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Published in:
Limnology and Oceanography

2003

Citation for published version (APA):
Romare, P., & Hansson, L.-A. (2003). A behavioral cascade: Top-predator induced behavioral shifts in planktivorous fish and zooplankton. *Limnology and Oceanography*, *48*(5), 1956-1964. http://aslo.org/lo/toc/vol_48/issue_5/1956.pdf

Total number of authors:
2

Limnol. Oceanogr., 48(5), 2003, 1956–1964

A behavioral cascade: Top-predator induced behavioral shifts in planktivorous fish and zooplankton

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Abstract

It is well known that the effects of direct (lethal) predator-prey interactions propagate through food webs (the trophic cascade). However, in the present study we show for the first time that, parallel to the trophic cascade, there exists a ''behavioral cascade'' in the sense that behavioral responses, induced by the nonlethal presence of a top predator, are transmitted down the food chain over more than one trophic link. By using a new method, horizontal echo sounding, in an enclosure study in a shallow lake in southern Sweden, we recorded the swimming activity and refuge use of young-of-the-year (0+) roach (*Rutilus rutilus*) in the presence and the absence of a caged predatory fish. By connecting the predator avoidance behavior of 0+ roach with that of zooplankton throughout summer, we show that species interactions are more dynamic than had been predicted earlier by food web theory. In our study, 0+ roach changed their behavior by becoming less active in early summer and by hiding in a refuge in late summer in the presence of a piscivore, and this caused *Daphnia* to spend more time feeding in the open water than when piscivores were absent. Thus, we conclude that, to explain patterns of habitat use in natural systems, it is of crucial importance that we recognize the existence of behavioral cascades.

Food web interactions have been one of the dominant research areas in ecology during the past two decades. Nowadays there is an almost complete consensus (*but see* Persson 1999) that effects of predator-prey interactions may cascade through the food web (Carpenter et al. 1985; Mazumder 1994; Pace et al. 1999). However, theoretical, as well as empirical, aspects of food chain theory are largely based on consumption; that is, most studies presuppose that the only important interaction between predator and prey is that they actually meet and that the prey is consumed.

During the past decade, evidence has emerged suggesting that the presence of a predator or grazer may induce a change in behavior (Lima and Dill 1990; Turner and Mittelbach 1990; Hansson 2000) or morphology (Brönmark and Miner 1992; Peacor and Werner 1997) of the prey. Such indirect interactions are termed behavioral indirect interactions (BIIs) (Miller and Kerfoot 1987), trait-mediated indirect interactions (Abrams et al. 1996), or interaction-modifications (Wootton 1993). It has been demonstrated that BIIs can be quantitatively important (Wootton 1994; Abrams et al. 1996), and it is believed that BIIs are widespread in many food webs and that their importance has been underestimated (Miller and Kerfoot 1987; Wootton 1993; Abrams et al. 1996; Sih et al. 1998; Persson 1999). Existing studies of behaviorally mediated indirect effects have shown that a shift in prey traits can affect the density of the prey's resources or the prey's competitors (Turner and Mittelbach 1990; Sih et al. 1998)—for example, indirect effects consisting of one behavioral link. It is, however, theoretically possible for shifts in prey behavior to in turn affect the behavior of the prey's resources or the prey's competitors, and these behavioral shifts may cascade through the food web and ultimately affect the abundance of distantly linked species. Such linked behavioral interactions are potentially important, because behavioral adjustments can occur much more rapidly and extend further than numerical effects. If behavioral effects often occur in tandem—that is, indirect effects consisting of two or more behavioral linkages—the power of behavioral interactions is multiplied, and the are likely to be especially important.

In the present study, we aim to show the existence of a behavioral cascade consisting of two behavioral links, and we focus on an aquatic food chain/web, a system in which trophic interactions are well studied (Persson 1999). We used piscivorous fish as the top predator, different-sized young-of-the-year (0+) fish as the intermediate predator, and zooplankton as prey. Because the antipredator strategy of 0+ fish changes during early ontogeny (Werner and Gilliam 1984; Eklöv and Diehl 1994), we expected several behavioral mechanisms to be involved. During early summer, schooling 0+ fish may decrease activity in response to the presence of a predator, and, later during the summer, larger 0+ fish may respond by seeking cover in a predator-free space, a refuge (Turner and Mittelbach 1990; Persson and Eklöv 1995; Christensen 1996). In aquatic systems, some vegetation may provide such a refuge for 0+ fish and also for their zooplankton prey. In shallow waters, various zooplankton groups have been shown to perform diel horizontal migrations in the presence of fish—that is, they hide in the vegetation during day and use open water during night (Timms and Moss 1984; Lauridsen and Buenk 1996; Lauridsen et al. 1996). This, however, means that, in the presence of a piscivorous predator, 0+ fish and their zooplankton prey may meet in the same refuge: zooplankton seek refuge in the presence of 0+ fish, and 0+ fish seek refuge in the

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Acknowledgments

We thank C. Brönmark, D. E. Schindler, and two anonymous reviewers for valuable comments on earlier version of this article. We also thank T. Nydén, N. Carlsson, M. Gyllström, J. Johansson, K. Nilsson, A. Olsson, and M. Svensson for help in the field and in the lab.

