality (the difference between average numbers of YOY and final numbers).

Statistical methods—At the end of both the June and August experiments, we had a gradient in numbers of YOY among enclosures. Therefore, we used regression analysis to test if total zooplankton, cladoceran, *Daphnia*, and copepod biomasses at the different sampling dates, as well as cladoceran size, could be explained by YOY average daily density. We also tested if final rotifer and algal abundances were explained by YOY average daily densities and if final algal abundances were explained by final cladoceran or rotifer biomass. Since many regression analyses were performed, we limited the analysis to five dates, and we applied the Bonferroni correction to the significance level. All zooplankton biomass data were log transformed. When testing for differences in Secchi depth between treatments in August, and when testing for differences in initial cladoceran biomass and abundance between the June and August experiments, analysis of variance (ANOVA) was used. For all tests, the statistical package Systat was used (Wilkinson 1992).

Results

YOY density and biomass—YOY fish densities at the end of the June experiment varied between 0.6 and 10.4 YOY m^{-3} , and average daily densities varied between 0.9 and 14.5 YOY m^{-3} (Table 1). YOY average daily total biomass varied between 0.06 and 0.42 g m^{-3} (Table 1). Mean fish size at the end of the experiment varied between 17 and 32 mm, and average daily size varied between 12 and 18 mm (Table 1). In the high-density enclosures, most larvae had not reached 20 mm by the end of the experiment. Fish densities in the enclosures at the end of the August experiment varied between 0.2 and 1.6 YOY m^{-3} , and average daily densities varied between 0.3 and 1.8 YOY m^{-3} (Table 1). YOY average daily total biomass varied between 0.6 and 2.4 g m^{-3} (Table 1). Mean fish size at the end of the experiment varied between 55 and 75 mm, and average daily size varied between 51 and 63 mm (Table 1).

Zooplankton community composition—In the June experiment, the percentage compositions of taxonomic groups in the zooplankton community were similar among treatments. The small cladoceran *B. coregoni* dominated zooplankton biomass in all enclosures throughout the experiment, except for a temporary increase in cyclopoid copepods during the first and/or second week (Fig. 1). During the first weeks of the experiment, *Bosmina* and cyclopoid copepods were also the dominant zooplankters in the lake (Fig. 1). Thereafter, the share of cladocerans was higher in the enclosures than in the lake, except on the last date (Fig. 1).

In the August experiment, the zooplankton community composition changed with time, and this change varied among treatments (Fig. 1). At the start of the experiment, cyclopoid copepods dominated zooplankton biomass in all enclosures as well as in the lake. At the highest mean average density of YOY fish (1.8 YOY m^{-3}), cyclopoid copepods continued to dominate throughout the experiment, whereas at all other densities (0–0.7 YOY m^{-3}), as well as in the lake, the share of cyclopoid copepods decreased, and the share of cladocerans (*D. cucullata*, *Ceriodaphnia quadrangula*, and *B. coregoni*, hereafter referred to as *Daphnia*,

