

Consequences of fish predation, migration, and juvenile ontogeny on zooplankton spring dynamics

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Abstract

In order to disentangle if and when resource supply and adult and young-of-the-year (0+) fish predation affect zooplankton dynamics during spring, we monitored zooplankton during three consecutive years in a lake in southern Sweden. We also experimentally assessed 0+ fish predation rates and estimated changes in predation rates of adult fish on zooplankton. Decline in abundances of large-sized zooplankters in early spring was not caused by 0+ fish predation. Instead, this decline was most likely a combined result of size-selective predation from adult fish (stationary in the lake and from those returning from surrounding streams) and competition for diminishing algal food resources. On the other hand, the decline in medium-sized zooplankton in the lake during spring was strongly affected by 0+ fish. Hence, during spring, zooplankton are facing predation both from adult fish selecting large prey and from 0+ fish, which start feeding on small-sized prey and eventually switch to larger. Neither predation by different ontogenetic stages of fish (adult and 0+) nor resource supply shape the zooplankton spring dynamics, but rather they affect the timing and strength of these events. 0+ cyprinids tend to have stronger effect on zooplankton dynamics than other taxa of 0+ fish. A combination of predation from adult and 0+ fish during spring is the main mechanism behind the crash of the zooplankton community, which in many lakes leads to the termination of the clear-water phase.

The spring, with its rapidly increasing temperature, is an important period for the development of the zooplankton summer community in temperate regions, mirrored in dramatic fluctuations in population densities. These conspicuous spring fluctuations are due to changes in reproductive rates and resource supply but also to increased feeding rates from predators. The total predation rate on zooplankton may be divided into several components. First, there is predation from adult fish present in the lake year-round, and the seasonal fluctuations in their predation rate is driven by temperature (Lessmark 1983) and is generally most intense on larger zooplankton size classes (Brooks and Dodson 1965). Second, a dramatic change in the predation rate occurs with the hatching and recruitment of young-of-the-year fish (0+) in the spring. They start their life by feeding on small zooplankton but are within a few weeks able to feed on larger size classes (Mills and Forney 1983; Mehner and Thiel 1999). Thus, smaller size classes of zooplankton should suffer from 0+ predation earlier in the season than larger ones. It has previously been suggested that 0+ predation drives succession in the zooplankton community (Cryer et al. 1986; Gliwicz and Pijanowska 1989), whereas other studies have concluded that 0+ fish

predation probably is too weak to explain zooplankton spring dynamics (Cushing 1983; Boersma et al. 1996) and that instead other processes, such as competition and resource supply (i.e., bottom-up processes) are more important. In a review, Mehner and Thiel (1999) suggested that 0+ larval fish may have only minor influence on smaller zooplankton species, whereas somewhat older 0+ fish can have a considerable influence on larger zooplankton, especially during late summer and fall.

A third—and hitherto almost completely neglected—component behind changes in predation rate on zooplankton is the return of winter migrating fish to the lake from tributaries and wetlands in spring (Brönmark et al. unpubl. data). Recent studies have quantified this winter migration of cyprinid fish to between 30% and 50% of the total cyprinid populations (Brönmark et al. unpubl. data), and, thus, the effect of the return of these predators on the zooplankton dynamics in spring cannot be neglected. These three different components of total predation rate (predation from stationary fish, winter migrating fish, and new recruits [0+]) may affect abundance and size of different zooplankton groups in different ways and at different times. Hence, in order to understand the development of the spring zooplankton community, it may be of importance to assess *when* 0+ fish start to feed on different size classes of zooplankton, *when* temperature allows adult fish to feed efficiently, and, finally, *when* migrating fish return to feed in the lake. The main aim with our study is to disentangle when each of these components is important for shaping the observed zooplankton community. To fulfill the aim, we have monitored zooplankton during

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three consecutive years in a lake in southern Sweden. As a way to quantify predation from adult fish, we estimated the proportion and timing of fish performing spring winter migrations between the lake and surrounding tributaries and wetlands. In order to assess 0+ fish predation rates on different size classes of zooplankton, we have performed repeated feeding experiments (Lehman and Sandgren 1985) starting when the first 0+ larvae were visible in the lake and continued until they were able to feed on the largest size fraction of zooplankton offered. In this way we could estimate relative predation rates from both adult and 0+ fish on different zooplankton groups. In our study, we have focused specifically on the spring dynamics in the zooplankton community and on the multitrophic interactions between fish predators, zooplankton grazers, and, finally, on the potential buildup of the summer algal biomass, that is, the breakdown of the “clear-water phase” (Lampert et al. 1986).

Material and methods

Lake Krankesjön is situated in southern Sweden (55°42'N, 13°28'E) approximately 20 km east of the city of Lund. The drainage area of Lake Krankesjön covers 53 km², consisting mainly of open fields (about 70%) and forests (15%). The lake covers a surface of 3.4 km² and has a mean depth of 1.5 m and a maximum depth of 3 m and is moderately eutrophic (Hargeby et al. 1994). The lake water is calcium rich with an average summer calcium concentration of 51 mg L⁻¹ (Blindow et al. 1993). Because of the calcareous bedrock, the pH is high (between 8 and 9 pH units). The mean spring–summer concentration of total phosphorus during 2003–2005 was $42 \pm 17 \mu\text{g L}^{-1}$ ($n = 6$). Lake Krankesjön has two tributaries, the river Länsmansbäcken, coming from west, and the river Silvåkrabäcken, coming from southeast. The outlet, the river Ålabäcken, runs out from the northern part of the lake.

The major part of the lake bottom is covered with submerged vegetation, mainly Charophytes, although this has not always been the case during past decades. Structural shifts between alternative states have been recorded in Lake Krankesjön (Blindow et al. 1993), where one state is characterized by submerged vegetation and clear water, the other by turbid water and sparse submerged vegetation.

The planktivorous fish roach (*Rutilus rutilus* L.) is the most abundant fish species in the lake. Other planktivorous and benthivorous species common in Lake Krankesjön are rudd (*Scardinius erythrophthalmus* L.), tench (*Tinca tinca* L.), bream (*Abramis brama* L.), and white bream (*Blicca bjoerkna* L.). Piscivorous fish species common in Lake Krankesjön are perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.).