We acknowledge financial support from the EC project SWALE, from MISTRA through the VASTRA program, from the Swedish EPA (to L.-A. H.) and from FORMAS (to P. R).

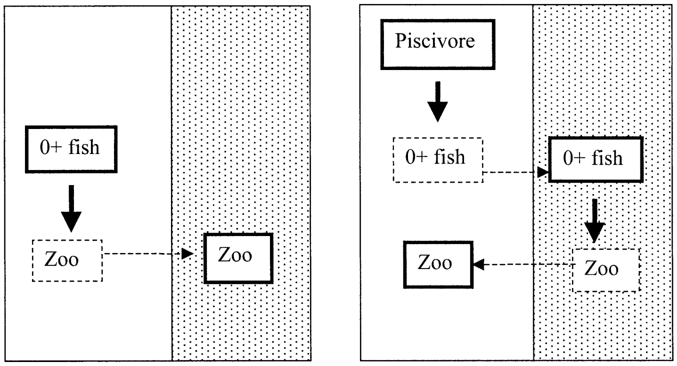

Fig. 1. A conceptual figure illustrating the expected behavioral cascade from piscivorous fish to zooplankton in the presence of a refuge (dotted area), acting in concert with the trophic cascade. Thick arrows indicate traditional lethal predator-prey links (cascading trophic interactions), whereas dotted arrows indicate the proposed nonlethal, behavioral cascade induced by the presence of a predator.

presence of piscivores (Fig. 1). In our study, done in a shallow area of a eutrophic lake, we studied the distribution of both 0+ fish and cladoceran zooplankton in large enclosures that included open water and vegetation. 0+ fish and zooplankton were present in the enclosures during the whole summer season; thus, 0+ fish were studied from the larval to the juvenile stage. To study the behavior of 0+ fish of all sizes, we used horizontal split-beam echo sounding, a new tool with considerable potential to study fish behavior in experimental setups even in shallow water (Romare 2001). Four of the eight enclosures in our setup were exposed to caged piscivorous fish during short periods (~24 h) at five occasions during the summer season. By exposing the intermediate predator to a nonlethal predator for relatively short intervals, we argue that any observed difference between treatments in the distribution of 0+ fish and of cladoceran zooplankton will largely be a result of behavioral responses.

Our main hypotheses were that the behavior of the intermediate predator (0+ fish) is affected by the presence of a top predator and that the behavior of the intermediate predator in turn affects refuge use by the prey (cladoceran zooplankton). We hypothesized that, if a behavioral cascade exists, cladoceran density will be higher in the vegetation than in open water in the absence of piscivores, because zooplankton seeks refuge from fish predation (Fig. 1). When (nonlethal) piscivores were added, however, this difference in zooplankton density between habitats would decrease or be reversed, because some cladoceran groups would move out from the vegetation into open water when 0+ fish moved into the vegetation (Fig. 1). Corroboration of these hypotheses would suggest that cascading trophic interactions are not merely based on direct confrontations between predator and prey but that they also include a more complex behavioral dimension—a "behavioral cascade."

Material and Methods

Performance—The experiment was carried out in the shallow Lake Krankesjön (area 2.9 km^2; mean depth 1.5 m; maximum depth 3.0 m), a moderately eutrophic lake in southern Sweden. (For a more thorough description of the lake, *see* Hargeby et al. 1994.) The experimental site was a nonvegetated area with a homogeneous, sandy/silty bottom. The water depth varied between 1.1 and 1.3 m, and the temperature varied between 19°C and 25°C during the experimental period.