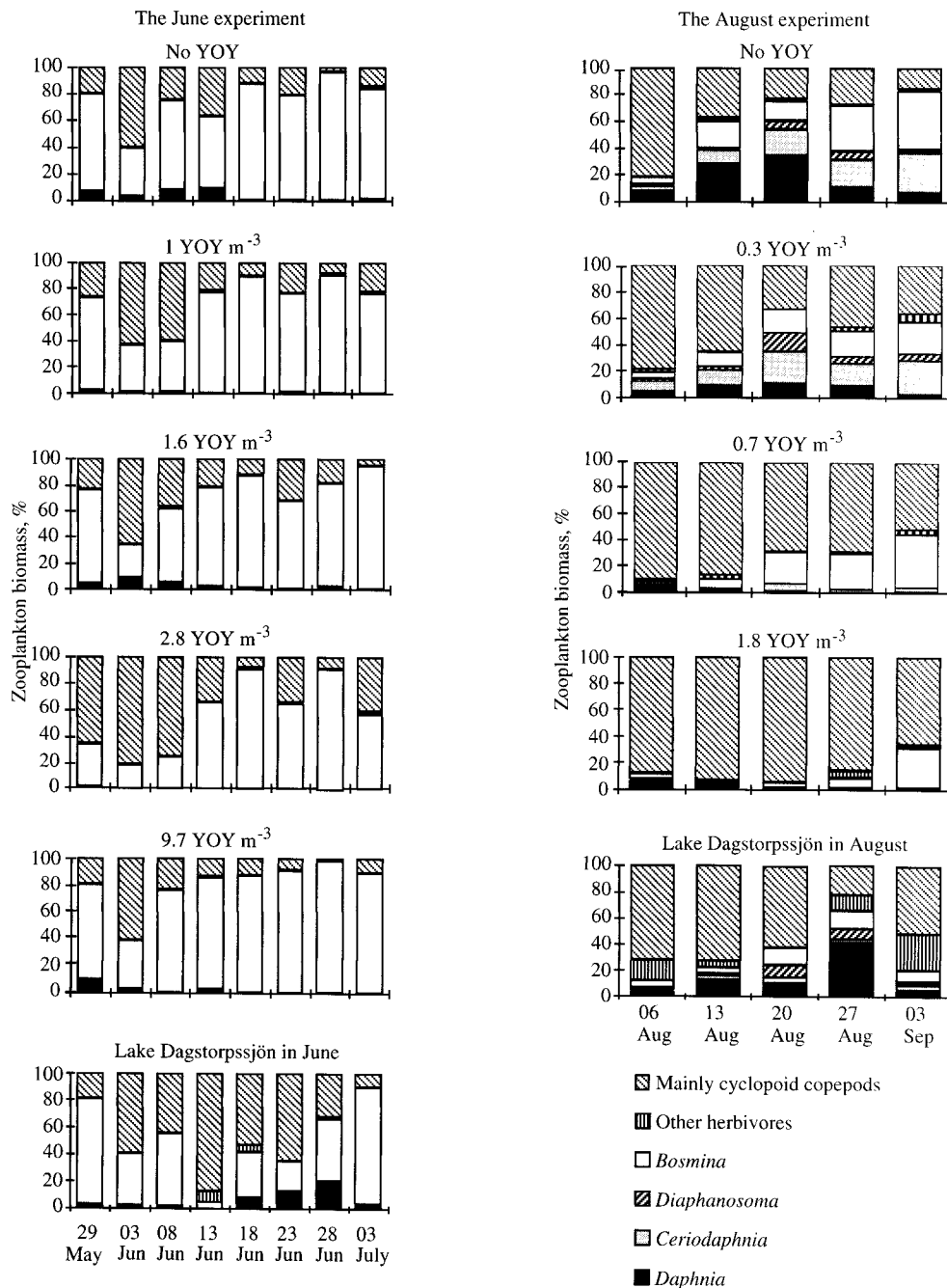


Fig. 1. Development of the zooplankton community, described as the percentage of total biomass of the following groups: *Daphnia*, *Ceriodaphnia*, *Diaphanosoma*, *Bosmina*, other herbivores (calanoid copepods and *Chydorus*), and mainly cyclopoid copepods (including the carnivorous cladoceran *Polyphemus*) at different YOY fish density groups (mean of average daily density, m^{-3}). To make figures easier to grasp, fish abundances from several enclosures were pooled into groups, expressed as the mean of these abundances. In June, $n = 1, 3, 3, 3,$ and in August, $n = 4$ in all groups. Data are from the enclosure studies in Lake Dagstorpssjön in June (left), August (right) 1996, and from the lake.

Ceriodaphnia, and *Bosmina*) increased (Fig. 1). The lower the density of YOY fish, the earlier cladocerans dominated the zooplankton biomass (Fig. 1). In the treatment without YOY fish, cladocerans reached 60% of total zooplankton biomass after 1 week. At 0.3 YOY m^{-3} , cladocerans reached

70% after 2 weeks, and at 0.7 YOY m^{-3} , cladocerans reached 50% of total zooplankton biomass by the end of the experiment (Fig. 1). Even within cladocerans, there were treatment differences by the end of the experiment. The share of daphnids (*Daphnia* and *Ceriodaphnia*) decreased