Monitoring

Zooplankton, chlorophyll *a* (Chl *a*), and temperature were monitored every 2 weeks, but between 16 March and 28 July 2005, samples were taken weekly. Sampling was performed at the same site (identified with GPS; SilvaTM) at the deepest part of the lake. Ten liters of water were taken

from the upper water column with a 1.2-m-long Plexiglas tube with a diameter of 36 mm and put into a bucket. The water for zooplankton analysis was filtered through a 45- μm net and preserved in Lugol's solution for further analysis in the laboratory. Zooplankton were examined at $\times 40$ magnification (Olympus CK 30 microscope) and determined to genus level with the exception of copepods, which were divided into cyclopoid and calanoid copepods. Twenty individuals of each genus or group were measured, and their biomass was determined using length–mass relationships (Bottrell et al. 1976). Zooplankton were categorized into three size classes: less than 0.2 mm (denoted “small zooplankton”; mainly nauplii and rotifers) and 0.2–0.55 mm, which was dominated by *Bosmina* and *Ceriodaphnia* constituting between 65% and 100% of this size class (by numbers), except for a few occasions during winter (denoted “medium-sized zooplankton”). The third zooplankton size class (larger than 0.56 mm; “large zooplankton”) was dominated by cyclopoid and calanoid copepods, which together constituted between 75% and 100% (by numbers) of this size class except for two occasions during the 3-yr investigation period. *Daphnia* spp. were rarely recorded in samples from the lake.

In the analysis we used maximum rather than mean size in each size class since mean size is strongly affected by reproduction leading to a smaller mean size during the reproductive period. Maximum size is, on the other hand, affected mainly by size-selective predation, which is the process in focus for this study.

In the same way as for zooplankton, pooled water samples were taken for analysis of Chl *a*. The Chl *a* concentration was determined by filtering lake water through a Whatman GF/F filter using a hand pump. In the laboratory, filters were put into test tubes with 10 mL of ethanol and stored in darkness for 20 h. The extract was then cleared by filtering it through a Whatman GF/F filter and absorbance of the supernatant was measured at 665 and 750 nm (Jespersen and Christoffersen 1987).

The predation rate by fish (*P*) is strongly temperature dependent and increases exponentially with temperature ($P = 0.2897e^{(0.1848 \text{ temp})}$; Lessmark 1983; Hansson 2004). Besides temperature, fish predation rate on zooplankton is also affected by the number of fish present in the lake. In many lakes, including Lake Krankesjön, a large portion of the cyprinid fish (mainly roach, *R. rutilus*, and bream, *A. brama*) migrate from the lake in fall and returns in March–April (Jepsen and Berg 2002; pers. obs.). During 2003–2005, we monitored the number of fish migrating in and out of the lake by means of PIT tagging (passive integrated transponder; Castro-Santos et al. 1996; Skov et al. 2005). Fish were caught by electrofishing in the lake at several occasions, and the PIT tag (Texas Instruments Radio Frequency Identification) was inserted through an incision into the body cavity of the fish. Because of the size of the tag (23 mm, 0.6 g in air), only cyprinids larger than approximately 120 mm were tagged. Swim-through PIT-tag readers were placed near the inlets and the outlet of the tributaries of Lake Krankesjön that registered migration activities of the tagged fish (Skov et al. 2005; Brönmark et al. unpubl. data).

Winter migration in fish should result in reduced predation rates on zooplankton during winter, not only because of lower predation rate as a result of low temperature but also because of a lower density of fish in the lake. In order to estimate the relative adult fish predation rate, we therefore set the fish abundance to 1.0 during summer when all migratory fish had returned to the lake and multiplied the temperature-dependent predation rate (see the equation in the previous paragraph) with the actual portion of fish present in the lake each day. In Lake Krankesjön this portion has ranged between 0.60 and 1.0 between 2003 and 2005.

In addition to PIT tagging, we assessed fish size and species distribution once every second year. Multifilament gill nets (Nord 12; 30 m long, 2.5 m deep, each consisting of twelve 2.5-m long sections of six mesh sizes ranging from 5 to 55 mm) were placed to evenly cover the lake area and different habitats during two nights. Fish were then determined to species, counted, and measured in the laboratory. The amount of fish on an areal basis was estimated from published relations between total phosphorus and standing crop (Hanson and Leggett 1982; Griffiths 2006).

Experimental design

In the laboratory experiment, we focused on the ontogenetic changes in feeding of roach (*R. rutilus*) larvae since roach is the most abundant planktivorous fish in Lake Krankesjön. Roach larvae were caught weekly with a zooplankton net in Lake Krankesjön from 23 May 2005, which was the first date fish larvae were visible at the shores of the lake. From 07 June on, the fish had reached a size where they were moving too fast to be caught with a net. From this date we used electrofishing to capture roach juveniles.

Zooplankton from Lake Krankesjön were caught weekly with a 50- μm net. Since the largest sizes of zooplankton occurred in too low numbers to be sampled for experimental purposes, we added large zooplankton species from cultures to the mixture of zooplankton presented to the fish. However, it should be noted that the majority of the zooplankton were harvested in the lake prior to each experimental run. The zooplankton slurry was thoroughly mixed, and equal volumes of the mixture were filled into five 8-L aquaria together with copper-free tap water that had been aerated for several hours. Samples for determination of initial zooplankton abundances in each aquarium were taken with a Plexiglas tube (diameter 70 mm). The sample was filtered through a 45- μm net and preserved with Lugol's solution. To each aquaria, 2, 4, 8, 16, or 32 roach larvae were added, but because of high mortality and difficulties in finding 0+ fish, the last two experiments (07 and 21 July) were performed using a reduced number of fish (0, 2, 8, 14, and 28 and 0, 2, 5, and 9, respectively). The fish larvae were allowed to feed on the zooplankton for between 77 h (24 May) and 13 h (07 July) as predation rates increased over time. At the end of each experiment, all fish were individually measured and then put together and dried (65°C). The batch of fish was then weighed together.

At the end of each experiment, also a zooplankton sample was taken using the same technique as for the initial sample. Samples were then analyzed in the same way as for the monitoring samples. Taxonomic groups were assigned to size classes (<0.20, 0.21–0.55, >0.56 mm, i.e., similar size classes as for the field study) for each experiment. Each experiment was run in a laboratory with approximately the same temperature as the lake water and total darkness between 20:00 and 08:00 h.

