Density dependent growth and size specific competitive interactions in young fish

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Body size is a major determinant affecting an individual's performance. In this study, four factors affecting an organism's competitive ability as related to body size: the attack rate, the maximum growth capacity, the metabolic demands and the size spectrum of available resources, were investigated for small stages of Eurasian perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*). The size dependence of the attack rate on a 0.5-mm cladoceran zooplankton of larval and juvenile perch was estimated and compared with the results from similar experiments for roach. At equal body sizes, roach always had a higher attack rate than perch. In contrast the reverse was the case for maximum growth capacity. The maintenance requirements at the same size were higher for perch than for roach. Based on the above data we were able to gain a mechanistic understanding of the outcome of two field enclosure competition experiments, one between perch larvae and 1-yr-old roach and one between perch larvae and roach larvae. In the first experiment, we found strong intraspecific density dependent growth in perch larvae, while the presence of 1-yr-old roach had no effect on perch larvae growth. High perch densities had strong negative effects on the zooplankton resource. Due to the larger size of 1-yr-old roach and consequently higher metabolic demands, 1-yr-old roach showed a stronger negative response in growth to high perch larvae densities than perch despite roach's higher attack rate on zooplankton. In the second experiment, perch larvae were negatively affected by high densities of roach larvae and had a reduced growth at high intraspecific densities. In contrast, the growth of roach larvae was not affected by perch larvae or high intraspecific densities. This difference between species could be related to the simultaneous lower attack rate and higher growth capacity of perch, leading to a higher sensitivity in growth of perch than of roach to decreasing resource levels. Temporal variation in competition intensity was present in both experiments. This variation could be related to the foraging efficiencies and different growth capacities of the competitors and the species composition and size structure of the zooplankton resource. Our study points to the potential for both intra- and interspecific competitive interactions in fish larvae in freshwater systems. Our results also suggest that species specific differences in how foraging, growth and food processing capacities relate to body size are of vital importance for interactions in ecological communities.

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Competition between individuals through similar use of limited resources has profound effects on individual growth rates, survival and fecundity and thus affects overall community dynamics (Connell 1983, Schoener 1983, Persson 1986, 1988, 1990, Olson et al. 1995, Byström et al. 1998). The competitive ability of an

individual is basically a function of two components: the per capita capacity to deplete shared resources (effect) and the ability to have a positive growth at low densities of resources (response) (Aarssen 1983, Persson 1985, Goldberg and Landa 1991, Werner 1994). The probably most important trait, affecting competitive

interactions is body size (Persson 1985, Werner 1988, 1994, Gliwicz and Lampert 1990). In size-structured populations individual body size can vary up to five orders of magnitude, leading to complex competitive interactions both within and between size structured populations (Neill 1975, Werner and Gilliam 1984, Persson and Greenberg 1990a, Werner 1994). Both foraging efficiency and metabolic demands depend on body size and because species differ in ontogenetic development rates and growth trajectories, competition is often asymmetric between species and within size classes of species, and may also change with body size and time (Persson 1987a, b, Wilbur 1988, Persson and Greenberg 1990a, Werner 1994).

In fish, the first year of life is the most dynamic phase, with rapid size development (increase in mass up to three orders of magnitude) and dramatic changes in morphology and foraging capacities (Miller et al. 1988, Noakes and Godin 1988, Werner 1988, Osse 1990). During early ontogeny most fish have a stage when they more or less exclusively feed on zooplankton (Post and Kitchell 1997). For some species, this stage is very transient, while for others it lasts for months to years and some species spend their entire life as zooplankti-vores (Werner 1986, Persson 1988, Olson et al. 1995, Mittelbach and Persson 1998). In temperate waters, the majority of fish larvae hatch during spring. During this period, the potential for complex intra- and interspecific competitive interactions both with larger zooplankti-vores and with other larval fish species for a shared zooplankton resource may be high. This potential for multifold competitive interactions during larval stages contrasts with the scarcity of studies on competitive interactions that have been directed towards these stages (but see Cushing 1983, Fortier and Harris 1989, Pope and DeVries 1994, Welker et al. 1994). This is a major weakness in current ecological research as it has been suggested that rather small changes in growth rates during the larval stage may have profound effects on subsequent survival (Houde 1987, Luecke et al. 1990). The otherwise well studied interaction between perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) is no exception to the rule of few experimental studies directed towards larval stages. However, a recent replicated whole-lake experiment suggested that the presence of $\geq$ 1-yr-old roach has no effect on the growth of larval perch (but on juvenile perch) (Byström et al. 1998).

In this study we explore, intra- and interspecific competitive interactions among larval perch, larval roach and 1-yr-old roach. We carried out two field enclosure experiments to answer the following questions: 1) Do perch larvae exhibit intraspecific density dependence in individual growth and survival over realistic density ranges? 2) Do perch larvae compete with roach of different size classes (larvae and 1-yr-old) for resources? 3) If so, how does the outcome of competi-tion (in terms of growth and mortality responses) depend on the body size and foraging efficiencies of the competitors? To analyse the last question more rigor-ously we performed laboratory trials to estimate the size dependence of the attack rates of larval perch and compared these with similar experiments carried out for roach. These results were then used to calculate the competitor's energetic maintenance requirements and combined with competitor diets, available zooplankton resources and literature data on growth capacities, this enabled us to gain a mechanistic understanding of the outcome of our enclosure experiments.

System studied

Perch and roach are found over most of Eurasia and are the numerically dominant fish species in many lakes (Svärdson 1976, Johansson and Persson 1986). The perch–roach interaction is characterized by a mixture of competitive and predatory processes (Persson 1988, Persson et al. 1991). Perch larvae hatch in the littoral zone and shift soon after hatching to the pelagic zone where they feed predominantly on zooplankton (Gu-ma'a 1978, Treasurer 1988, 1990, Wang and Eckmann 1994). They gradually develop into juveniles and at a size of approximately 20 mm they shift habitat and become more littoral, but continue to feed mainly on zooplankton (Craig 1978, Guma'a 1978, Coles 1981, Persson 1987c, Treasurer 1988, 1990, Byström et al. 1998). As perch grow, they potentially undergo two ontogenetic niche shifts, first from feeding on zooplank-ton to feeding on macroinvertebrates and second from feeding on macroinvertebrates to feeding on fish (Persson 1988). Roach undergo less dramatic shifts in diet during their ontogeny, from feeding on zooplank-ton as larvae and juveniles and zooplankton, macroin-vertebrates, algae and plant material as adults and gradually exhibit a shift to become more pelagic in terms of habitat use (Persson 1983, 1988, Rheinberger et al. 1987).

Material and methods

Field experiments

We conducted two field enclosure experiments in order to examine intra- and interspecific competitive interac-tions between perch larvae and 1-yr-old roach and between perch larvae and roach larvae. The experi-ments were carried out in 1996 in a small unproductive lake (Lake Abborrtjärn 3), situated in central Sweden (64°29'N, 19°26'E). Detailed information on the lake is given in Persson et al. (1996). Each of 32 enclosures was built as follows. An iron ring with a diameter of 1.6 m was attached to the interior of the wood frame (2 × 2

m) with attached polystyrene floating devices. The ring held a plastic (polyethylene) transparent bag sealed at the bottom with a diameter of 1.6 m, a depth of 9 m and was anchored to the bottom with a weight. The total volume of the bag was 18 m^3 and the water volume above the thermocline was never less than 8 m^3. Shortly after the break-up of the ice (10–12 May), the enclosures were placed in the lake and filled (16–19 May) with unfiltered lake water. The enclosures were placed in rows of four (0.5 m apart), the distance between rows was approximately 7 m and each row was oriented in an east–west direction. To ensure that a natural community of zooplankton developed in the enclosures before the start of the experiment, each enclosure was inoculated on 29 May with a filtered sample of zooplankton from the lake corresponding to a volume of 1000 l of lake water.