Eight triangular enclosures were built in a fanlike configuration, and each enclosure was 4.0 m long, 2.4 m wide in the back end, and 0.7 m wide in the front end. Along one side of each enclosure, we placed artificial vegetation (untwined nylon ropes) that functioned as a refuge from predators. For further details on the experimental setup, see Romare (2001). We assigned four of these enclosures to a piscivore treatment. For practical reasons, because we needed to have open water to be able to rotate the transducer pole, the inner part of the experimental arena was only sealed off between the two treatments; thus, the four enclosures in each treatment had to be placed next to each other (for further description, *see* Romare 2001). In each of the eight enclosures, one small, covered cage was put in the nonvegetated corner, furthest away from the transducers. Twenty-four hours before monitoring the enclosures, two piscivorous perch (15–20 cm total length) were put in each of the cages placed in the four enclosures of the piscivore treatment. When the piscivores were inside the cage, 0+ roach could not detect them visually. Prior to being placed in the cages, the perch had been kept in aquaria and fed 0+ roach.

The artificial vegetation was put in the enclosures on 7 June 1999, and, during the following week, zooplankton could enter the enclosures from the lake through 1-mm mesh windows (most zooplankton were <1mm in the lake at that time; Romare unpubl. data). Before the start of the experiment, the enclosures were completely sealed off from the lake but were open to the sediments. About 60 roach larvae (mean length, 15 mm) caught in the lake were added to each enclosure by 17 June. Additional 0+ roach (20 roach on the first two occasions and 10 roach on the following occasions) were caught in the lake and added to the enclosures the day before each sampling, to compensate for expected mortality. The mean size of 0+ roach was 20 mm at the start of the experiment, 24 mm in early July, 33 mm in late July, and 40 mm at the end of the experiment. On six occasions during the experimental period, an inoculum of mixed zooplankton from the lake was added to each enclosure.

The 0+ roach distribution was monitored on five occasions during the experiment: 23 and 29 June, 13 and 30 July, and 11 August 1999 (hereafter called weeks 25, 26, 28, 30, and 32, respectively). Monitoring the behavior of 0+ fish of all sizes in large-scale field enclosures is not possible using traditional techniques, such as direct observations, so we used the horizontal echo sounding technique (Kubecka 1996; Romare 2001) to record the distribution and the swimming behavior of 0+ fish. Monitoring of 0+ fish distribution was performed by means of a SIMRAD EY500 120 kHz echo sounder, using two split-beam transducers. The two transducers were put on top of each other, to monitor the entire water depth. We monitored the fish distribution in each enclosure for 4 min at noon and at midnight and at the same time zooplankton were collected. We considered these sampling periods to be representative for day and night fish behavior, respectively (based on two 24-h samplings; Romare unpubl. data). Zooplankton were sampled with a 1-m-long tube sampler (diameter, 48 mm) at three sites in the open water (a pooled total of 10 liters) and at two sites within the artificial vegetation (a pooled total of 7 liters) at noon. Because of practical problems with sampling in the vegetation in darkness, only the pelagic volume was sampled at midnight. The sampled water was filtered through a 45-μm net, and zooplankton was preserved in Lugol solution and later counted and size measured at 40× magnification.

Data analysis and statistics—A detailed description of the echo sounding data analysis is presented in Romare (2001), so the basic data analysis will only be outlined in brief here. Data analysis was performed using a combination of an echo processing system (echo counting and trace tracking) and direct observations of printed echograms. Because of the integration of noise, a direct quantification of fish numbers was not possible. Instead, we manually defined ‘‘fish echoes’’ from echograms and assessed where in the transducer beam these echoes were located (Romare 2001). From the registered patterns on the echograms and the distribution of ‘‘fish echoes’’ in the beam, we observed different behavioral patterns of 0+ roach. These behavioral patterns were divided into four categories: (1) 0+ fish swimming as active single fish in the open water, (ASF, observed as short lines of consecutive echoes on the echogram), (2) 0+ fish appearing in schools in the open water, (observed as swarms of echoes in changing patterns on the echogram), (3) 0+ fish aggregating close to the vegetation (‘‘fish echoes’’ present on the echogram and located near the ‘‘vegetation side’’ of the beam), and (4) all 0+ fish hiding inside the vegetation (no, or very few, ‘‘fish echoes’’ present on the echogram). When a mixture of two behaviors was observed in one enclosure, we considered this enclosure to belong by 50% to the first behavioral group and by 50% to the second group.

We used the proportion of daytime number of fish echoes (the number of daytime echoes divided by the sum of daytime and nighttime echoes) as a relative estimate of 0+ fish presence in open water during daytime. The abundance estimate was standardized in this way because the exact number of 0+ roach present in each enclosure was not known. To test whether the daytime proportion of 0+ fish echoes present in the open water changed over time and whether this differed between treatments, we used repeated-measures analysis of variance (RMA) with season as the repeated factor, including all sampling occasions. Because Levene's test showed that variances differed between treatments, proportions were arcsine transformed prior to analysis.