To compare changes in the zooplankton composition during the experiment, we used the equation developed by Lehman and Sandgren (1985). This method has been used mainly to assess zooplankton grazing rates on phytoplankton (Lehman and Sandgren 1985; Hansson 1996; Hansson et al. 1998). Here we apply the same methodology to fish predation on zooplankton and calculated net observed growth rate of the zooplankton prey (r) as

$$r = \ln(N_t/N_0)/\Delta t$$

where N_0 = initial number of individuals per taxonomic group or size class, N_t = final number of individuals per taxonomic group or size class, and Δt = duration of the experiment expressed as light hours.

The net observed growth rate (r) is, theoretically, a result of reproduction of and predation on the prey organism, but since our experiments lasted for only a maximum of 77 h and neonates and nauplii were not included in the counts, only predation was effective. Fish mortality during the experiments was low, and only one fish died in each of three experimental runs. Dead fish were counted as 0.5 fish when calculating predation rates since they were alive for at least half of the feeding time in all these cases. Since roach is a visual feeder (Lessmark 1983), we based the Δt on number of hours with light. For each genus, group, and size class of zooplankton, net observed growth rate was calculated for all the treatments. A linear regression relating net observed growth rates (r) to the number of fish present in the experiment was computed (Lehman and Sandgren 1985). The slope of this regression was used as an estimate of 0+ predation rate on zooplankton. The F - and p -values of the linear regressions (Table 1) were generally high, indicating that the per capita predation rates were relatively similar regardless of predator and prey abundances. To normalize the scales of 0+ and adult fish predation rates (see the previous discussion), the highest value of each data set was set to 1.0. These normalized data are used in all results presented.

Results

Monitoring—Since the monitoring in Lake Krankesjön started in late May 2003, early spring dynamics for this year was not possible to include in the analysis. During the 3 yr of investigation, water temperature ranged between 0°C and 26°C (Fig. 1). The algal biomass, expressed as Chl a , was generally between 10 and 20 $\mu\text{g L}^{-1}$ in winter (October–March; Fig. 1). In both 2004 and 2005, it reached a maximum of between 50 and 60 $\mu\text{g chlorophyll L}^{-1}$ in

Table 1. Linear regression analysis on fish density versus net growth rate (r) of zooplankton in experiments performed 24 May, 03 June, 17 June, 30 June, 07 July, and 21 July 2005. The negative slope of the regression is proportional to the number of zooplankton from each size class eaten per fish and time unit (Lehman and Sandgren 1985). A positive slope indicates that the size class is positively related to fish abundance. The coefficient of determination (r^2), F -statistics (including p -values) of the regressions, and experimental (lake) temperatures are also given.

Date/size class	Equation	r^2	F	p	Temp. (°C)
24 May					
<0.2 mm	$y = -0.00002x - 0.00952$	0.02	0.062	>0.150	18.8
0.2–0.55	$y = -0.00031x + 0.00031$	0.19	0.698	>0.150	
>0.56	$y = -0.00003x - 0.00274$	0.04	0.119	>0.150	
03 June					
<0.2	$y = -0.00068x - 0.02006$	0.61	4.782	0.117	15.2
0.2–0.55	$y = -0.00094x + 0.00419$	0.82	14.490	0.032	
>0.56	$y = -0.00011x - 0.00092$	0.02	0.039	>0.150	
17 June					
<0.2	$y = 0.00229x - 0.07409$	0.82	13.285	0.036	18.9
0.2–0.55	$y = -0.00216x - 0.02925$	0.80	12.050	0.040	
>0.56	$y = -0.00256x + 0.00794$	0.99	295.939	0.001	
30 June					
<0.2	$y = 0.00659x - 0.47702$	0.65	5.667	0.097	21.0
0.2–0.55	$y = -0.01135x - 0.06728$	0.92	34.244	0.010	
>0.56	$y = -0.00438x + 0.00779$	0.99	245.081	0.001	
07 July					
<0.2	$y = 0.00396x - 0.16883$	0.86	18.489	0.023	22.9
0.2–0.55	$y = -0.00461x - 0.04973$	0.96	65.297	0.004	
>0.56	$y = -0.00853x + 0.02330$	0.96	71.648	0.003	
21 July					
<0.2	$y = 0.03059x - 0.35094$	0.97	56.739	0.017	20.9
0.2–0.55	$y = -0.01884x - 0.05280$	0.83	9.594	0.090	
>0.56	$y = -0.03783x + 0.00389$	0.94	32.370	0.030	

mid-April (Fig. 1). Algal biomass then declined at the end of April in both years (Figs. 1, 2).

The main fluctuations in zooplankton abundances occurred in spring between mid-April and mid-June in all years when numbers often fluctuated more than 20-fold (Fig. 3). The large zooplankton showed maximum abundances in late April, whereas medium-sized zooplankton peaked in mid-May 2004 and in the beginning of June in 2005 (Fig. 2).

From May to September, all fish were present in the lake, but fish started to migrate from the lake and into the tributaries in late September (Fig. 1). In midwinter, a maximum of 26%, 30%, and 42% of the roach population had migrated out of the lake in 2003, 2004, and 2005, respectively (Fig. 1). Fish started to return to the lake in March, and all fish had returned in late April (Brönmark et al. unpubl. data). The predation rate on zooplankton from adult fish were generally low between October and late March as a result of low water temperature and a lower proportion of fish present in the lake. In spring, predation rate eventually increased as a result of increasing temperatures and returning migratory fish and peaked in mid-July and early August (Fig. 3).

The maximum size within the zooplankton size class 0.2–0.55 mm, which was completely dominated by *Bosmina* spp. and *Ceriodaphnia* spp., varied considerably but showed no obvious seasonal trend and showed no, or even

a tendency for a positive, relation with higher fish predation ($r^2 < 0.071$; $F_{1,49} = 3.759$; $p < 0.06$; Fig. 4). The larger size class of zooplankton, however, showed a negative relation between maximum size and predation rate from fish ($r^2 = 0.20$; $F_{1,50} = 12.900$; $p < 0.001$; Fig. 4).