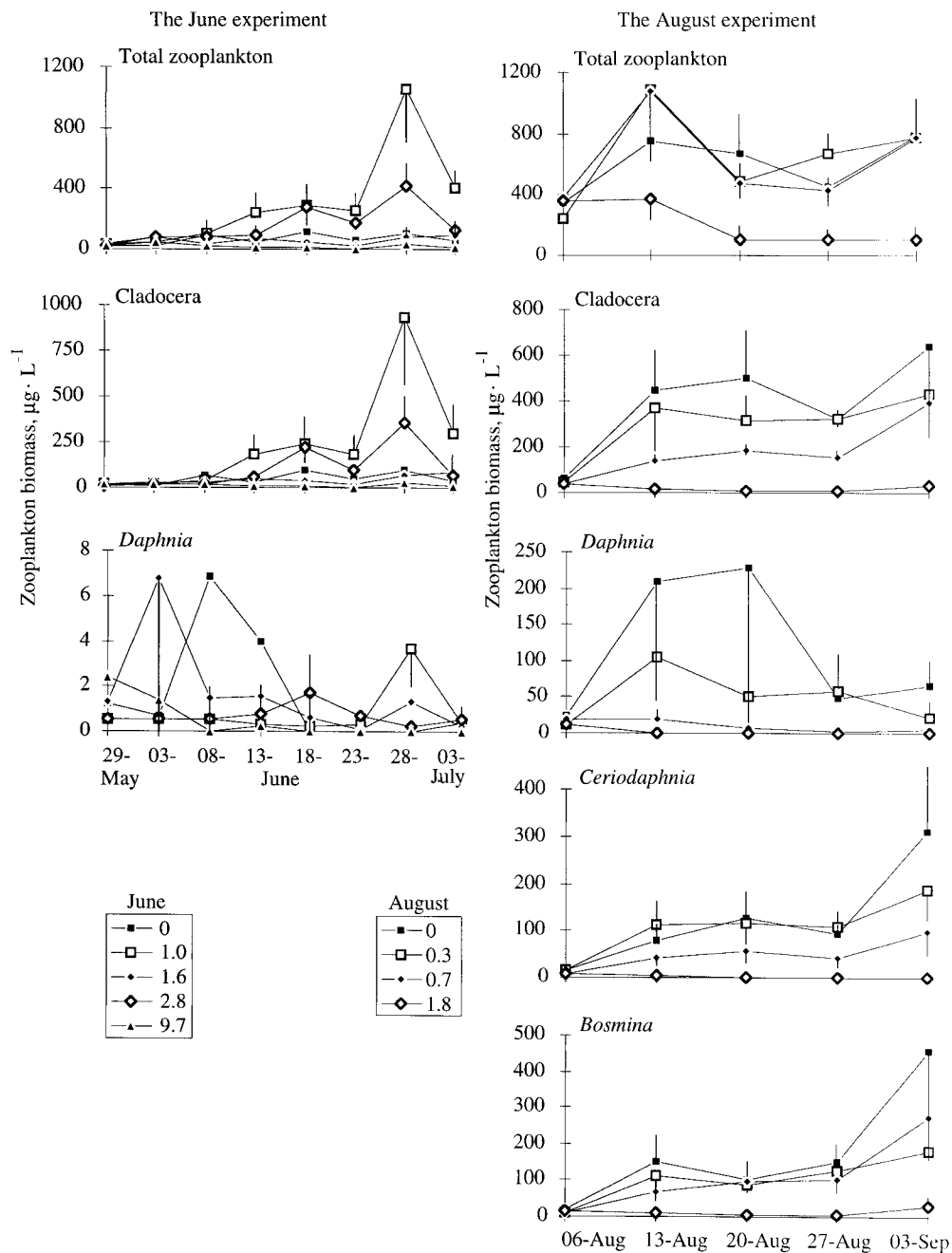


Fig. 2. The development of biomasses ($\mu\text{g liter}^{-1} \pm \text{SE}$), of total zooplankton (cladocerans and copepods), total cladocerans, and *Daphnia* at different YOY fish density groups (mean of average daily density, m^{-3}) in Lake Dagstorpssjön, in the June experiment (left) and in the August experiment (right), 1996. Also shown is the development of *Ceriodaphnia* and *Bosmina* biomass in the August experiment. Since *Daphnia* biomass was very low in the June experiment, and *Ceriodaphnia* was absent, the graph on total cladoceran biomass also represents the development of *Bosmina* biomass in June. For explanation of groups, see Fig. 1.

with increasing YOY fish density, from nearly 50% of cladoceran biomass in the treatments with no fish and low fish density to <10% in the medium and high fish treatments (Fig. 1).

Zooplankton abundance and biomass—In the June experiment, zooplankton biomass (i.e., mainly the cladoceran *Bos-*

mina) developed differently among enclosures (Fig. 2). However, average daily density of larval fish in the enclosures could not explain these differences in total zooplankton, cladoceran, *Daphnia*, and copepod biomass at any date (Table 2).

In the August experiment, both total zooplankton and cladoceran biomass differed across YOY fish densities (Fig. 2).

Table 2. Linear regression of the effects of average daily YOY perch density (No. m⁻³) on the biomass ($\mu\text{g m}^{-3}$) of total zooplankton, cladocerans, *Daphnia*, and copepods in the June 1996 experiment at Lake Dagstorpssjön. Biomass values were log transformed (*Daphnia* biomass $\log(x + 1)$). With the Bonferroni correction, the significant level was set to 0.01 (0.05/5). NS, not significant.

Date	F	df	P
Total zooplankton			
29 May	0.0	1,10	0.975 (NS)
08 Jun	2.5	1,10	0.142 (NS)
18 Jun	3.5	1,10	0.092 (NS)
28 Jun	1.7	1,10	0.222 (NS)
03 Jul	3.0	1,10	0.115 (NS)
Cladocerans			
29 May	0.0	1,10	0.897 (NS)
08 Jun	0.5	1,10	0.503 (NS)
18 Jun	4.1	1,10	0.071 (NS)
28 Jun	1.5	1,10	0.247 (NS)
03 Jul	1.9	1,10	0.201 (NS)
<i>Daphnia</i>			
29 May	5.5	1,10	0.041 (NS)
08 Jun	3.0	1,10	0.113 (NS)
18 Jun	0.3	1,10	0.594 (NS)
28 Jun	0.6	1,10	0.459 (NS)
03 Jul	1.3	1,10	0.280 (NS)
Copepods			
29 May	0.0	1,10	0.979 (NS)
08 Jun	1.4	1,10	0.269 (NS)
18 Jun	1.2	1,10	0.302 (NS)
28 Jun	1.1	1,10	0.312 (NS)
03 Jul	2.3	1,10	0.163 (NS)

Table 3. Linear regression of the effects of average daily YOY perch density (No. m⁻³) on the biomass ($\mu\text{g m}^{-3}$) of total zooplankton, cladocerans, *Daphnia*, and copepods in the August 1996 experiment at Lake Dagstorpssjön. Biomass values were log transformed ($\log(x + 1)$). With the Bonferroni correction, the significant level was set to 0.01 (0.05/5). NS, not significant.

Date	F	df	P
Total zooplankton			
06 Aug	0.31	1,14	0.585 (NS)
13 Aug	10.3	1,14	0.006
20 Aug	11.8	1,14	0.004
27 Aug	15.8	1,14	0.001
03 Sep	36.0	1,13	0.001
Cladocerans			
06 Aug	1.3	1,14	0.266 (NS)
13 Aug	38.3	1,14	0.001
20 Aug	71.4	1,14	0.001
27 Aug	112.3	1,14	0.001
03 Sep	44.0	1,13	0.001
<i>Daphnia</i>			
06 Aug	1.9	1,14	0.186 (NS)
13 Aug	16.0	1,14	0.001
20 Aug	29.9	1,14	0.001
27 Aug	27.5	1,14	0.001
03 Sep	8.0	1,13	0.014 (NS)
Copepods			
06 Aug	0.5	1,14	0.478 (NS)
13 Aug	0.3	1,14	0.581 (NS)
20 Aug	0.5	1,14	0.501 (NS)
27 Aug	2.2	1,14	0.161 (NS)
03 Sep	5.3	1,13	0.038 (NS)