Experiment I

This experiment was designed to examine density dependent growth of larval perch and the competitive interaction between perch larvae and 1-yr-old roach. We randomly assigned 16 enclosures to the eight treatment combinations of a factorial design with two factors: perch density (7, 15, 30 or 60 individuals per enclosure corresponding to 3.5, 7.5, 15 or 30 individuals/m^2) and roach presence/absence (presence with two 1-yr-old roach per enclosure, corresponding to 1 roach/m^2). Each treatment was replicated twice. The chosen densities of perch larvae were within the range found in different lakes (Coles 1981, Treasurer 1988, Byström et al. 1998). The chosen density of 1-yr-old roach corresponds to densities in lakes of similar productivity as the experimental lake (M. Appelberg unpubl.).

Experiment II

This experiment was designed to reveal differences in the response of perch and roach larvae to intraspecific and interspecific competition (Underwood 1986, Morin and Johansson 1988). We used a design with four treatments: 20 perch (10/m^2) only; 20 roach only; 10 perch (5/m^2) + 10 roach (5/m^2) and 20 perch + 20 roach. All treatments were replicated four times and we randomly assigned the four enclosures in one row to the four treatments.

Egg strands of perch were collected from two lakes in the vicinity of Umeå and perch larvae were hatched between 2–3 June in laboratory tanks. Perch larvae were fed with a mixture of zooplankton from a nearby pond in Umeå until transfer to the enclosures. Newly hatched roach larvae were caught with a scoop net along the shore line in a lake close to Umeå on 9 June. 1-yr-old roach were collected in late May by electrofishing in a lake close to Umeå and kept in a large outdoor holding pond. Perch larvae (6.4 ± 0.06

mm, 0.84 ± 0.03 mg, mean ± 1 SE, $n = 20$) and 1-yr-old roach (28.4 ± 0.30 mm, 0.15 ± 0.01 g, $n = 44$) were introduced to the enclosures on 5 June and roach larvae (6.0 ± 0.04 mm, 0.67 ± 0.02 mg, $n = 20$) were introduced on 10 June. With respect to hatching patterns, this procedure simulates the natural conditions in lakes in the experimental region, where perch hatch during the first week of June and roach appear free-swimming approximately one week later (P. Byström unpubl.). Fish in the two experiments were sampled on 23 June and 14 July with a large dipnet (diameter 1.6 m). The first haul always caught approximately 75% of the recovered fish and the hauling was ended when two subsequent hauls had resulted in no captures. The fish sampled on 23 June were all withdrawn from the enclosures and preserved (see below). On 24 June new similarly sized fish were introduced into the enclosures at the same densities as at the start of the experiment. Perch larvae (13.8 ± 1.3 mm, 17.1 ± 5.2 mg, $n = 51$) from the first introduction were cultivated in tanks and additional individuals were caught with a scoop-net in a pond close to Umeå. New roach larvae (9.9 ± 1.0 mm, 3.6 ± 1.9 mg, $n = 49$) were caught with a scoop-net from the same lake as in the first sampling occasion. Finally, 1-yr-old roach (30.8 ± 0.46 mm, 0.20 ± 0.01 g, $n = 37$) were taken from the large outdoor holding pond.

Sampled fish were preserved in Lugol's solution and in the laboratory measured to the nearest 0.1 mm (total length) and, after being blotted dry, weighed to the nearest 0.1 mg (wet weight). Stomach contents (whole gut for roach) were identified to suborder, family or genus. If possible, 10 prey of each category were measured. Lengths of prey were transformed to dry weights by using weight-length relationships (Dumont et al. 1975, Bottrell et al. 1976 for zooplankton and Persson and Greenberg 1990b for macroinvertebrates). The stomach contents of 15 (all if fewer) perch and all 1-yr-old roach were analysed from the density dependence experiment. From the experiment with perch and roach larvae, the stomach content of 10 individuals (all if fewer) of each species were analysed.

Zooplankton were sampled with a 100-μm-mesh net (diameter 250 mm) drawn at a speed of 0.5 m/s on three occasions (4 June, 23 June and 13 July). Zooplankton were sampled from the thermocline to the surface and preserved in Lugol's solution. In the laboratory, animals were counted and classified to suborder, family or genus and the body lengths of 15 individuals (all if fewer) of each category from each sample were measured. Lengths were transformed to biomass using regressions relating length to dry weight (Dumont et al. 1975, Bottrell et al. 1976). The water temperature in the enclosures during the experimental period increased from 14°C at the start of the experiments to 17.5°C at the end of the experiment.

Laboratory foraging experiments

Perch used in the experimental trials were hatched from egg strands collected from lakes close to Umeå, central Sweden. The smaller size classes used (14, 19, and 25 mm, weight range 0.016–0.15 g) were raised in two large tanks (600 l) and were fed a natural zooplankton mixture collected from a nearby pond in Umeå. Larger size classes (30, 35, 40 and 45 mm, weight range 0.30–0.87 g) were cultured in large outdoor holding ponds and caught with a large scoop-net. The largest size class of perch (75 mm, 3.3 g) was elecrofished in Lake Abborrtjärn 3 (see Field experiments above). After capture, the larger size classes of perch were held for three days in the same holding tanks and fed with the same natural zooplankton mixture as the smaller size classes before experiments started. Approximately 16 h before the experiments started, perch were transferred to 20-l holding aquaria without food in order to acclimatize the animals and standardize hunger levels between experiments. The temperature in holding and experimental aquaria was 19°C and a 20-W fluorescent tube was placed 15 cm above the water surface. The bottom colour of each aquarium was black and the back and side-walls were pale green. Feeding experiments were carried out with one size class of *Bosmina* (0.53 ± 0.03 mm, mean ± 1 SE) at five densities (1, 2, 4, 8, and 16 ind./l). For all size classes of perch, each feeding trial lasted between 6 and 60 s. The desired *Bosmina* density was established in the experimental aquarium (20 l) and one perch (size classes 14–45 mm) was then gently introduced into the aquarium. Perch almost immediately started to feed (normally between 5 and 20 s) and perch that did not start feeding after 45 s were discarded from further analyses. For the largest size class (75 mm), the experimental procedure was changed, as these perch were more sensitive to disturbance. Two perch (focal perch and companion) were introduced into the aquarium 1 h before experiments started. The reason for having two perch in the aquarium was that perch became less stressed and also started to feed faster in the presence of a conspecific. The desired *Bosmina* density was gently introduced from above into the aquarium. Focal perch that did not start feeding within 45 s were discarded from further analyses.

After that perch had consumed one prey, the capture rate was estimated by visually recording the time to consume 5 (14-mm perch) or 7 *Bosmina* (all other size classes). If less than 5 or 7 prey were consumed during a 60-s trial, the number consumed during that time period was used. Trials where fish were not displaying pelagic feeding behaviour (e.g. feeding in the corners of the aquarium) were discarded. Each density-size combination was replicated five times and no fish were used more than once. A type II Holling's functional response equation was fitted to the relationship between capture

rate and zooplankton density using nonlinear regression techniques (see Persson 1986, 1987a). The following equation were fitted to the data on attack rates of differently sized perch (additional data for perch were obtained from Persson and Greenberg 1990c) and roach (J. Hjelm unpubl.):

$$a(w) = A\left[\frac{w}{w_0}\exp\left(1 - \frac{w}{w_0}\right)\right]^\alpha \tag{1}$$

where $a(w)$ is the attack rate at weight w, A is the maximum attack rate, w_0 is the body weight at maximum attack rate and α is the rate of initial increase in attack rate with body size (see Persson et al. 1998). The general shape of eq. (1) is hump shaped with maximum at w_0. As the experiments focused on small stages, we restrict our presentation of data to fish weights below 3.5 g. The maintenance requirements of differently sized fish in terms of resource density were calculated by setting energy gain (capture rate × prey weight × assimilation efficiency) minus metabolic requirements equal to zero, assuming 12 h/d spent foraging. Capture rate was described by a type II functional response function, where attack rate was taken from eq. (1) and handling time was taken from Lessmark (1983). Metabolic data (at 19°C) were for perch obtained from Claesson et al. (unpubl.) and for roach obtained from Persson et al. (1998).