In 2005, fish larvae were first detected in Lake Krankesjön at the end of May and had then an individual mean dry weight of 0.21 mg and a mean length of 6.4 mm (± 0.43 mm SD). Already after about a week, they had doubled their length (11.5 ± 1.44 mm). At the final experiment (21 July; age of fish about 59 d), the length had increased more than five times and the mean weight more than 300 times to 68 mg.

Estimates of fish abundance and feeding rates—The amount of adult fish in the lake estimated from published relations between total phosphorus and standing crop based on the mean total phosphorus value of $42 \mu\text{g L}^{-1}$ was between $8,300 \text{ kg km}^{-2}$ (Griffiths 2006) and $8,500 \text{ kg km}^{-2}$ (Hanson and Leggett 1982). Since these estimates are very concordant, we have used $8,400 \text{ kg km}^{-2}$ as an estimate of fish standing crop in Lake Krankesjön. The feeding rate of roach (individual weight 56 mg; 20°C) under laboratory conditions has been determined to 99 large or 129 small zooplankton per hour (Mikheev and Wanzenböck 1999). The estimated fish biomass in Lake Krankesjön is 8400 kg km^{-2} , and according to net fishing,

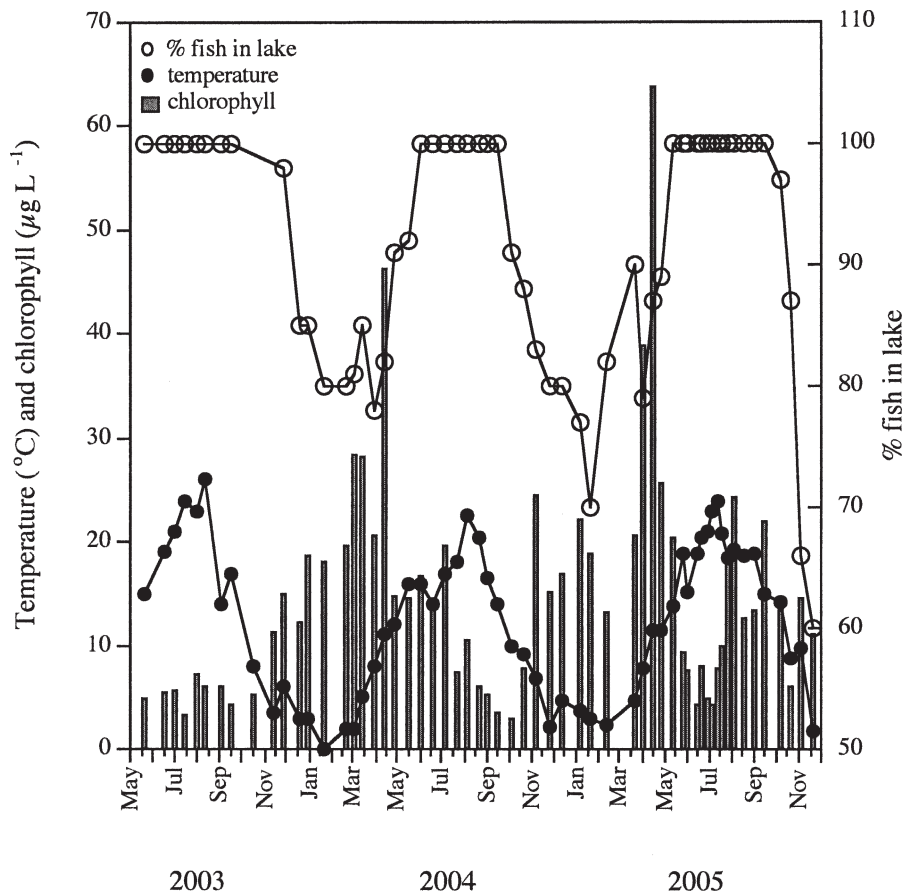


Fig. 1. Temperature and Chl *a* concentration ($\mu\text{g L}^{-1}$) and percentage fish present in Lake Krankesjön (i.e., not migrating to tributaries) from May 2003 to December 2005.

36% of these are roach (Svensson, unpubl. data). The maximum numbers of medium-sized zooplankton in the lake were 325 and 1,600 individuals L^{-1} during spring 2005 and 2004, respectively, and the corresponding values for large zooplankton were 125 and 175 individuals L^{-1} (Fig. 2). Based on these data, fish predation can potentially remove between 5% and 25% of the standing crop of medium-sized and between 37% and 52% of large zooplankton from the lake per day, assuming a feeding period of 12 h d^{-1} (Persson 1983). In addition to the predation pressure from adult fish, the accelerating predation from 0+ fish during spring adds to the mortality rate of zooplankton.

Experiment—During the first feeding experiment (24 May 2005), 0+ fish predation was not detectable on any of the zooplankton size classes (<0.20, 0.21–0.55, and >0.56 mm, respectively; Table 1). Ten days later (03 June), when fish mean size was 11.5 mm, the predation rate on the zooplankton size classes <0.2 mm and 0.2–0.55 mm was detectable but still low (Table 1). Thereafter, the smallest size class of zooplankton always showed a positive response to fish density, that is, a positive slope of the regression line between fish density and net growth rate (Table 1). From 03 June to 07 July, the slopes of the feeding regression for the medium-sized class, consisting mainly of *Bosmina* and

Ceriodaphnia, were significantly different from zero, suggesting that from a size of about 11 mm the 0+ fish were able to feed on this size class. The maximum predation rates on medium-sized zooplankton occurred on 30 June, when the slope was -0.0114 . At 17 June, when the 0+ fish were about 15 mm, they also started feeding on zooplankton larger than 0.56 mm (Table 1).