In contrast to in the June experiment, this difference in biomass among enclosures could be explained by the difference in average daily YOY density (Table 3). The effect of YOY fish density on total zooplankton, cladoceran, and *Daphnia* biomass was detected already after 1 week; at each date, zooplankton biomass decreased with increasing YOY fish density (Table 3). At the start of the August experiment, cladoceran and total zooplankton biomasses were low in all

enclosures as well as in the lake (Figs. 2, 3). After the first week, cladoceran biomass increased in all treatments except in the high-density treatment (Fig. 2). There was also a temporary increase in copepod biomass in the low and medium density treatments after 1 week, which is reflected in the increase in total zooplankton at the same time (Fig. 2). Copepod biomass then decreased and remained unchanged throughout the rest of the experiment. *Daphnia* numbers and

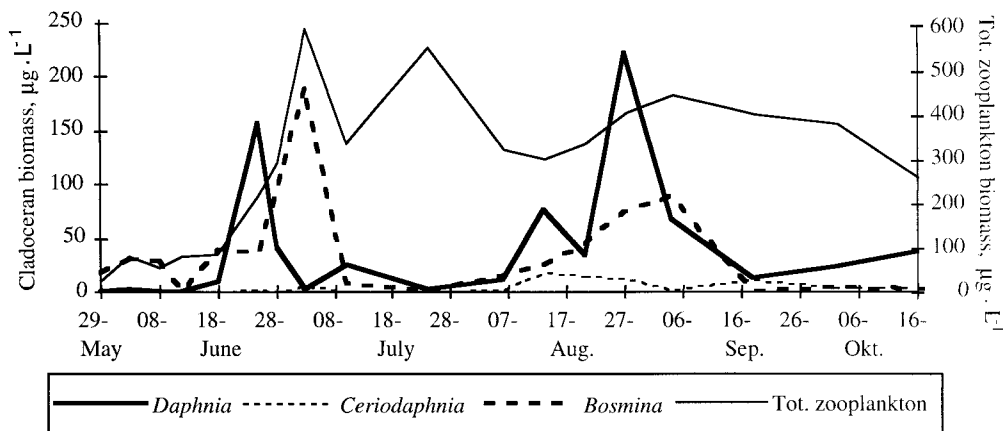


Fig. 3. The development of total zooplankton (cladocerans and copepods), *Daphnia*, *Ceriodaphnia*, and *Bosmina* biomasses ($\mu\text{g liter}^{-1}$) in Lake Dagstorpssjön during the summer of 1996.

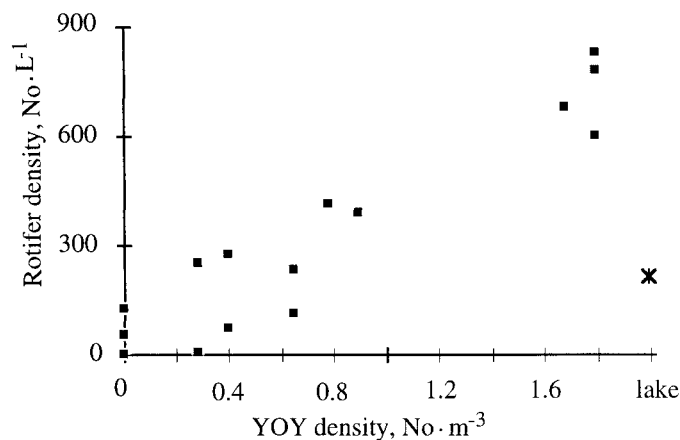


Fig. 4. The abundance ($\text{liter}^{-1} \pm \text{SE}$) of rotifers at different YOY fish density groups (average daily density, m^{-3}) in the enclosures (closed square) and in the lake (cross) in Lake Dagstorpssjön at the end of the August 1996 experiment.

biomass also increased during the first week in treatments, with no or low density of YOY fish, but decreased at the end of the experiment (Fig. 2). In the treatments with medium and high YOY fish density, *Daphnia* numbers and biomass decreased from the first week (Fig. 2). Initial cladoceran biomass in the August experiment was higher than in the June experiment (ANOVA: $F_{1,26} = 17.05$, $P < 0.001$), while initial cladoceran abundance did not differ (ANOVA: $F_{1,26} = 1.87$, $P = 0.183$). Initial total zooplankton biomass was also higher in August (Fig. 2). The higher biomass in August was due to a higher abundance of daphnids and cyclopoid copepods (Figs. 1, 2).

Final rotifer abundance varied between 2 and 330 ind liter^{-1} in the June experiment, but there was no effect of average daily larval density on rotifer abundance (linear regression: $F_{1,10} = 0.18$, $P = 0.91$, $R^2 = 0.00$). In August, final rotifer abundance was higher in the enclosures than in the June experiment, up to 820 ind liter^{-1} (Fig. 4), and final rotifer abundance increased with increasing average daily YOY density (linear regression: $F_{1,13} = 106.7$, $P < 0.001$). The increase in rotifer numbers was mainly due to an increase in *Keratella cochlearis*.

Table 4. Linear regression of the effects of average daily YOY perch density (No. m^{-3}) on the length (mm) of total cladocerans in the June and August 1996 experiments at Lake Dagstorpssjön. With the Bonferroni correction, the significant level was set to 0.01 (0.05/5). NS, not significant.