To test whether the piscivore treatment had any effect on 0+ roach behavior during the period when 0+ roach were present in open water, we compared the number of enclosures during weeks 25, 26, and 28 (a total of 12 enclosures per treatment) in which the behavioral group ‘‘active single fish’’ was registered. Because this test was not based on real numbers of fish but on the presence or absence of behavioral categories, we used Fisher's exact test and tested for day- and nighttime differences separately.

We tested for spatial and temporal differences in cladoceran density (expressed as biomass) using one-factor RMA, with season as the repeated factor. We tested whether cladoceran enclosure density (open water *and* vegetation daytime densities) differed between the two treatments over the season and whether overall cladoceran density (data from *all* enclosures included) differed between open water and vegetation and between day and night. To test for treatment effects on the spatial distribution of cladocerans, we compared the proportion of cladoceran biomass present in open water (cladoceran daytime open water density divided by the sum of open water and vegetation daytime densities) between treatments, and, to test for effects on the temporal distribution, we compared the proportion of cladocerans present during daytime (cladoceran daytime open water density divided by the sum of daytime and nighttime open water densities).

To test for a difference in *Daphnia* size distribution between habitats (using data from weeks 25 and 26, when large *Daphnia* were abundant), we used a paired Kolmogorov-Smirnov test, lumping all *Daphnia* measurements together among replicates. The differences in cladoceran enclosure biomass and in spatial and temporal distribution within the enclosures were analyzed for the three dominant zooplankton taxa (*Daphnia, Ceriodaphnia,* and *Bosmina* spp.). Zooplankton biomass data were log or arcsine transformed (proportions) prior to analysis.

Results

The 0+ roach changed their daytime behavior during summer from schooling in the open water, to staying close to, or inside the vegetation (Fig. 2). During nighttime, 0+ roach mainly occurred as single fish swimming in the open water throughout the summer (Fig. 2). In the absence of piscivores, 0+ individuals were actively swimming (feeding) during daytime in early summer (weeks 25–28). In the presence of piscivores, however, such behavior was only detected the first week (Fig. 2). Hence, there was a difference in the daytime behavior (ASF) of 0+ fish between treatments in early summer (Fisher's exact test $p < 0.05$) but no difference between treatments during nighttime (Fisher's exact test, not significant).

The mean proportion of 0+ roach that stayed in open water during day (the daytime share of fish echoes) is shown through time for both treatments in Fig. 3. There was no significant effect of season or treatment alone. The significant interaction between treatment and season (RMA), however, indicated that the development over the season differed between treatments (season × treatment, sums of squares = 0.8, mean squares = 0.2, $F_{4,12} = 4.8$, $p = 0.015$, Greenhouse-Geisser = 0.04). As seen in Fig. 3, the proportion of 0+ roach in open water declined when piscivores were present, whereas, when piscivores were absent, there was no decrease in the proportion of 0+ roach outside the vegetation during summer (Fig. 3). Although 0+ roach did not enter the vegetation in the absence of piscivores, they also changed their behavior during late summer to aggregating close to the vegetation (Fig. 2).

The dominant cladoceran groups, seen over the whole season, were *Ceriodaphnia, Daphnia,* and *Bosmina* spp. Also