Data on maximum specific growth rates (G_w) of roach were derived from Keckeis and Schiemer (1992). We were only able to find two values for the maximum specific growth rate in perch at weights below 1 g: at 1.8 mg (Wang and Eckmann 1994) and at 1 g (Lessmark 1983). We therefore included complementary field data from our experimental lakes on larval perch growth in the size interval between those two data points (Byström et al. 1998). The lake growth data should be regarded as conservative and is probably an underestimate of the growth capacity of perch larvae. Total metabolic mass (a measure of total energy requirements) in one enclosure in the middle of each experimental period of perch and 1-yr-old roach was calculated as $n \times W^{0.77}$ where n is the number of fish at the start of the experimental period, W equals mean weight over the experimental period and 0.77 is the metabolic exponent, see Persson et al. (1998).

Statistical analyses

All analyses were performed on enclosure means. Most data were analysed with repeated-measures analysis of variance (ANOVA) and regression analysis. The sphericity assumption of univariate repeated-measures designs similar to homoscedasticity, was satisfied (Bartlett and Mauchly tests, $P > 0.05$) when it was possible to test it. In some cases in the competition

experiment between perch and roach larvae, we also used standard ANOVAs. Weights were log-transformed and proportions were arcsine square root transformed because homoscedasticity and linearity were clearly improved. All factors of linear models were considered as fixed effects (i.e. model I). The survival analysis of 1-yr-old roach was, due to the bounded distribution of the response variable, analysed with a generalized linear model, using binomial errors with the total number of surviving roach as the binomial denominator. To compensate for overdispersion (McCullagh and Nelder 1989), we implemented the method of Williams (1982) before the analysis.

Results

Experiment I. Density dependence and competition with 1-yr-old roach

Zooplankton resources
The total zooplankton biomass and the biomasses of the most abundant zooplankton taxa decreased as a function of perch density and time (Fig. 1, Table 1). Total zooplankton biomass tended to decrease in the presence of roach but no species or categories apart from copepod nauplii (a decrease with roach presence) showed any significant effect (Table 1). We therefore pooled data from roach present/absent treatments in Fig. 1 and partly in Fig. 2. On 23 June, there was no effect of perch density on total zooplankton resources (linear regression, $r^2 = 0.069$, $F_{1,14} = 1.04$, $P = 0.32$). However, on 23 June, *Holopedium* was not included in the diet of perch because perch were still gape-limited at that time (see Results: diet and Discussion). When *Holopedium* was excluded from the analysis, a negative effect of increasing perch density on available zooplankton was present (linear regression, $r^2 = 0.32$, $F_{1,14} = 6.54$, $P = 0.023$). Cyclopoid copepods were the only abundant prey category that decreased over time at all perch densities. *Holopedium* increased with time at low perch densities but was almost absent in high perch densities (Table 1, time × perch density interaction). Among the less abundant zooplankton categories, *Ceriodaphnia* decreased with increasing perch density and *Daphnia* decreased with time in all densities whereas copepod nauplii increased with time in all treatments (Table 1, biomasses too low to be visible in Fig. 1).

Diets
In June, perch larvae at all densities fed mainly on cyclopoid copepods, copepod nauplii and *Bosmina*. The diet of 1-yr-old roach in all treatments consisted mainly of *Bosmina* and *Daphnia* in spite of *Daphnia* being very rare in our enclosures (Fig. 2). Although present in the enclosures in June, *Holopedium* was not eaten by perch larvae nor 1-yr-old roach (Fig. 2). Although cyclopoid

copepods were the most abundant zooplankton, they were rarely included in the diet of 1-yr-old roach in June (Fig. 2). In July, the diet of perch larvae at low perch densities changed to become dominated by *Holopedium*, whereas the diet of perch larvae at high perch densities was dominated by *Bosmina* (Fig. 2, Table 1). There was also an increase of *Daphnia* and a decrease of nauplii in the diet of perch (Fig. 2, Table 1). In July, cyclopoid copepods were very rare in the enclosures, but were still included in the diet of perch (Fig. 2). The diet of 1-yr-old roach in July consisted mainly of *Holopedium* at low perch densities and of chironomids at high perch densities (Fig. 2, Table 1).

Growth
The growth of perch larvae was strongly intraspecific density-dependent, especially in July (Fig. 3a, b), while the presence of 1-yr-old roach did not affect perch growth (repeated-measures ANOVA: roach presence $F_{1,8} = 0.96$, $P = 0.35$, roach × perch density; $F_{3,8} = 0.34$, $P = 0.79$, time × roach $F_{1,8} = 0.00$, $P = 0.96$, Fig. 3a, b).
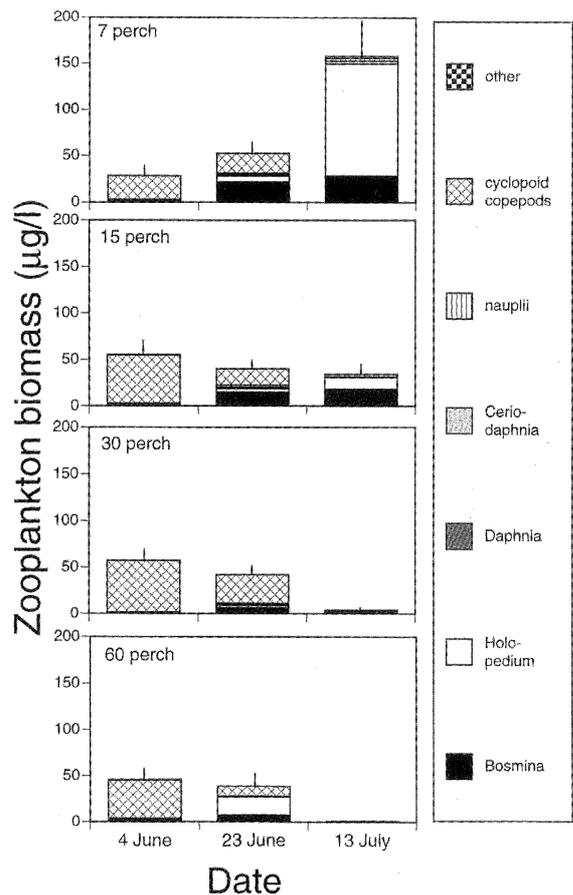

Fig. 1. Zooplankton biomasses (mean + 1 SE, for total biomass) at different densities of perch larvae on 4 June (start of the experiment), 23 June and 13 July. Roach absence and presence treatments have been collapsed to one figure.

Table 1. Repeated-measures ANOVAs (*F*-values) of 1) the effects of perch larvae density, 1-yr-old roach presence and time on the zooplankton community (total biomass of zooplankton and biomass by zooplankton group, log-transformed), 2) the effects of perch larvae density, 1-yr-old roach presence and time on the diet of perch (mean proportion of biomass of food categories, arcsine square root transformed) and 3) the effects of perch density and time on the diet of 1-yr-old roach (mean proportion of biomass of food categories, arcsine square root transformed). Significance level: $^+ = 0.05 < P \leq 0.1$; $* = 0.01 < P \leq 0.05$; $** = 0.001 < P \leq 0.01$; $*** = P \leq 0.001$. n.f. = food category not found in the diet of 1-yr-old roach.