Date	F	df	P	R^2
29 May	0.1	1,10	0.775 (NS)	0.01
08 Jun	0.2	1,9	0.630 (NS)	0.03
18 Jun	1.6	1,10	0.239 (NS)	0.14
28 Jun	6.7	1,10	0.027 (NS)	0.40
03 Jul	6.6	1,9	0.031 (NS)	0.42
06 Aug	0.2	1,14	0.688 (NS)	0.01
13 Aug	4.7	1,14	0.047 (NS)	0.25
20 Aug	26.6	1,13	0.001	0.67
27 Aug	32.4	1,14	0.001	0.70
03 Sep	57.2	1,13	0.001	0.82

In the lake, cladoceran biomass remained low until the end of June, when there was an increase in first, *Daphnia*, and later, *Bosmina* biomass (Fig. 3). Cladoceran biomass crashed in early July, and copepods dominated zooplankton biomass during July. In August, the development of zooplankton in the lake resembled that of the enclosures with no fish or low density of YOY fish (Figs. 2, 3).

Zooplankton size—In the June experiment, initial cladoceran lengths were 0.2–0.25 mm (*Bosmina*), and in the August experiment, they were 0.35 (*Bosmina*) – 0.7 mm (*Daphnia*). In June, there seemed to be a weak effect of larval fish density on cladoceran size toward the end of the experiment; cladoceran size decreased with increasing larval fish density. However, if the Bonferroni correction is applied and the significant level is set to 0.01, this effect is nonsignificant (Table 4). Only the size of *Bosmina* was included in this test since the *Daphnia* sp. were too few in June to allow for a test on size. In August, the density of YOY fish had an effect on the size of total cladocerans (including *Daphnia*, *Ceriodaphnia*, and *Bosmina*). Total cladoceran size decreased with increasing YOY density from the third sampling date and onward (Table 4).

Phytoplankton—In the June experiment, common algal species were *Cryptomonas* sp. and *Rhodomonas* sp. as well as unidentified small cells with a GALD (greatest axilar linear dimension) of $< 5 \mu\text{m}$ (hereafter called small algal cells). Final algal abundance varied among treatments: total algae (484–1,919 ind liter^{-1}), *Cryptomonas* sp. (0–190 ind liter^{-1}), *Rhodomonas* sp. (7–1,516 ind liter^{-1}), and small algal cells (132–1,524 ind liter^{-1}). However, no trends in abundance of any algal group were recorded among larval fish treatments at the end of the June experiment, and there was no effect of average daily larval density on total algal, cryptomonad, or small algal cell abundance (linear regression: total algae $F_{1,10} = 1.06$, $P = 0.33$, $R^2 = 0.10$; cryptomonads $F_{1,10} = 0.15$, $P = 0.711$, $R^2 = 0.01$; and small algal cells $F_{1,10} = 2.10$, $P = 0.178$, $R^2 = 0.17$). Nor was there any effect of cladoceran density on algae abundance at the end of the

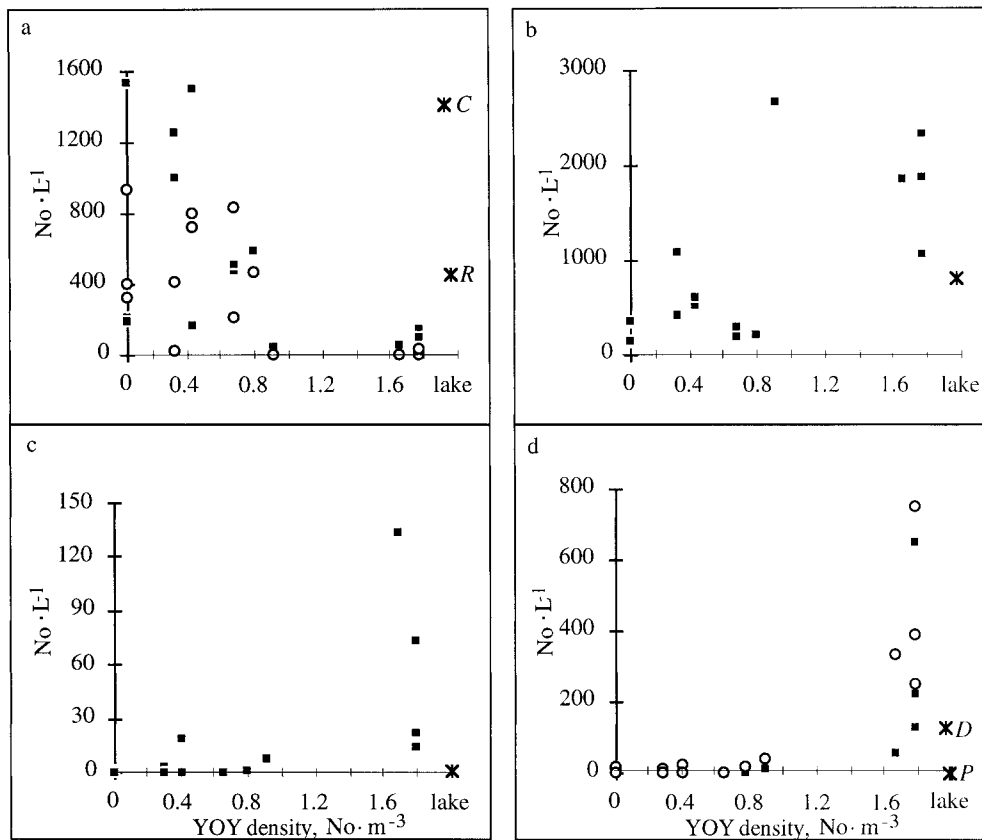


Fig. 5. The abundance ($\text{liter}^{-1} \pm \text{SE}$) of *Cryptomonas* (closed square) and *Rhodomonas* (open circle) (a), small algal cells (unidentified) (b), blue-green algae (c), and *Peridinium* (closed square) and *Dinobryon* (open circle) (d) at different YOY fish density groups (average daily density, m^{-3}) in Lake Dagstorpssjön at the end of the August 1996 experiment. The abundance of *Cryptomonas* and *Rhodomonas* (cross C and cross R), small algal cells (cross), blue-green algae (cross), and *Peridinium* and *Dinobryon* (cross P and cross D) in Lake Dagstorpssjön at the last sampling date in August is also shown in each diagram.