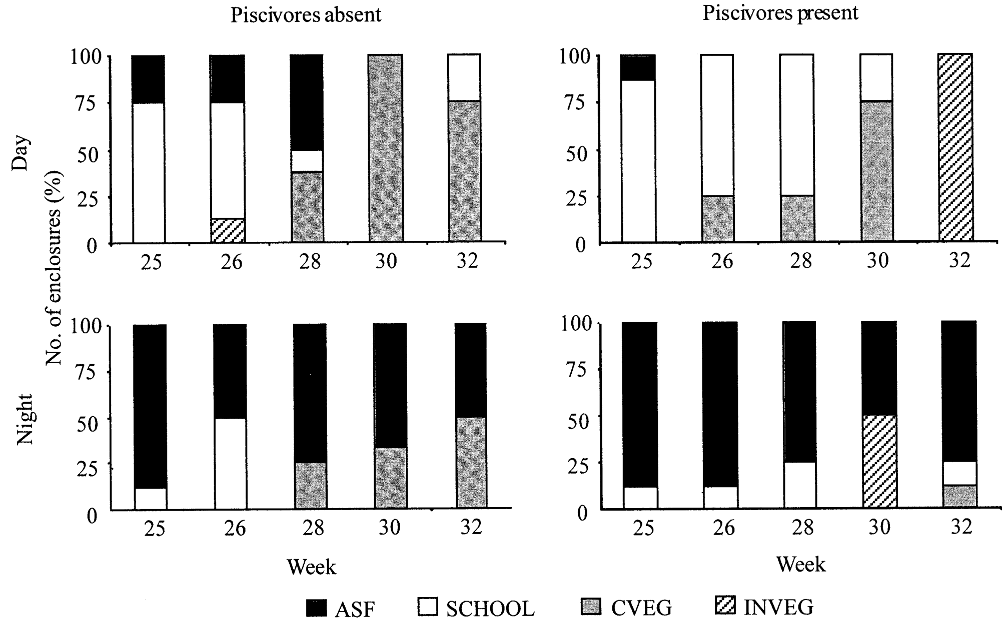

Fig. 2. The proportion of enclosures in which 0+ roach appeared as active single fish (ASF), in schools (SCHOOL), staying close to the vegetation (CVEG), or hiding inside the vegetation (INVEG). The figures show the distribution during day and night, with and without piscivores. There were four enclosures used in the analysis at all occasions except in the no-piscivore treatment week 30 day and weeks 26 and 30 night, when we used three.

occurring in occasional high numbers were *Diaphanosoma* and *Polyphemus* spp., but they were not present all through the summer and are therefore not included in the analysis. Total cladocerans, *Daphnia, Ceriodaphnia,* and *Bosmina* mean densities (log mg L^{-1}) during daytime in vegetation versus open water (Fig. 4A–D) and during night versus day (Fig. 4E–H) are shown in Fig. 4.

There was no difference in total cladoceran, *Daphnia, Ceriodaphnia,* or *Bosmina* enclosure biomass between treatments (RMA, total cladocerans, treatment: $F_{1,6} = 0.4$, not significant; season: $F_{4,24} = 0.4$, not significant, treatment × season: $F_{4,24} = 0.9$, not significant; *Daphnia,* treatment: $F_{1,6} = 0.9$, not significant; season: $F_{4,24} = 6.4$, $p = 0.003$; treatment × season: $F_{4,24} = 0.4$, not significant, Fig. 5). The change in diel distribution of cladocerans, observed in both treatments, showed a higher cladoceran density in open water during night than during day. This was evident for *Daphnia* and *Bosmina* but not for *Ceriodaphnia* (Table 1). Total cladocerans, *Daphnia,* and *Ceriodaphnia,* but not *Bosmina,* also showed a significantly higher density in the vegetation than in open water during day (RMA, Table 1). For *Daphnia,* the magnitude of the habitat separation during day differed between treatments—that is, depending on whether piscivores were present. The proportion of *Daphnia* (biomass) in open water during day was significantly higher when piscivores were present than where no piscivores were present (RMA, Table 2, Fig. 6). On the first two sampling dates, large *Daphnia* (>1.0 mm) were present in the enclosures, and during that time the size distribution of *Daphnia* differed between habitats in the absence but not in the presence of piscivores (Kolmogorov-Smirnov paired test, without piscivores: week 25 $p = 0.01$, $n = 65, 27$; week 26 $p = 0.000$, $n = 65, 32$; with piscivores: weeks 25 and 26, not significant, $n = 61, 60$ and $26, 32$; Fig. 7). For *Ceriodaphnia* and *Bosmina,* the addition of piscivorous fish had no effect on refuge use (RMA, Table 2), and the diel distribution did not differ between treatments for any of the cladoceran groups (RMA, Table 2).

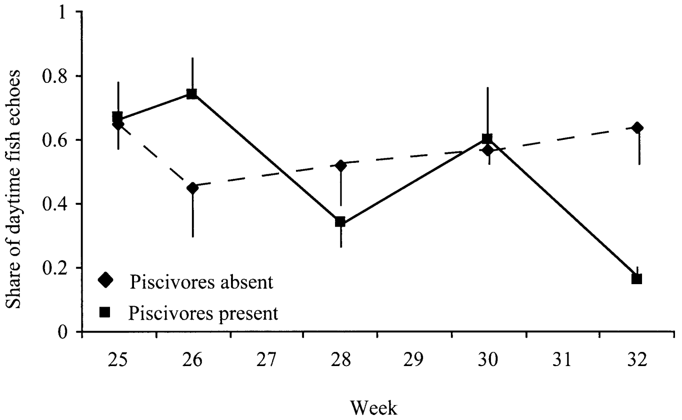

Fig. 3. Mean numbers (± standard error) of fish echoes (expressed as the daytime share of the total number of echoes registered both day and night) at all monitoring occasions, without and with piscivores present. Note that, in the treatment without piscivores, only three enclosures were included at each date because the noise level in one of the replicates was too high to get a reliable number of fish echoes.