Source of variation	df	Total biomass	*Bosmina*	*Holopedium*	*Daphnia*	*Ceriodaphnia*	Copepod nauplii	Cyclopoid copepods	Other	Chironomidae
Zooplankton										
perch density	3,8	15.5***	10.7**	11.6**	0.27	4.93*	14.3***	0.94	0.82	–
roach	1,8	4.50+	0.75	1.15	1.44	0.73	6.51*	0.47	0.13	–
perch density × roach	3,8	1.66	0.82	1.87	0.38	0.50	0.60	1.40	3.92+	–
time	2,16	30.4***	30.3***	18.7***	13.8***	2.37	14.6***	88.0***	18.8***	–
time × perch density	6,16	21.3***	3.98*	11.4***	2.11	1.43	3.40*	1.26	0.82	–
time × roach	2,16	0.32	1.46	0.22	2.52	0.53	0.25	0.06	0.13	–
time × perch density × roach	6,16	0.63	0.68	1.04	1.63	0.24	0.38	0.70	3.92*	–
Perch diet										
perch density	3,8	–	1.33	19.6***	1.63	0.55	1.61	0.19	0.26	0.51
roach	1,8	–	1.73	0.08	0.08	0.81	1.04	0.07	0.71	0.77
perch density × roach	3,8	–	0.51	0.07	1.38	0.12	2.04	0.72	1.34	1.65
time	1,8	–	2.68	120.9***	19.8**	4.86+	6.65*	97.2***	0.10	4.19+
time × perch density	3,8	–	7.50**	19.6***	0.37	0.88	1.42	6.88*	0.45	0.51
time × roach	1,8	–	0.09	0.08	2.42	0.10	0.00	0.16	0.83	0.77
time × perch density × roach	3,8	–	0.64	0.07	2.25	0.53	0.19	0.76	0.80	1.65
Roach diet										
perch density	3,2	–	0.93	1.05	0.81			0.43	0.44	43.9*
time	1,2	–	1.75	2.52	2.41	n.f.	n.f.	0.26	0.33	364.5**
time × perch density	3,2	–	0.47	1.05	0.31			0.17	0.44	43.9*

The growth of 1-yr-old roach was negatively affected by perch density in July but not in June (Fig. 3c, d). At the lowest perch density (7 individuals), roach had similar growth in June and July whereas roach had a lower growth in July than in June at the higher perch densities (Fig. 3c, d). At the highest perch density, roach had almost no growth in July. In contrast, perch increased more than twofold in weight even at the highest perch density (Fig. 3b, d). The growth rate of roach was thus lower during the second time period, which is the opposite pattern to that found for perch. Two replicates, one with 30 perch and one with 60 perch had no surviving roach in July at the end of the experiment. However, perch still had a positive growth in the enclosures with high perch density where roach had survived (Fig. 3b, the lowest data points for the 30- and 60-perch density treatments).

Survival

The survival of larval perch was high (range: 83–100% in June and 63–92% in July) and neither perch density nor 1-yr-old roach presence had any effect on the survival of perch (repeated-measures ANOVA: perch density; $F_{3,8} = 1.67$, $P = 0.25$, roach presence; $F_{1,8} = 1.06$, $P = 0.33$). There was no effect of perch density on 1-yr-old roach survival in June (range; 75–100%) (Generalized linear model, $\chi^2 = 0.004$, df = 1, $P = 0.95$). In July 1-yr-old roach survival tended to be negatively affected by increasing perch density (100, 75, 50 and 25% for the 7, 15, 30 and 60 perch densities, respectively) (Generalized linear model, $\chi^2 = 3.09$, df = 1, $P = 0.079$). There was, however, at the latter sampling date a high between replicate variation.
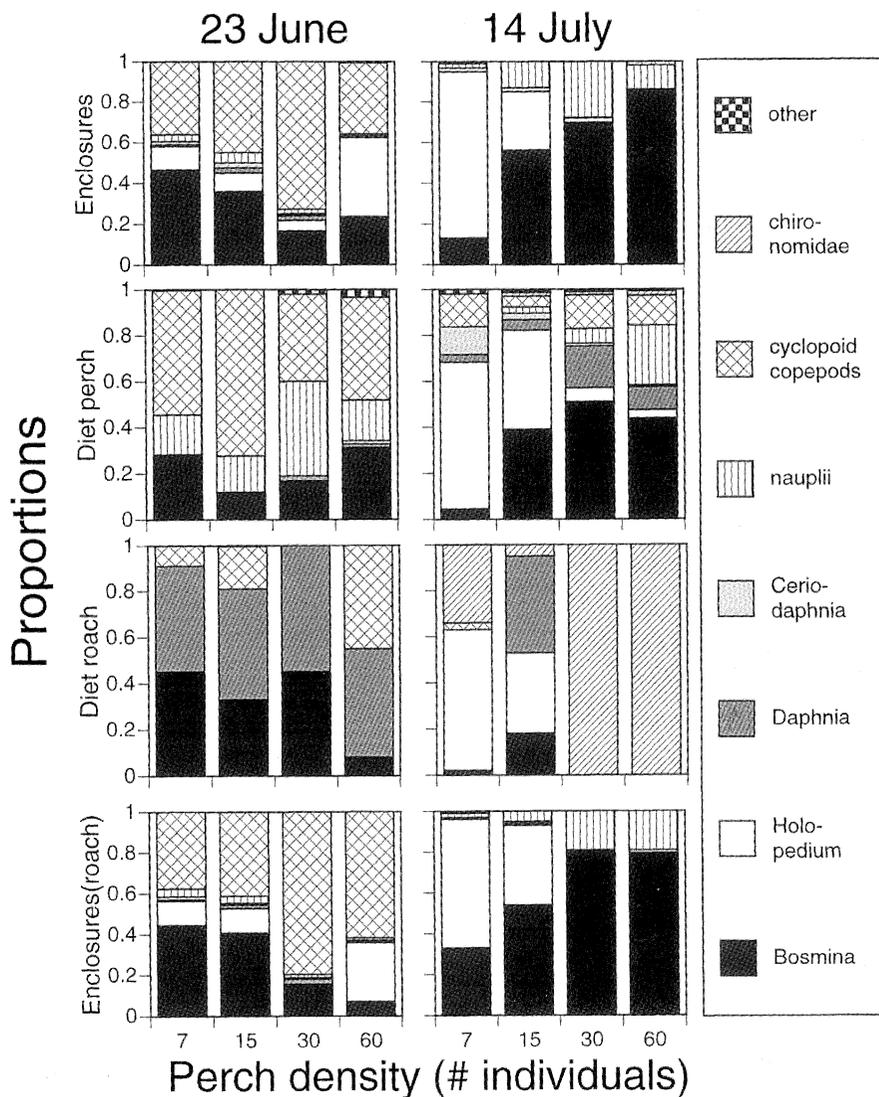

Fig. 2. Diet (mean proportion of biomass) of perch larvae and 1-yr-old roach and relative zooplankton biomasses in the enclosures on 23 June and 14 July. The two top panels are relative zooplankton biomasses and the diets of larval perch both collapsed for absence/presence treatments of roach. The two bottom panels are the diet of roach and relative zooplankton biomasses in the roach presence treatments only.
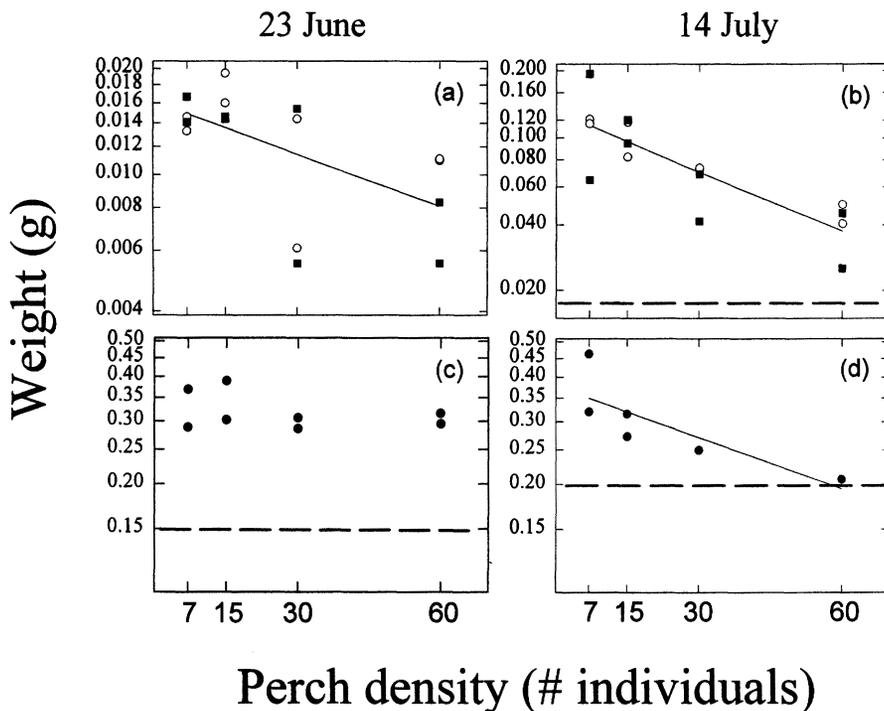
23 June