The experimental data on zooplankton dynamics shows that there was predation, albeit low, on the smallest size class (rotifers and nauplii; <0.2 mm) in mid-May and the beginning of June (Fig. 5). In mid-June, however, the predation rate from 0+ fish was negative, indicating that the smallest size class of zooplankton actually benefited from the presence of 0+ fish. Until the beginning of June, the predation rate from 0+ fish on medium-sized (0.2–0.55 mm) zooplankton was low but then gradually increased (Fig. 5). The abundance of this size class in the lake declined drastically between 03 and 16 June, simultaneously with the onset of 0+ fish predation (Fig. 5). 0+ predation on large (>0.56 mm) zooplankton was not detectable before mid-June, but in mid-July the predation rate from 0+ fish on this size class was about twice as high as on medium-sized zooplankton (Fig. 5). Combining the timing of the relative estimates of 0+ and adult fish feeding for 2005 reveals that the increase in predation rate on zooplankton started in early May for adult fish, whereas

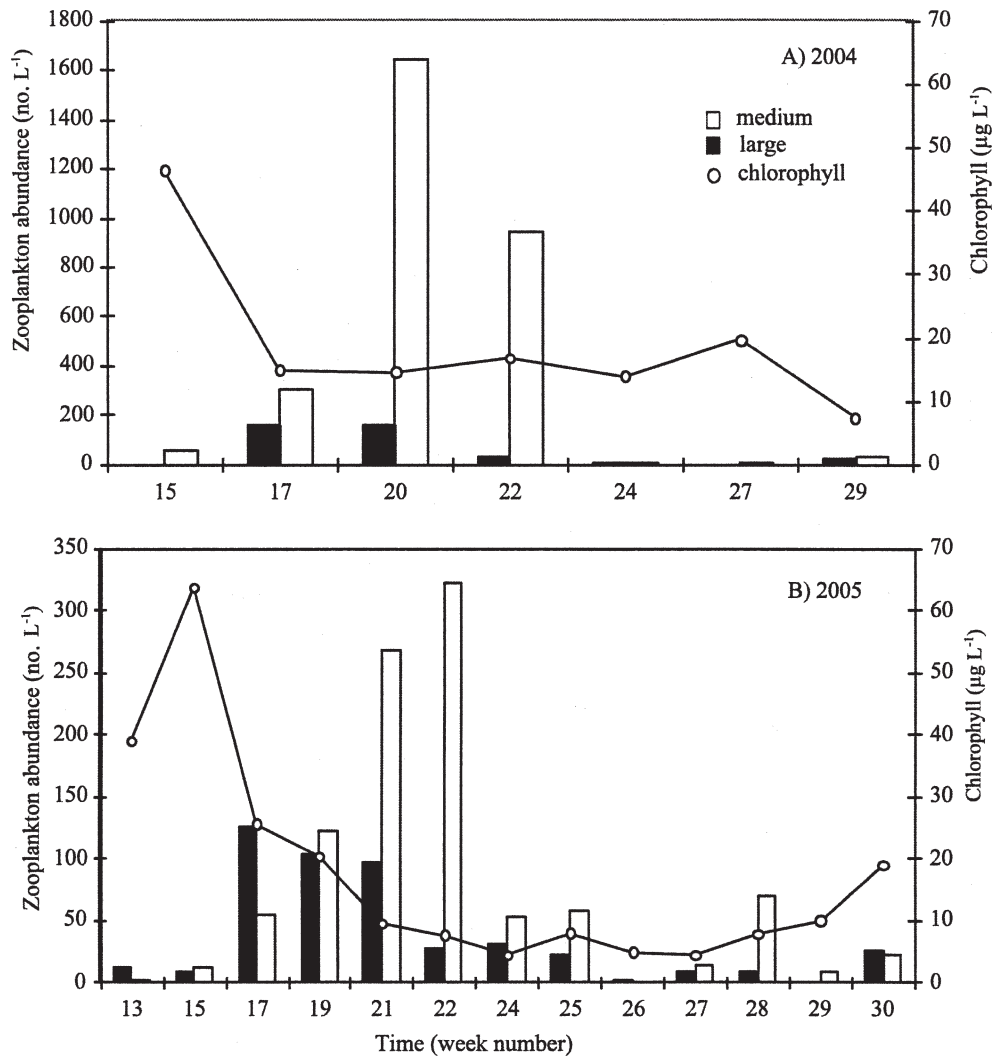


Fig. 2. Spring and early summer development—(A) 2004 and (B) 2005—of medium-sized and large classes of zooplankton (abundance; no L⁻¹) and food resources, expressed as chlorophyll (µg L⁻¹). Week numbers are given on the time axis. In 2004, weeks 15–18 correspond to April, weeks 19–22 to May, weeks 23–26 to June, and weeks 27–29 to July. In 2005, weeks 13–17 correspond to April, weeks 18–21 to May, weeks 22–25 to June, and weeks 26–30 to July.

the 0+ fish predation on medium-sized and large zooplankton was not efficient before early June (Fig. 5). Abundances of both medium-sized and large zooplankton started to increase in late April (Fig. 5). However, while the medium-sized zooplankton continued to become more abundant during early spring, the abundance of larger zooplankton declined already in the beginning of May, simultaneous with the eventual increase in adult fish predation (Fig. 5).

Discussion

The spring period, with strong alterations in temperature-driven processes, such as predation and resource supply, is important in shaping the summer zooplankton community. It should therefore be of crucial importance to focus on this period in order to understand the zooplankton population and community dynamics. In our study, the

fluctuations in abundance of larger zooplankton (>0.56 mm) during early spring were related more to predation rates by adult fish (migrators and stationary) than was the case for medium-sized classes (0.20–0.55 mm), which showed no major decline before the 0+ fish started feeding. A likely explanation is that medium-sized zooplankton are not much affected by adult fish, which select for larger size classes (Brooks and Dodson 1965). Similar results were reported by Cryer et al. (1986), suggesting that adult fish may affect the zooplankton community in early spring, but as soon as the 0+ fish are large enough, they also constitute a major predation risk for zooplankton. This leads to the fact that medium-sized zooplankton are allowed to establish and reproduce in early spring before the 0+ fish have reached a gape size suitable for feeding on this size class. Larger zooplankton, on the other hand, suffer from a high predation rate from adult fish already when temperature starts rising in mid-April, whereas this