Discussion

Trophic cascades have been identified as one of the major structuring forces for both fish and zooplankton communities

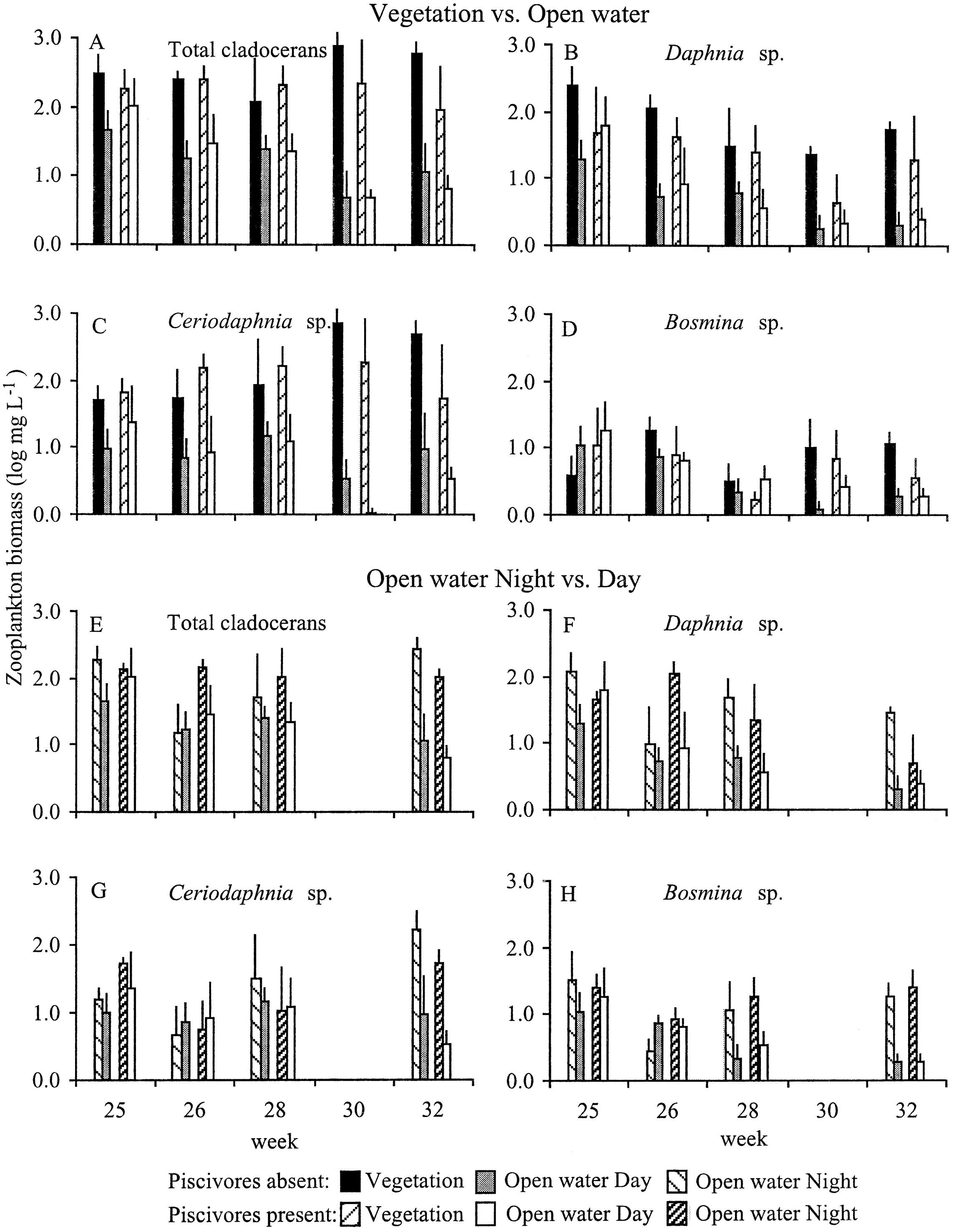

Fig. 4. Mean density of total cladocerans and dominant cladoceran taxa (mg L^{-1}) in open water and in vegetation during the day (A–D) and during night and day in open water (E–H) of the experimental enclosures with and without piscivores present. Each bar represents the mean ± standard error ($n = 4$) at one sampling occasion. Data were log transformed. Cladoceran groups included are *Daphnia, Ceriodaphnia,* and *Bosmina* spp. Note that open-water day densities are shown in both A–D and E–H and that there were no data from night samplings during week 30.