14 July

Fig. 3. Mean weight of perch larvae on (a) 23 June and (b) 14 July as a function of perch density in the different treatments (filled squares: roach presence, open circles: roach absence) and mean weight of 1-yr-old roach in the different perch densities on (c) 23 June and (d) 14 July. Regression analysis (weight, log-transformed): a) perch larvae, June ($r^2 = 0.35$, $F_{1,14} = 7.59$, $P = 0.016$), b) perch larvae July ($r^2 = 0.69$, $F_{1,14} = 31.7$, $P = 0.0001$), c) 1-yr-old roach, June ($r^2 = 0.12$, $F_{1,6} = 0.81$, $P = 0.40$) and d) 1-yr-old roach, July ($r^2 = 0.68$, $F_{1,4} = 8.31$, $P = 0.045$). Dashed lines show initial weights (at the introduction to the enclosures).

Weight (g)

Perch density (# individuals)

Experiment II. Competition between perch and roach larvae

Zooplankton resources

Total zooplankton biomass and the biomasses of the dominant zooplankton groups (*Holopedium* and *Bosmina*) decreased strongly over time at high perch and high perch/roach densities (Fig. 4, Table 2). In contrast, total zooplankton biomass, *Holopedium* and *Bosmina* biomasses increased over time at high roach and low perch/roach densities. Cyclopoid copepods were the only dominant prey that decreased over time in all perch treatments but were still abundant in the treatment with only roach (Fig. 4). Among the less abundant zooplankton categories, *Ceriodaphnia* were negatively affected in all treatments with perch, *Daphnia* decreased with time, whereas copepod nauplii increased with time in all four treatments (Table 2, biomasses too low to be visible in Fig. 4). Overall, roach larvae had a lower effect on the abundance of zooplankton than perch larvae. Although large effects on biomasses were present, the relative composition of the zooplankton was similar among treatments with the exception that cyclopoid copepods were relatively more abundant in the roach only treatment (Fig. 5).

Diets

There were no treatment effects on the diet of perch larvae except that *Ceriodaphnia* were eaten less in the low perch/roach treatment (Table 2, Bonferroni post

hoc test, $P < 0.05$). In June, the diet of perch larvae in all treatments consisted mainly of cyclopoid copepods, with *Bosmina* as the second most important prey item (Fig. 5). At the same time, the diet of roach larvae in all treatments consisted mainly of *Bosmina* and copepod nauplii. Although present in the enclosures, *Holopedium* was only occasionally found in the diets of perch and roach larvae in June. In July, the diet of perch larvae changed to be dominated by *Holopedium*, *Bosmina* and cyclopoid copepods (Fig. 5, Table 2). Cyclopoid copepods were very rare in our enclosures in July, but still important in the diet of perch. The diet of roach larvae was mainly composed of *Holopedium*, *Bosmina* and copepod nauplii in July (Fig. 5). In July roach consumed less *Holopedium* in the high perch/roach density treatment than in the other treatments (Fig. 5, Table 2, Bonferroni post-hoc test, $P < 0.05$). With respect to taxonomic composition, diet overlap between perch and roach larvae was low in June but high in July (Fig. 5). However, with respect to prey size diet overlap was low concerning *Holopedium*, which was the largest dominant prey taxa in our enclosures in July. Perch larvae consumed most of the available size range of *Holopedium*, whereas roach larvae only consumed the smallest *Holopedium* (Fig. 6).

Growth

Over the whole larval period the growth of perch was much higher than that of roach (Fig. 7). The growth of

perch larvae varied among treatments (Fig. 7, repeated-measures ANOVA: treatment, $F_{2,9} = 6.69$, $P = 0.017$; time × treatment, $F_{2,9} = 1.50$, $P = 0.27$). In June, the growth of larval perch was lower at the high perch/roach density than at high perch and low perch/roach density where growth was similar (Fig. 7, one-way ANOVA: $F_{2,9} = 6.4$, $P = 0.019$). In July, there was a tendency for the growth of perch to be negatively affected by high intraspecific density, whereas roach had no effect on perch growth (Fig. 8, one-way ANOVA: $F_{2,9} = 3.29$, $P = 0.085$). By contrasting the low perch/roach versus the high perch and high perch/roach treatments this tendency became significant ($t = 2.60$, df = 10, $P = 0.026$). The growth of roach larvae was similar in all treatments (Fig. 7, repeated-measures ANOVA: treatment, $F_{2,9} = 1.0$, $P = 0.39$; time × treatment, $F_{2,9} = 0.63$, $P = 0.54$).

Survival

The overall survival was higher for perch ($87 \pm 2\%$, mean ± 1 SE, range: 60–100%, average over both experimental periods) than for roach ($74 \pm 3.5\%$, range: 30–100%) (repeated-measures ANOVA: species, $F_{1,22} = 7.58$, $P = 0.012$; time × species, $F_{1,22} = 0.06$, $P = 0.81$; time, $F_{1,22} = 0.62$, $P = 0.44$). There were no effect of treatment or time on the survival of neither perch larvae (repeated-measures ANOVA: treatment, $F_{2,9} = 1.98$, $P = 0.19$; time × treatment, $F_{2,9} = 2.44$, $P = 0.14$; time, $F_{1,9} = 0.107$, $P = 0.33$) nor roach larvae (repeated-measures ANOVA: treatment, $F_{2,9} = 0.36$, $P = 0.71$; time × treatment, $F_{2,9} = 0.68$, $P = 0.53$; time, $F_{1,9} = 0.10$, $P = 0.76$).

Size dependent attack rate, maintenance requirements and maximum growth

The attack rate of perch on *Bosmina* increased with size (Table 3) to reach maximum at a weight of 1.55 g (length of 56 mm) (Fig. 8a). The difference between perch and roach in attack rate on *Bosmina* increased with size, with perch having a lower attack rate than roach for most sizes investigated (Fig. 8a). For a given size, the critical resource level was always higher for perch than for roach (Fig. 8b). Perch had a lower critical resource level than 1-yr-old roach but a higher critical resource level than larval roach at the end (14 July) of our experiments (Fig. 8b). In experiment I, the resource levels at high perch densities decreased to levels similar to the critical levels for both perch and 1-yr-old roach (Fig. 8b). With respect to growth capacity the pattern was reversed, with perch having a higher growth capacity than roach at a given size (Fig. 8c). Although perch were numerically dominant over 1-yr-old roach in experiment I, the calculated total metabolic demands on 14 June were higher for roach at low perch densities but not at higher perch densities. In the second part of the experiment perch had a higher calculated total metabolic demand than roach at all perch densities (Fig. 8d).