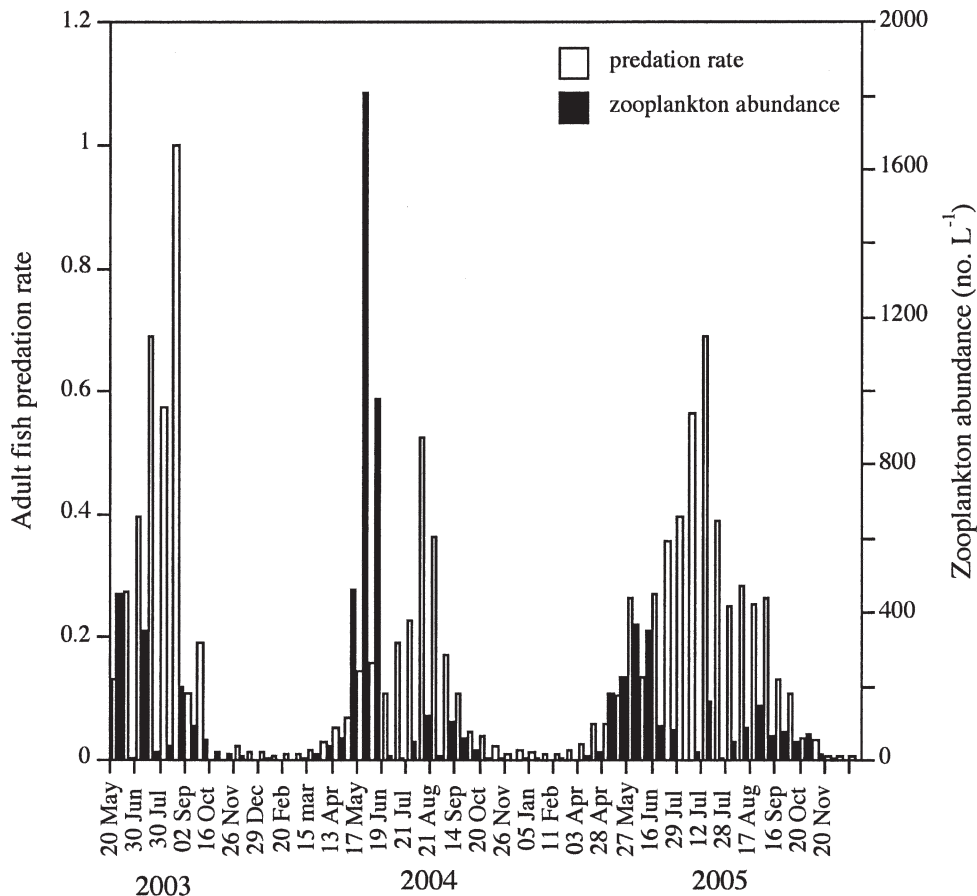


Fig. 3. Relative adult fish predation rate and the total abundance of zooplankton larger than 0.2 mm (i.e., medium-sized and large classes) from 2003 to 2005.

size class of zooplankton was not the major target for 0+ fish before mid-June. Therefore, medium-sized zooplankton should have a temporal refuge from predation until 0+ fish start feeding on them in the beginning of June or mid-June, when water temperature increases above about 15°C (Fig. 1). The period for exponential population growth, that is, when predation is low and resource supply and temperature are high, is therefore longer for medium-sized than for larger zooplankton. In our study this period lasted 49 d (15 April and 03 June) for medium-sized zooplankton but only 13 d (15 and 28 April) for zooplankton larger than 0.56 mm (Fig. 5). Hence, during spring, medium-sized and large zooplankton are “sandwiched” between selective predation from adult (selecting large prey) and 0+ fish (starting with small-sized prey and eventually switching to large). The consequences for the zooplankton community of this temporal variation in predation rate should be that medium-sized zooplankton are less affected by fish predation than larger ones, not only because of size-selective predation by adult fish but also because of a shorter period of, and less pronounced, predation from 0+ fish. This development is also commonly observed in many lakes with high 0+ fish recruitment (Post and McQueen 1987; Hansson et al. 1998; Vakkilainen et al. 2004). It may also be noted that after the decline in zooplankton abundances, neither medium-sized nor large zooplankton populations

recovered (Fig. 5). This may be a result of the accelerating predation pressure from both adult and 0+ fish, of resource depletion, or of a combination of both bottom-up and top-down processes (Gliwicz 2002; Wagner et al. 2004).

Despite the risk of extrapolating laboratory and monitoring data to natural systems, it may be worth performing a thought experiment to test whether the obtained fluctuations in zooplankton abundances could have been caused by fish predation. We calculated the daily maximum roach predation rate in Lake Krankesjön on medium-sized zooplankton to between 5% and 25% and on large zooplankton to between 37% and 52% of the lake standing crop. In addition to this predation pressure from adult fish, the accelerating predation from 0+ fish during spring adds to the mortality rate of zooplankton. Although these calculations are very rough, they show that fish feeding rate is in the same order of magnitude as zooplankton standing crop and that fish predation has the potential to cause the observed population and community fluctuations among zooplankton.

There has been a long-standing controversy whether the zooplankton decline in early summer, marking the breakdown of the clear-water phase, is caused by 0+ fish predation or resource limitation (Luecke et al. 1990; Mehner and Thiel 1999; Hülsmann and Voight 2002). This controversy may partly be a result of the fact that

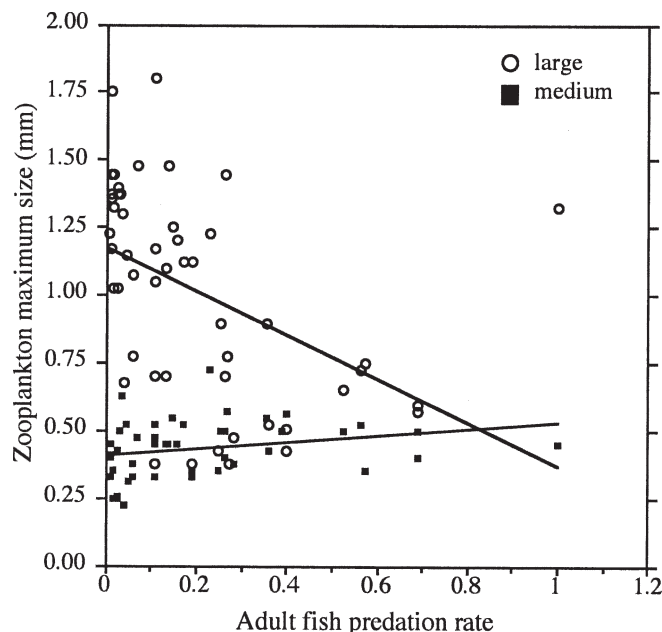


Fig. 4. Relative adult fish predation rate versus the maximum sizes of zooplankton in the size classes 0.2–0.55 mm ($r^2 = 0.07$; $y = 0.125x + 0.407$; $F = 3.759$; $p < 0.05$) and larger than 0.56 mm ($r^2 = 0.21$; $y = -0.8101 + 1.1804$; $F = 12.90$; $p < 0.001$). Note the outlier at the highest value of adult fish predation rate, which is based on one exceptionally large individual calanoid copepod. All other individuals were smaller. The data point is included in the regression.