experiment (linear regression: total algae $F_{1,10} = 0.32$, $P = 0.587$, $R^2 = 0.03$; cryptomonads $F_{1,10} = 2.48$, $P = 0.146$, $R^2 = 0.20$; and small algal cells $F_{1,10} = 1.62$, $P = 0.231$, $R^2 = 0.14$) or of rotifer densities (total algae $F_{1,10} = 1.49$, $P = 0.250$, $R^2 = 0.13$; cryptomonads $F_{1,10} = 0.86$, $P = 0.377$, $R^2 = 0.08$; and small algal cells $F_{1,10} = 0.03$, $P = 0.857$, $R^2 = 0.00$). In the August experiment, final total algae abundance was nearly twice as high as in the June experiment (888–3,392 ind liter^{-1}). *Cryptomonas* sp. and *Rhodomonas* sp. were dominant species in treatments with low YOY fish abundance (Fig. 5a). *Cryptomonas* and *Rhodomonas* decreased in abundance with increasing average daily YOY density, whereas small algal cells (Fig. 5b), as well as *Peridinium* sp. and *Dinobryon* sp. (Fig. 5c), all increased with increasing fish density (linear regression: cryptomonads $F_{1,14} = 12.80$, $P = 0.003$; small algal cells $F_{1,14} = 15.81$, $P < 0.001$; and *Peridinium* sp. and *Dinobryon* sp. $F_{1,14} = 29.80$, $P < 0.001$). Blue-green algal (*Anabaena*, *Microcystis*, and *Pseudanabaena*) abundances increased with increasing average daily YOY density (Fig. 5d, linear regression: blue-green algae $F_{1,14} = 10.54$, $P = 0.006$). The change in algal species composition, i.e., the decrease in cryptomonads and the increase in small algal cells, could also partly be ex-

plained by decreasing cladoceran biomass (linear regression: cryptomonads $F_{1,13} = 14.6$, $P = 0.002$, $R^2 = 0.53$, and small algal cells $F_{1,13} = 22.78$, $P < 0.001$, $R^2 = 0.64$) and by the increase in rotifer abundance (linear regression: cryptomonads $F_{1,13} = 11.41$, $P = 0.005$, $R^2 = 0.47$, and small algal cells $F_{1,13} = 12.56$, $P = 0.004$, $R^2 = 0.49$). The abundance of cryptomonads, blue-green algae, *Peridinium* sp., and *Dinobryon* sp. in the lake at the end of the August experiment was similar to that of the no-fish enclosures (Fig. 5).

Secchi depth and temperature—In the June experiment, Secchi depth increased in all enclosures during the first weeks and showed little variation among treatments at the end of the June experiment (Fig. 6). In the August experiment, Secchi depth increased and reached the bottom of enclosures within 2–3 weeks in the no-fish and low and medium fish densities (Fig. 6). At high densities, however, Secchi depth did not increase after the first week and remained low throughout the experiment. At the end of the experiment, Secchi depth was considerably lower in the treatment with the high YOY fish density than in the other treatments (ANOVA: $F_{3,12} = 37.23$, $P < 0.001$, and Tukey's post hoc test: $P < 0.001$). Secchi depth in the enclosures in