Discussion

Competition and density dependent mortality in young stages

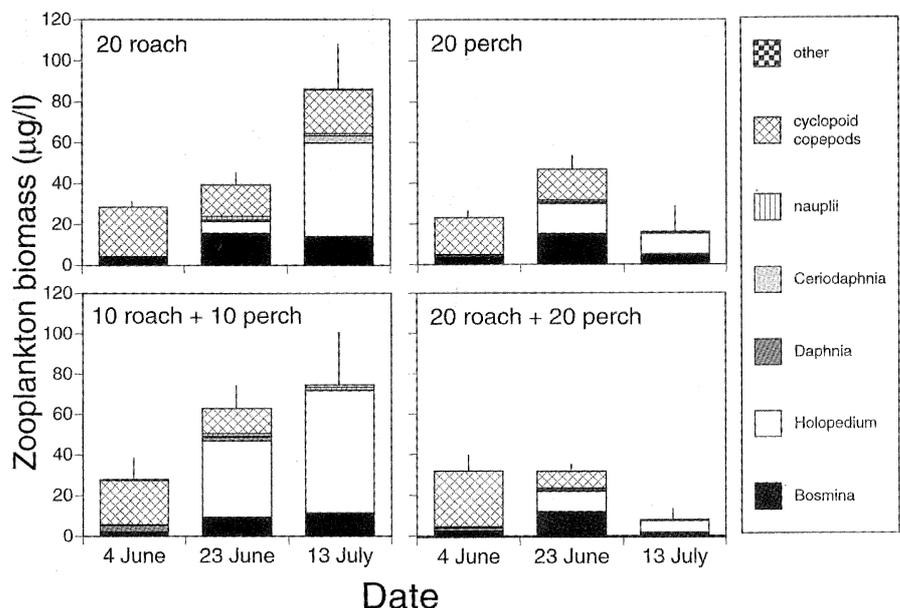Our results from the experiments demonstrated both

Fig. 4. Zooplankton biomasses (mean + 1 SE, for total biomass) in the different treatments (20 perch larvae, 20 roach larvae, 10 perch + 10 roach larvae and 20 perch + 20 roach larvae) on 4 June (start of the experiment), 23 June and 14 July.

Table 2. Repeated-measures ANOVAs (F-values) of the effects of treatment (20 perch larvae, 20 roach larvae, 10 perch larvae + 10 roach larvae and 20 perch larvae + 20 roach larvae) and time on the zooplankton community (total biomass of zooplankton and biomass by zooplankton group, log-transformed) and on the diet of perch and roach larvae (mean proportion of biomass of food categories, arcsine square root transformed). Significance level: $+ = 0.05 < P \leq 0.1$; $* = 0.01 < P \leq 0.05$; $** = 0.001 < P \leq 0.01$; $*** = P \leq 0.001$.

Source of variation	df	Total biomass	Bosmina	Holopedium	Daphnia	Ceriodaphnia	Copepod nauplii	Cyclopoid copepods	Other	Chironomidae
Zooplankton										
treatment	3,12	4.49*	6.46**	1.99	1.35	3.88*	2.15	5.79**	0.46	—
time × treatment	6,24	7.45***	2.16+	6.70***	1.16	9.17***	1.59	7.26***	2.03+	—
time	2,24	7.31**	15.1***	36.0 ***	12.4 ***	8.84***	14.1***	82.9***	0.82	—
Perch diet										
treatment	2,9	—	1.64	1.95	1.10	11.4**	1.96	0.29	3.19+	0.64
time × treatment	2,9	—	1.32	1.65	0.75	0.69	1.00	0.14	4.41*	0.64
time	1,9	—	9.10**	85.1***	3.79+	0.22	132.3***	0.72	13.2**	5.46*
Roach diet										
treatment	2,9	—	0.88	5.98*	2.04	2.08	0.26	1.00	5.87*	1.34
time × treatment	2,9	—	0.55	4.52*	0.76	0.22	0.42	1.00	5.88*	1.34
time	1,9	—	7.64*	49.6***	11.7**	0.01	27.0***	1.00	8.20*	5.00*

intra- and interspecific competitive effects on perch larvae. The competitive effects were present only on growth but not on survival. Experiment I demonstrated strong density-dependent growth in perch larvae and a strong impact of perch density on the zooplankton community with corresponding diet shifts in perch. The persistence of abundant large zooplankton (*Holopedium*) at low perch densities can be suggested to be the main cause of the higher growth rates at low perch densities in July (cf. Arts and Sprules 1989). In experiment II, perch larvae were also negatively affected by high densities of roach (see below, Species specific traits and size dependent interspecific competition for explanations). Thus, in contrast to what has been suggested for marine systems (Cushing 1983, Fortier and Harris 1989) our results point to the potential for both intra- and interspecific competitive interactions between fish larvae in freshwater systems during early summer (cf. Welker et al. 1994). Due to small body size and low energy reserves, starvation has been suggested to be a major mortality factor in larval fish (Miller et al. 1988, Cushing 1990). Although the resource levels in July at high perch densities in experiment I were similar to the critical resource levels for perch, we found, however, no density dependent effects on the survival of larval perch. This suggests that mortality due to starvation is unlikely during the pelagic larval stage of perch and that the frequently observed high mortality rates of pelagic perch larvae (e.g. Coles 1981, Treasurer 1989) should be related to other factors such as predation (cf. Treasurer 1989, Mason and Brandt 1996). Intra- and interspecific competition may, however, indirectly increase mortality by increasing the time an individual spend in size classes vulnerable to predation (Werner and Gilliam 1984, Houde 1987, Post and Prancevicius 1987, Fuiman 1989, Luecke et al. 1990).

High mortality during early life often leads to growth compensation in surviving individuals (Wilbur 1988). Thus, if strong competition causes high starvation mortality, survivors could benefit from this competitive release and show compensatory growth later in the season. However, in spite of strong density dependence in growth, we did not observe any corresponding density dependence in mortality of larval perch. A lack of density dependence in mortality combined with density dependence in growth has also been observed in perch during the latter part of their first growing season (Persson 1987c, Persson and Greenberg 1990b, Byström et al. 1998). This general lack of density dependence in survival of underyearling perch may be related to the significant time lag between the effect of competition (resource limitation) and the response to it (starvation mortality) (see also Byström et al. 1998). Thus, growth compensation due

Fig. 5. Diets (mean proportion of biomass) of perch and roach larvae and relative zooplankton biomasses (mean proportion of biomass) in the enclosures for the different treatments on 23 June and 14 July.
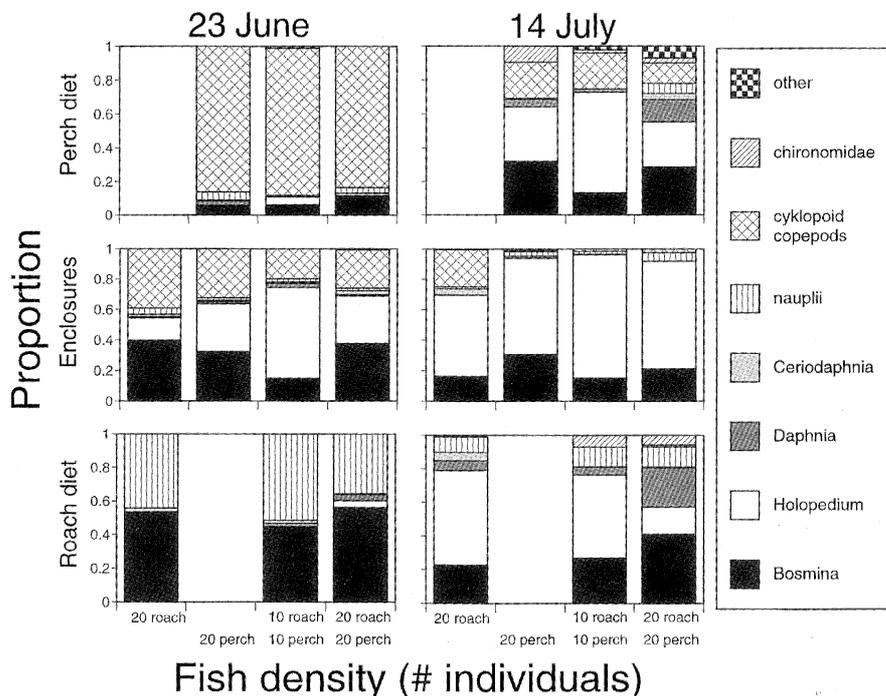
to starvation mortality should be low in the first growing season and under a scenario of strong competition, underyearlings at the end of the growing season should be small and in poor condition. This may in temperate climates result in total recruitment failure because of strong size-selective winter mortality on small individuals (Oliver et al. 1979, Post and Evans 1989, Byström et al. 1998). In many systems, however, this scenario may be counteracted by high predation mortality of underyearling perch (Nielsen 1980, Treasurer 1989, Byström et al. 1998), which in turn opens up an opportunity for growth compensation later in the season.