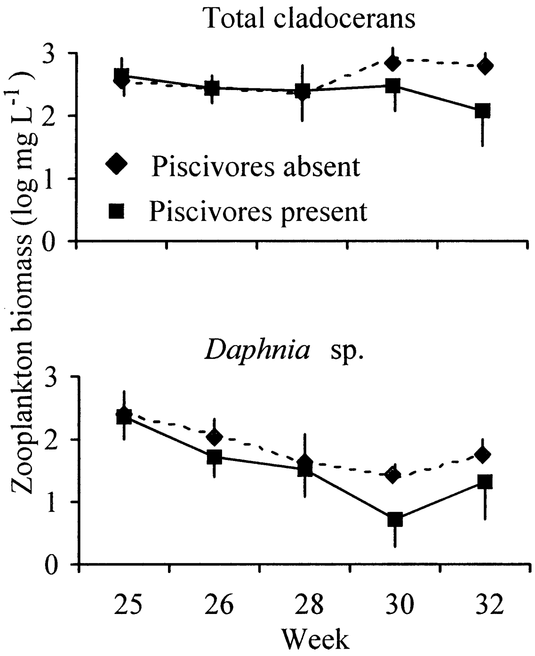

Fig. 5. Mean enclosure density (daytime open water and vegetation densities) of cladocerans (mg L^{-1}) in the experimental enclosures without and with piscivores present. Each data point represents the mean ± standard error ($n = 4$) at one sampling occasion. Values are log transformed.

(Carpenter et al. 1985; Hansson 1992; Mazumder 1994). In contrast to density-mediated trophic cascades, behaviorally mediated interactions may lead to a rapid redistribution of prey and thereby to a rapid change in the number of prey encountered in different habitats. In our study, the behavioral responses in 0+ roach, as well as in *Daphnia,* were induced when they were exposed to caged piscivores for just 24 h. When piscivores were added, 0+ roach lowered their feeding activity in the open water (i.e., showed less single fish activity) during early summer and hid in the vegetation during late summer, and at the same time the proportion of *Daphnia* biomass present in open water increased.

Table 1. Habitat (vegetation vs. open water) and diel (day vs. night) effects on overall cladoceran density (mg L^{-1}) in the experimental enclosures, including data from both treatments. Data were log transformed prior to analysis. Differences tested with one-factor RMA with season as the repeated factor.

Season × Habitat	Habitat (df = 1, 14)		Season (df = 4, 56)		Habitat × Season	
	F	*p*	*F*	*p*	*F*	*p*
Total cladocerans	34.0	0.000	1.3	NS	2.7	NS
Daphnia sp.	13.5	0.002	9.6	0.000	0.9	NS
Ceriodaphnia sp.	34.8	0.000	0.2	NS	3.2	0.305
Bosmina sp.	4.0	NS	3.6	0.024	2.2	NS
Season × Diel	**Diel (df = 1, 3)**		**Season (df = 3, 39)**		**Diel × Season**	
	F	*p*	*F*	*p*	*F*	*p*
Total cladocerans	14.3	0.002	2.0	NS	2.7	NS
Daphnia sp.	15.6	0.002	6.5	0.003	1.2	NS
Ceriodaphnia sp.	1.8	NS	2.1	NS	3.0	NS
Bosmina sp.	30.6	0.000	2.8	NS	3.3	NS

NS: not significant.

Table 2. Treatment effects (piscivores present vs. absent) on cladoceran spatial (vegetation vs. open water) and diel (day vs. night) distribution in the experimental enclosures. Comparing the proportion of cladoceran density present in open water tested spatial distribution, and comparing the proportion of cladocerans present during daytime tested diel distribution. All proportions were arcsine transformed prior to analysis. Differences tested with one-factor RMA with season as the repeated factor.

Spatial distribution	Treatment			Season			Treatment × Season	
	df	*F*	*p*	df	*F*	*p*	*F*	*p*
Daphnia sp.	1, 4	9.1	0.039	4, 16	0.4	NS	0.1	NS
Ceriodaphnia sp.	1, 5	0.9	NS	4, 20	2.4	NS	0.4	NS
Bosmina sp.	1, 3	4.4	NS	4, 12	1.1	NS	0.8	NS
Diel distribution	**Treatment**			**Season**			**Treatment × Season**	
	df	*F*	*p*	df	*F*	*p*	*F*	*p*
Daphnia sp.	1, 5	0.1	NS	3, 15	0.4	NS	2.9	NS
Ceriodaphnia sp.	1, 3	1.5	NS	3, 9	2.3	NS	0.9	NS
Bosmina sp.	1, 3	0.2	NS	3, 9	3.5	NS	0.5	NS