recruitment of 0+ fish differs between years within lakes as well as among lakes, which, of course, will lead to differences in predation rates on zooplankton. Another reason for the controversy may be difficulties in accurately assessing 0+ fish abundances (Mehner and Thiel 1999). Furthermore, the controversy may be due to the focus on adult *Daphnia* as a response variable since 0+ fish are not able to feed on such large prey before they reach a size of approximately 15–20 mm (about 25 d old). Instead, our study shows that the main effect from 0+ fish may be on smaller herbivores, at least during early spring. Mehner and Thiel (1999) reviewed 18 studies with the aim to assess whether 0+ fish may be a major factor affecting the often observed decline in zooplankton abundance in late spring. The major conclusions from their review were that the smallest 0+ stages may affect abundances of small but not large zooplankton, a conclusion in line with our results. Larger 0+ may, however, have some effect also on larger zooplankton size classes, although other factors, such as low resource supply, cannot be excluded as causing the decline in zooplankton abundance. In order to upgrade the literature basis, we complemented the review by Mehner and Thiel (1999) and also included dominant fish species into the analysis (Table 2). Notable is that the majority (75%; six of eight) of the studies reporting strong impact from 0+ fish on zooplankton dynamics were dominated by cyprinids (roach, bream) or clupeids (gizzard shad), whereas the majority (66%; 8 of 12) of the studies reporting weak effects from 0+ fish were dominated by noncyprinid

fish species (Table 2). These results may be explained by higher foraging efficiency of cyprinids (e.g., roach) than of, for example, perch (Persson 1983). Hence, we may add to the understanding of the controversy regarding the effect of 0+ fish predation on zooplankton by concluding that in lakes where cyprinids are dominant, the impact is likely to be stronger than where other fish groups dominate, given similar abundances.

Studies based on monitoring of natural systems have the strength of pointing out general patterns and suggesting likely scenarios but cannot assess mechanistic relations. Our study, based on long-term monitoring combined with mechanistic laboratory studies, suggests the following scenario regarding the interactions between the zooplankton community and the three components of predation, including 0+, as well as stationary and migrating adult fish: Large zooplankters are strongly affected by size-selective predation from adult fish from early spring throughout the summer. Medium-sized zooplankters, on the other hand, are less affected by adult fish and are therefore almost completely released from predation until the 0+ fish reach a size of about 11 mm and the water temperature is about 15°C. The predation rate from fish on the smallest zooplankton (<0.2 mm), including nauplii and rotifers, is most probably low and occurs only during a short period of the 0+ fish ontogeny.

Despite the fact that predation from fish is likely to be a strong regulating process for the zooplankton spring dynamics, algal food resources most probably also play a role. In our study, the abundance of large zooplankton started to decline simultaneously with the decline in algal chlorophyll, which may indicate that food shortage, in combination with high predation rate, was responsible for the decline of this zooplankton size class. With respect to medium-sized zooplankton, food shortage seems, however, to be a less important regulating factor during spring since the abundance of this size class continued to increase despite a declining algal biomass (Fig. 2). Hence, it may be concluded that it is not predation or resource supply that shape the zooplankton spring dynamics but rather a matter of when and how much, that is, a matter of timing and magnitude (Gliwicz 2002; Hansson et al. 2004; Wagner et al. 2004). Moreover, since the timing of predation rates on different size classes of zooplankton from both adult and 0+ fish are very subtle, occurring on a temporal scale of days, even a minor change in spring mean temperatures may have considerable effects on the zooplankton size and community composition. Although a warmer climate is likely to increase the predation rate on zooplankton (Mehner 2000), fine-scaled predator–prey interactions may also be indirectly affected by other processes, such as temporal mismatch of algal food resources and growth rates of zooplankton, and the overall effect on zooplankton from a global warming perspective may therefore be difficult to predict (Winder and Schindler 2004).

Our study points out interactions between resource supply and predation during the spring period as crucial for the development of zooplankton and phytoplankton communities later in the season. We also show that size-selective predation from adult fish on large size classes of