Species specific traits and size dependent interspecific competition

Body size is a major factor affecting the performance of an organism through its effects on foraging capacity and metabolic demands (Peters 1983, Calder 1984, Persson 1985, Lundberg and Persson 1993, Werner 1994). Based on our size-dependent functional response experiments and literature data presented in the result section (i.e. Fig. 8), we can gain a mechanistic understanding of the outcome of our experiments. At equal sizes, roach had a higher attach rate than perch on small zooplankton (Fig. 8a) but perch had a higher capacity for growth compared to roach (Fig. 8c, Lessmark 1983, Keckeis and Schiemer 1992, Wang and Eckmann 1994). This suggests that roach are more limited by total handling (including diges-

tion) of prey and have a lower conversion efficiency than perch (Lessmark 1983), hence roach are more limited in their food processing capacity (cf. Lundberg and Persson 1993). Roach thus have a lower consumption capacity than perch (Lessmark 1983) and perch may therefore have a stronger per capita impact on the resource than roach over time (cf. Kurmayer and Wanzenböck 1996). As a result of the combination of high growth capacity and a low attack rate, the growth of perch should respond negatively and earlier than roach to declining resource levels. In contrast, roach may show no or only small growth responses to moderate decreases in resource
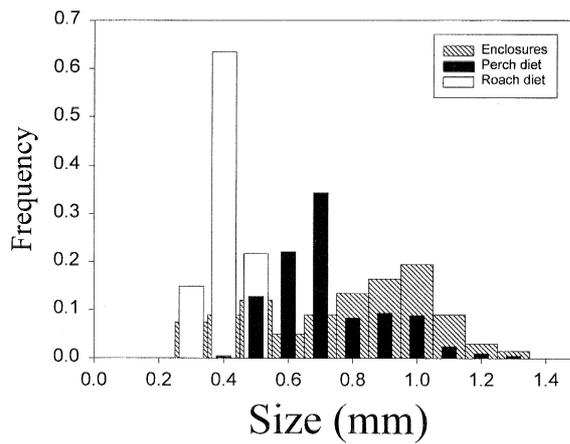

Fig. 6. The size distribution of *Holopedium* in the enclosures and in the diet of perch and roach larvae on 14 July (data taken only from the 10 perch + 10 roach treatment).
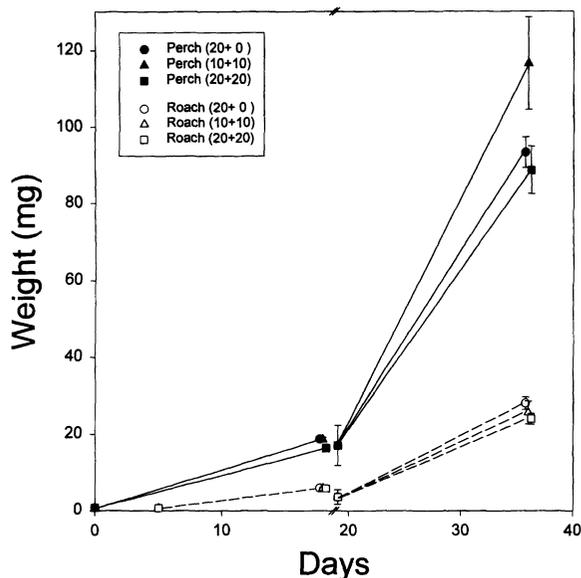
Fig. 7. Mean weight (± 1 SE) of perch and roach larvae in the different treatments (20 perch larvae, 20 roach larvae, 10 perch + 10 roach larvae and 20 perch + 20 roach larvae).

levels due to their, relative to perch, high attack rate but low growth capacity. However, if resource levels decrease to very low levels, 1-yr-old roach may show a larger negative response in growth than perch, despite their high attack rate on zooplankton as a result of their larger size than perch (cf. Fig. 8b; Persson 1985, Lundberg and Persson 1993, Werner 1994). In the experiment between perch and 1-yr-old roach (experiment I), perch were the smaller competitor and were also the competitor that had an impact on its opponent when the resource levels became very low which was the case in July. However, despite the fact that the metabolic mass of 1-yr-old roach amounted to a substantial fraction of the total metabolic mass in our enclosures, we found no effect of the presence of 1-yr-old roach on neither resource levels (although there was a tendency for total zooplankton biomass to be lower in roach treatments) nor the growth and diet of perch larvae. As roach have a lower consumption than perch (cf. Lessmark 1983), the impact of 1-yr-old roach especially in July on the resource may be small in comparison to perch even at low perch densities and undetectable with our experimental design. In June there was also a clear differentiation in diet between perch larvae and 1-yr-old roach, where perch larvae fed mainly on cyclopoid copepods and nauplii whereas roach fed mainly on *Daphnia* and *Bosmina*. Thus, although both competitors fed on zooplankton, they diverged in their resource use by feeding on different zooplankton species and therefore reducing their competitive effects on each other. This was also evident by the fact that perch density had no effect on the growth of 1-yr-old roach in June, which suggests that the

resource segregation was not a consequence of a competition induced niche shift (cf. Werner and Hall 1979, Persson 1988, Osenberg et al. 1992). The food overlap increased between perch larvae and 1-yr-old roach in July, indicating the potential for interspecific competition when resources became limited. Evidently, zooplankton resources became very low at high perch densities and in the range of the critical resource levels for both perch and 1-yr-old roach. 1-yr-old roach also shifted diet at high perch densities from zooplankton to chironomids and had almost zero growth in these treatments. In contrast, perch increased more than twofold in weight even at high perch densities. Thus, although perch larvae have a lower foraging efficiency than 1-yr-old roach, their per capita weight gain was higher than that of 1-yr-old roach at high resource limitation because of perch's lower metabolic demands (cf. Fig. 8b). There was also a concomitant tendency for an increased mortality for 1-yr-old roach at high perch densities.

In the experiment between perch and roach larvae (Experiment II), roach larvae were the competitor that had a negative impact on its opponent and roach larvae also showed a lower response than perch to high densities of competitors. Roach larvae actually showed no response in growth to high intraspecific densities nor interspecific competition. The negative impact of roach larvae on perch growth was only present in June while perch larvae were negatively affected by high intraspecific densities in July. This was supported by the stronger effect of high densities of perch compared to roach larvae on the zooplankton resource. Both the negative growth response in perch and the negative effect on the zooplankton resource of high perch density correspond well with the results in experiment I between perch larvae density and growth and impact on the zooplankton resource (cf. Figs 1 and 4, and Figs 3 and 7). Although perch larvae showed a decreased growth in June at high perch/roach densities, diet data and zooplankton biomasses in June showed no evidence of competition between perch and roach larvae. Two mechanisms may be advanced to explain this discrepancy. First, the growth response observed in perch larvae may have been a result of previous consumption during the experiment as both newly hatched perch and roach larvae feed on very small zooplankton like copepod nauplii (Hartman 1983, Hammer 1985). Second, as roach larvae in June to a large extent fed on copepod nauplii, they may also have had a negative effect on copepod recruitment, which may have negatively affected copepod availability for perch. Although not significant there was a tendency for lower densities of copepods in the high perch/roach enclosures in June (contrasting high perch/roach versus high perch and low perch/roach treatments, $t = 1.86$, df = 10, $P = 0.09$). The absence of a competitive effect of roach

larvae on perch in July may be related to the increased difference in size leading to a size-based differentiation in food utilisation (Wilson 1975, Werner and Gilliam 1984). This becomes important considering that the zooplankton resource was size-structured and species diverse and the fact that small fish generally are gape-limited (Hunter 1981, Schmitt and Holbrook 1984, Tessier 1986). As a piscivore, perch hatch with a larger gape-size than roach (cf. Hartman 1983, Arts and Evans 1987, Kurmayer and Wanzenböck 1996). Perch can thus, due to both higher growth capacity and larger gape, shift diet earlier in life to larger zooplankton and hence have access to a larger resource spectrum than roach (cf. Wilson 1975, Hall et al. 1976). The presence of an external gelatinous coat makes *Holopedium* less vulnerable to gape-limited zooplanktivorous fish (Tessier 1986). This was also evident in our experiment, where perch larvae consumed most of the present size range of *Holopedium* whereas roach larvae only used the smallest fraction of *Holopedium*. The fact that perch

larvae, in contrast to roach larvae, consumed most size classes of *Holopedium*, also suggests that perch were able to shift to feed on *Holopedium* earlier in time than roach. The increased size differentiation between perch and roach larvae over time also causes the relative impact of roach on the resource to decrease even further compared to the impact of perch. This further decreases the interspecific competitive effects of roach larvae on perch larvae in comparison with the intraspecific effects of perch on themselves.