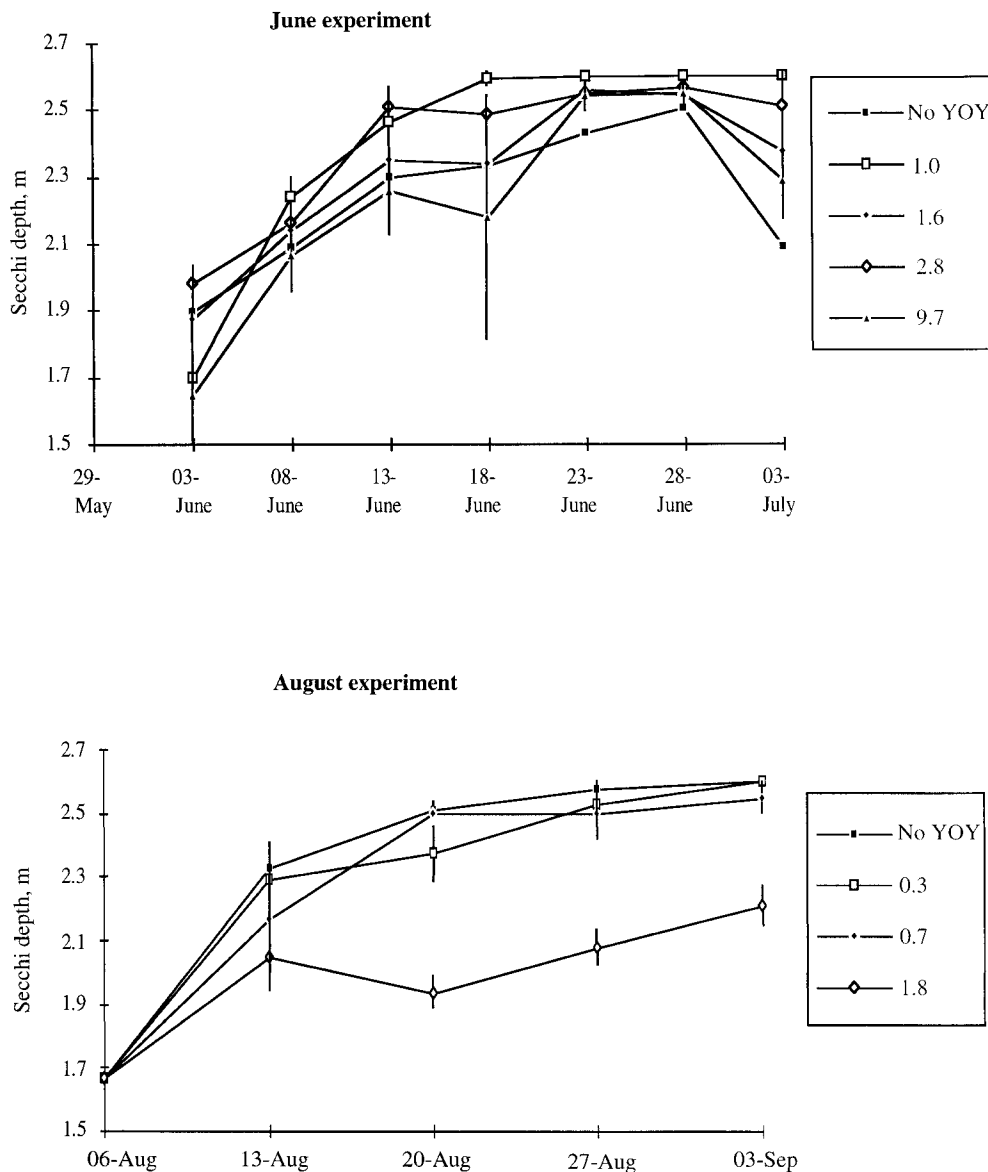


Fig. 6. Development of mean Secchi depth ($m \pm SE$) at different YOY fish densities (mean of average densities, m^{-3}) in the June (upper) and August (lower) experiments in Lake Dagstorpssjön in 1996. The bottom of the enclosure was visible when Secchi depths were >2.5 m. For explanation of groups, see Fig. 1.

both the June and August experiments was higher than in the lake from the second sampling date and onward, probably because of higher sedimentation rates of suspended matter.

The mean water temperature was lower in the June experiment than in the August experiment, with a mean temperature of $17.5^{\circ}C \pm 0.4$ (SE) in June and $20.2^{\circ}C \pm 0.1$ (SE) in August.

Discussion

In this study, we were able to evaluate how different ontogenetic stages of YOY perch structured the early and late summer plankton communities. The two experiments were

performed under conditions that represented late spring/early summer and mid/late summer conditions in a northern temperate lake. Water temperatures in late spring 1996 were unusually low, and during the first week of the June experiment, the water temperature was still $<15^{\circ}C$. YOY perch were still in the larval stage, and cladoceran biomass was increasing. Our August experiment was carried out after the midsummer decline in zooplankton abundance, when cladoceran biomass had again started to increase (Fig. 3) and when water temperatures were high, and perch had become fully developed juveniles.

In the August experiment, average densities as low as 0.3 YOY fish m^{-3} (0.7 g m^{-3}) affected the recovery of *Daphnia* after the midsummer decline. Other enclosure studies have

shown that densities of two to three YOY perch m^{-3} suppress *Daphnia* biomass throughout the summer (Kurmayer and Wanzenböck 1996; Hülsmann and Mehner 1997), whereas our experiment showed that *Daphnia* recovery was totally suppressed at mean YOY fish densities of 0.7 YOY m^{-3} . There was also a gradual change in cladoceran species composition as a result of increasing YOY fish density in the August experiment. This shift from large to small zooplankton species with increasing fish predation is well known from studies of adult fish in general (Brooks and Dodson 1965; Lynch and Shapiro 1981; Ramcharan et al. 1996) as well as from a study of YOY yellow perch (Post and McQueen 1987).

In August, the effects of YOY fish predation also cascaded down to the algal community. The increase in abundance of small algal cells ($<5 \mu m$) and blue-green algae at higher fish densities was most likely a result of the decreased abundance, and thereby grazing pressure, from the macrozooplankters. It is also possible that the increase in nutrient input from fish excretion affected the algal community (Vanni and Findlay 1990). However, the algal genera *Cryptomonas* and *Rhodomonas* showed the opposite response and decreased with increasing fish density. This unexpected result may be due to the increased importance of rotifer grazing. In contrast to macrozooplankton, rotifer abundance was positively affected by increasing fish density in the August experiment, probably because of decreased competition from larger cladocerans with increasing fish density. We found that the cryptomonad abundance was negatively correlated to rotifer density. According to Pourriot (1977), *K. cochlearis*, which was one of the dominant rotifer species, feeds mainly on chryomonads and cryptomonads. Hence, a possible explanation for the decrease in cryptomonad abundance as fish biomass increased was grazing by a growing *Keratella* population. The increase in abundance of small algal cells and in blue-green algae led to a decrease in water transparency in the high-density treatment. Previous studies have also shown that YOY fish at high densities (>1.5 YOY m^{-3}), but not at low densities, result in decreased Secchi depth (Post and McQueen 1987; Kurmayer and Wanzenböck 1996).

In the June experiment, larval fish density could not explain the variation in cladoceran, copepod, or phytoplankton densities found among enclosures, which was contrary to our predictions. However, the result is in agreement with a field study of larval perch (<20 mm) (Treasurer 1992) and with an enclosure study on larval gizzard shad (15–23 mm, 0–60 m^{-3}) (Welker et al. 1994). In the study on gizzard shad, however, copepod biomass was affected by larval predation.