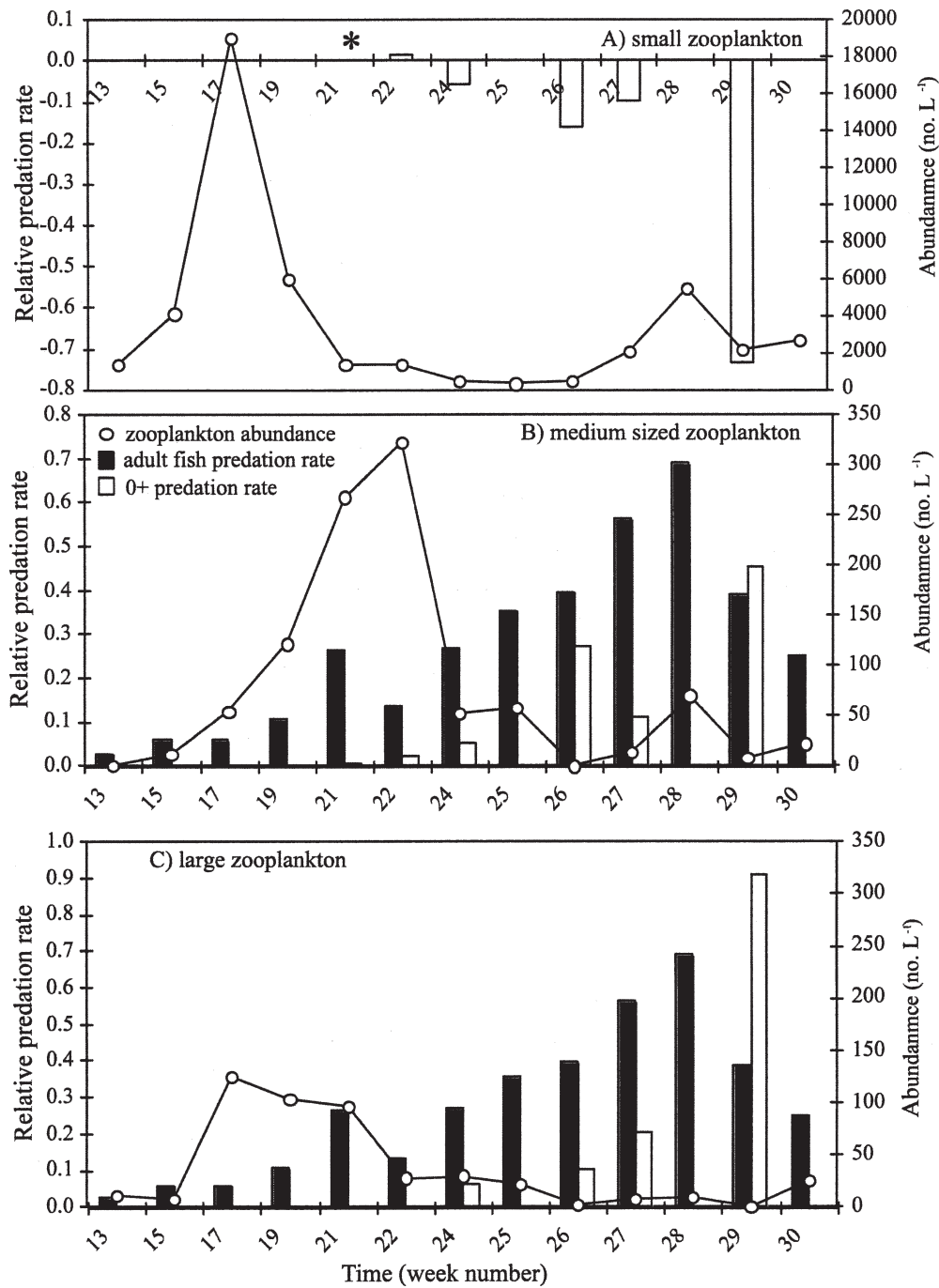


Fig. 5. Spring and early summer development in abundances of zooplankton (line) in Lake Krankesjön divided into size classes smaller than 0.2 mm (rotifers and nauplii), 0.2–0.55 mm (*Bosmina* and *Ceriodaphnia*), and larger than 0.56 mm (calanoid and cyclopoid copepods). Along each time series are also given the relative predation rate from 0+ fish on each of the size classes (white bars). For the medium-sized and large fractions, adult fish predation rate is also shown (black bars). Note that predation rates of adult and 0+ fish cannot be quantitatively compared since total fish biomasses in the lake are unknown. An asterisk (*) in panel (A) denotes that there was a predation rate on small zooplankton that was too low to be visible in the graph. Week numbers are given on the time axis, and weeks 13–17 correspond to April, weeks 18–21 to May, weeks 22–25 to June, and weeks 26–30 to July.

Table 2. Effects (strong or weak) of 0+ fish on zooplankton and suggested reason for decline in zooplankton abundance in early summer. Cyprinid fish species are roach (*Rutilus rutilus*) and bream (*Abramis brama*). Other fish species are perch (*Perca* spp.), sander (*Sander lucioperca*), cisco (*Coregonus* spp.), smelt (*Osmerus eperlanus*), bluegill sunfish (*Lepomis macrochirus*), and gizzard shad (*Dorosoma cepedianum*).

Source	Location	Mean depth	Dominant fish	Suggested reason	0+ effect
Mehner et al. (1998)	Bautzen reservoir, Germany	7.4	Perch, sander	Low food	Weak
Luecke et al. (1990)	Lake Mendota, WI, U.S.A.	12.4	Perch, cisco	Low food	Weak
Hülsmann et al. (1999)	Bautzen reservoir, Germany	7.4	Perch, sander	Low food (0+ pred.)	Weak
Mehner et al. (1997)	Bautzen reservoir, Germany	7.4	Perch, sander	0+	Weak
Mehner et al. (1995)	Bautzen reservoir, Germany	7.4	Perch, sander	Low food	Weak
Mills et al. (1987)	Oneida Lake, U.S.A.	6.8	Walleye, perch	0+	Strong?
Mills and Forney (1983)	Oneida Lake, U.S.A.	6.8	Walleye, perch	0+	Strong
Hülsmann and Mehner (1997)	Experimental enclosures	—	Perch	Low food	Weak
Treasurer (1992)	L. Kinrod, U.K.	1.2	Perch	Low food	Weak
Treasurer (1992)	L. Davan, U.K.	1.5	Perch	Low food	Weak
Boersma et al. (1996)	Tjeukemeer, The Netherlands	1.5	Bream, smelt	Low food	Weak-medium
Dettmers and Stein (1992)	Kokosing Lake, U.S.A.	2.0	Gizzard shad (low)	Adult fish pred.	Weak
Dettmers and Stein (1992)	Knox Lake, U.S.A.	9.6*	Gizzard shad (high)	0+	Strong
Wu and Culver (1994)	Western L. Erie, U.S.A.	—	Perch	Low food	Strong
Bergman et al. (1999)	Lake Ringsjön, Sweden	6.1	Roach, bream	0+	Strong
Persson et al. (2004)	Lake Abbotjärn 2 & 4	2.4 and 7.3	Perch, roach	0+	Strong
Cryer et al. (1986)	Alderfen Broad, U.K.	0.8	Roach	0+	Strong
Vijverberg et al. (1990)	Tjeukemeer, The Netherlands	1.5	Bream, smelt	0+	Strong
Kairesalo and Säppälä (1987)	Pääjärvi, Finland	14.4	Roach	0+	Strong
Welker et al. (1994)	L. Shelbyville, U.S.A.	18.0*	Gizzard shad, bluegill	0+	Strong

* Denotes that the given depth is the maximum depth.

zooplankton in combination with 0+ fish predation on somewhat smaller zooplankton size classes during spring are likely to cause the crash of the zooplankton community, which opens up for an expansion of phytoplankton and, ultimately, for the termination of the clear-water phase.

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