In this study we have explored four major factors affecting an organism's competitive ability as related to body size, namely the attack rate, growth capacities, metabolic demands and the size spectrum of available resources. The last factor has been suggested to favour larger competitors, because they have access to a larger size range of resources including all resources used by smaller competitors (Brooks and Dodson 1965, Wilson 1975, Hall et al. 1976). However, the attack rate for a particular feeding organism on a given prey size has
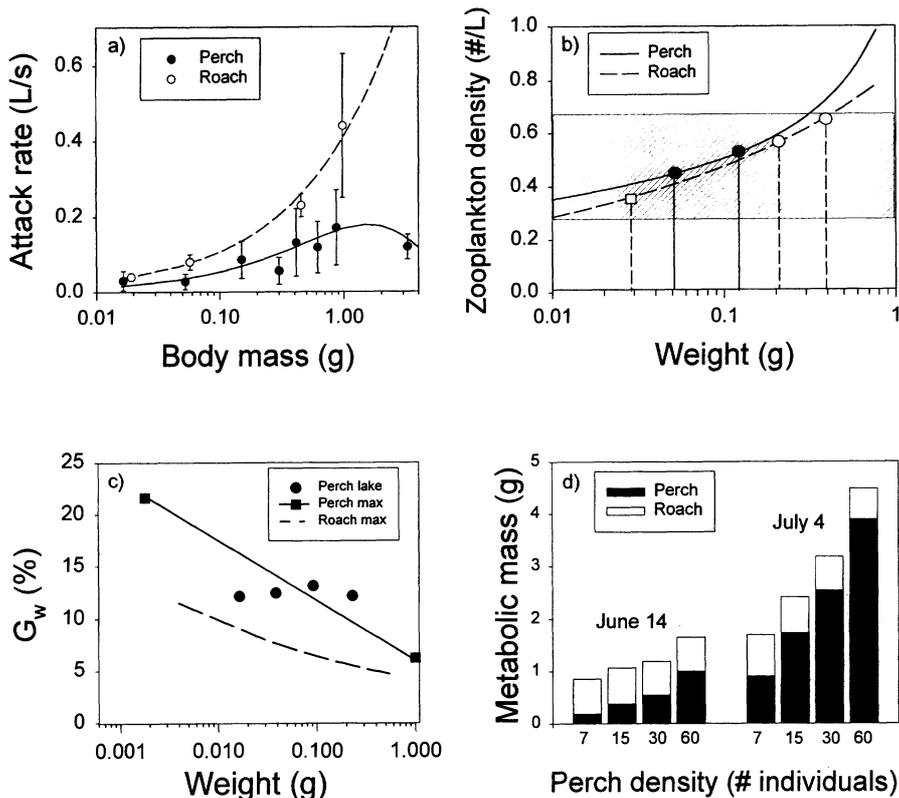

Fig. 8. a) The size dependence of the attack rate of perch and roach feeding on 0.5 mm *Bosmina*. Parameter estimates in equation (1) were: $A = 0.179$ L/s, $W_0 = 1.55$ g and $\alpha = 0.671$ for perch, and $A = 2.35$ L/s, $W_0 = 50.7$ g and $\alpha = 0.59$ for roach (J. Hjelm unpubl.). b) Critical resource levels of 0.5-mm cladocerans (*Bosmina*) for the maintenance of different sizes of perch and roach. Shaded area represents the variation in resource levels of *Bosmina* in our enclosures with 60 perch on 13 July. Filled circles are minimum and maximum weights of perch, open squares weight of roach larvae and open circles minimum and maximum weights of 1-yr-old roach in July in our experiments. c) Maximum growth capacity (G_w) of perch and roach expressed in % of body wet weight per day. As only two data points were available for perch, growth data from Lake Abborrtjärn 3 are also included in the figure. d) Total metabolic mass of perch and 1-yr-old roach in the enclosures in the middle of each experimental period.

Table 3. Estimated (mean with 95% CL) attack rates and handling times for different sizes of perch foraging on 0.5-mm *Bosmina* derived from fitting a type II Holling's functional response equation to the data.

Size (mm)	Weight (g)	Attack rate (L/s)	Handling time (s)	R^2
14	0.016	0.03 (0.026)	4.20 (1.86)	0.40
19	0.053	0.03 (0.021)	2.54 (1.51)	0.54
24	0.15	0.09 (0.054)	2.08 (0.61)	0.50
30	0.30	0.06 (0.036)	3.04 (0.95)	0.53
35	0.41	0.13 (0.09)	2.01 (0.59)	0.48
40	0.61	0.12 (0.069)	2.24 (0.48)	0.52
45	0.87	0.17 (0.103)	1.47 (0.34)	0.54
75	3.3	0.12 (0.033)	1.05 (0.16)	0.86

been shown to first increase to a maximum and thereafter decrease with consumer body size (Wilson 1975, Werner 1977, 1988). The size at which the maximum attack rate occurs depends on both prey size and consumer species. Thus, depending on the abundance of different resource sizes, different species and size classes within species may have a foraging advantage over other species/size classes (Werner 1977, Mittelbach 1981, Persson 1987a, b). This was the case in our study concerning the perch and roach larvae interaction. The larger gape-size of perch larvae and the higher capacity for growth compared to roach larvae gave perch larvae a temporal escape from the competitive effect of roach larvae in July due to the presence of large prey not consumed by roach larvae. In contrast, 1-yr-old roach had no advantage concerning prey size use in the perch larvae and 1-yr-old roach interaction, as perch larvae were able to consume all available size classes. The combined effects of size dependent foraging capacities and metabolic rate have been theoretically analysed and applied in several experimental studies to analyse competitive interactions (Wilson 1975, Hall et al. 1976, Persson 1985, 1987a, b, Werner 1994). When the metabolic rate increases with body size with a higher exponent than foraging capacity (including both attack rate and handling constraints) smaller individuals are favoured when resources decline (Persson 1985, Lundberg and Persson 1993, Werner 1994), which was the case for the smaller perch larvae compared to 1-yr-old roach. In cladocerans, the gain curve has been suggested to increase faster than the cost curve with size leading to that larger individuals are favoured (Brooks and Dodson 1965, Hall et al. 1976, Gliwicz and Lampert 1990). This hypothesis is, however, largely based on interspecific comparisons between differently sized species. There is also contradictory evidence suggesting that smaller species of cladocerans may be competitively superior under low food levels (Neill 1975, Lynch 1977, Tillman and Lampert 1984, Tessier and Goulden 1987). This apparent contradiction in results may be due to the fact that interspecific differences in foraging efficiencies have not clearly been differentiated from intraspecific size scaling.

In conclusion, size and species specific foraging and growth capacities of consumers may, even during the

short temporal window and narrow size range of competitors studied by us, lead to temporal variation in competitive interactions as a result of changing size structures of consumers and resources. Knowledge of how foraging, growth and food processing capacities scale to body size is of major importance for the understanding and prediction of competitive interactions and ultimately for the understanding of population and community dynamics.

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