There are several factors that may explain why predation from perch larvae alone was not a major structuring force in our June experiment. For one thing, the low temperature in June probably delayed development of larger cladoceran species in spring/early summer (Sommer et al. 1986) by affecting the population dynamics of daphnids negatively (Luecke et al. 1990; Boersma and Vijverberg 1996). The fact that the initial zooplankton community consisted of fewer and smaller cladoceran species in the June compared to the August experiment may have influenced the outcome of our June experiment directly through a reduced ability of the fish to detect such small-sized cladocerans (Kerfoot 1980; Gli-

wicz and Pijanowska 1989), as well as through a lower effect of predation on the production of small-sized cladocerans (Vanni 1987). Another process that could have been operating in our enclosures is predation from fourth instar *Chaoborus* larvae, which also feed on cladocerans (Moore et al. 1994). Since *Daphnia* numbers did not increase in any of our enclosures, not even in the fishless or low-density treatments, we do not consider it likely that predation by larval fish alone was responsible for this lack of increase. *Chaoborus* larvae, however, were observed, but not quantified, in the lake and in some of our enclosures in June, including the fishless enclosure. The presence of this additional source of predation may also explain the large variation in *Bosmina* biomass among treatments. Fourth instar *Chaoborus* larvae were not present in the August experiment.

A final factor that could have affected the outcome of the June experiment is the combination of low water temperature and lack of larger cladoceran species, which would have led to poor growth by larval perch (Romare pers. comm.). The resulting small-sized YOY would have had less of an effect on the zooplankton community, since, during the early ontogeny of perch, the ability to move and orient, as well as to detect, capture, and digest large prey, improves with body size as fins, gape size, and sensory and digestive systems develop (Blaxter 1986; Govoni et al. 1986; Miller et al. 1988, 1992, 1993). Also, because of the slow growth, we had consistently lower average daily biomasses of YOY perch in the June experiment than in the August experiment, and thus, predation rates in the two experiments are not really comparable. In August, the predation effect of YOY perch on *Bosmina* was evident at an average daily biomass of 2 g m^{-3} , which is five times higher than the YOY biomass used in the highest density treatment in June. So even if the maximum mass specific consumption rate of an equal biomass of YOY perch was three to four times higher in the June than in the August experiment (Post 1990; Karjalainen et al. 1997), only the highest density treatment in June should have been expected to exert a predation pressure on zooplankton similar to that of the 2-g m^{-3} treatment in August.

Recent studies indicate that the impact of YOY fish on *Daphnia* in early summer is a function of *Daphnia* biomass and production, YOY fish biomass, and time of maximum predation (Post and Kitchell 1997; Mehner et al. 1998a). According to Mehner et al. (1998b), maximum predation by YOY fish occurs when YOY are large enough to selectively prey on large, mature daphnids, and the timing of peak predation will thus be influenced by species-specific variation in spawning time, initial size, and gape size of the fish (Kurmayer and Wanzenböck 1996; Mehner et al. 1998b). Although we did not evaluate the impact of larval perch on daphnids in this study, our experiment indicates that the growth of larval perch is enhanced by the occurrence of larger cladocerans in the diet (Romare pers. comm.). Thus, we suggest that the timing of peak predation of perch is also dependent on the occurrence and abundance of larger cladoceran species that may enhance perch growth during the larval stage.

During mid- and late summer, zooplankton dynamics in enclosures have been shown to be affected by predation of

juvenile fish: both juveniles of the piscivorous European perch (Kurmayer and Wanzenböck 1996; Hülsmann and Mehner 1997; this study) and juveniles of planktivorous or omnivorous fish such as yellow perch (*Perca flavescens*), gizzard shad, roach, and bleak (*Alburnus alburnus*) (Post and McQueen 1987; Dettmers and Stein 1996; Kurmayer and Wanzenböck 1996). Thus, the combination of many species reaching the juvenile stage at the same time and the high water temperatures in mid- and late summer increases the likelihood that high densities of juvenile fish will have an impact on large *Daphnia*. Still, species-specific differences in foraging behavior and gape size will play an important role in determining the impact of different species on lower trophic levels (Kurmayer and Wanzenböck 1996). However, it is important to consider that enclosures are artificial systems, forcing zooplankton to be continually affected by YOY fish. Processes involving ontogenetic habitat shifts of YOY fish and migrations of both fish and zooplankton will modify the impact of YOY fish in a natural system; thus, these processes also need to be considered. When we compare data on algae and rotifer abundances and macrozooplankton biomass between the enclosures and Lake Dags-torpssjön at the end of August, the predation pressure seems to have been low in the lake. It is not known if this is due to low densities of YOY fish in the lake as a whole or only in the pelagic zone.

In conclusion, our experiments showed that there was a strong effect of YOY perch predation on both zooplankton and phytoplankton dynamics and community composition in late summer but no clear effect in early summer. The lack of an effect of YOY perch on zooplankton in early summer may occur when the abundance of larger cladocerans is low, precluding most larval perch from growing large enough to be able to prey on large mature *Daphnia* at the time when *Daphnia* biomass is increasing. Later, however, when YOY perch have become fully developed juveniles, high predation pressure prevents recovery of large herbivores and drives the algal community toward small algal cells and blue-green algae, typically found in late summer. Thus, when restoring many European lakes by manipulating the fish community (biomanipulation), a subsequent increase in the abundance of juvenile perch during mid- and late summer may counteract the intent of the biomanipulation. High predation pressure of juvenile perch in late summer may promote the formation of blue-green algal blooms and thereby reduce water transparency considerably.

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