We show that the antipredator strategy of 0+ roach changed during ontogeny. Small 0+ fish have a high metabolic rate and are forced to feed often, trading off the safety of a refuge against food (Pitcher and Parrish 1993). When no predation threat is perceived, juvenile fish prefer to feed as single fish (Irving and Magurran 1997), and accordingly, in the absence of piscivores, 0+ roach in our study were actively feeding as single fish (ASF) during daytime. When piscivores were present, however, single-fish activity was rare, and all fish were schooling, a behavior that reduces predation risk (Christensen 1996). Large 0+ fish are less affected by food deprivation than small fish and may there-

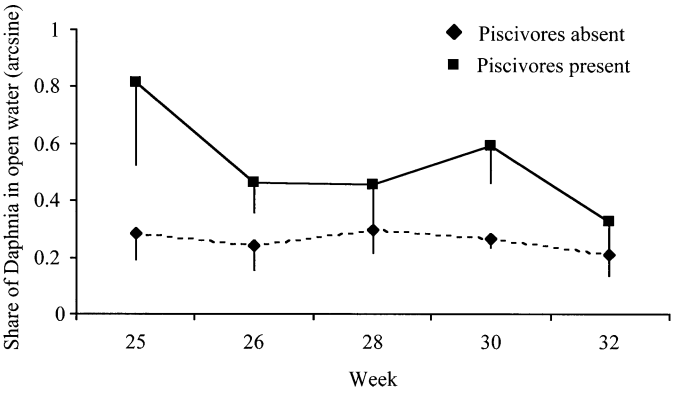

Fig. 6. Mean proportion of daytime *Daphnia* spp. biomass (mg L^{-1}) in open water (daytime open water density divided by the sum of open water and vegetation daytime densities) in the experimental enclosures without and with piscivores present. Shown are the mean of arcsine-transformed proportions ± standard error ($n = 4$).

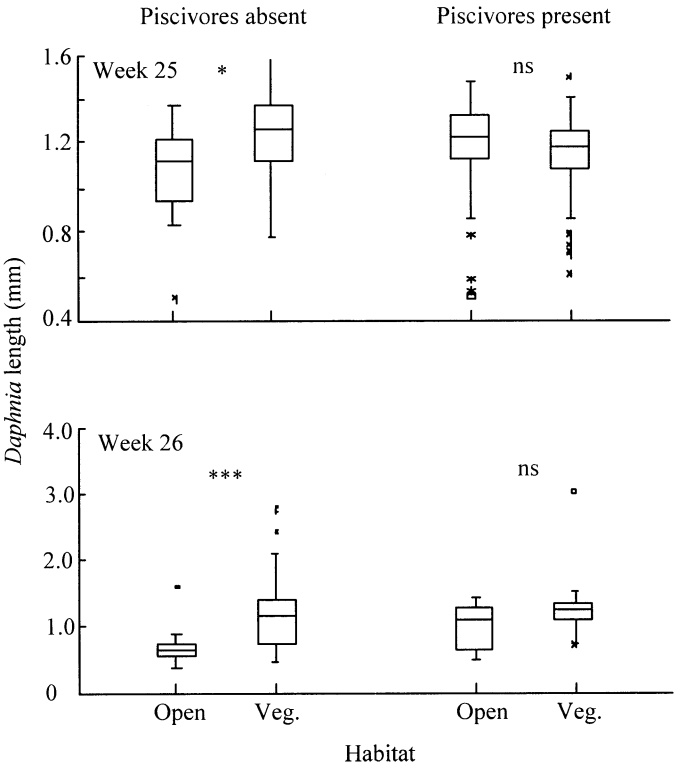

Fig. 7. *Daphnia* spp. size distribution (mm) in open water and in vegetation in the experimental enclosures without and with piscivores. Shown are data from the first two sampling occasions, when large *Daphnia* were present in all enclosures (weeks 25 and 26). Prior to analysis, *Daphnia* length measurements for all replicates within each treatment were lumped together. A paired Kolmogorov-Smirnov test showed significant differences between habitats in the absence but not in the presence of piscivores, as indicated on the graph (* and ns, respectively).

fore be able to stay longer in a refuge (Krause et al. 1998); thus, we expected 0+ roach to move into the vegetation during late summer in the presence of piscivores. This behavior was observed on the last daytime sampling in our study, when no or very few 0+ roach were observed outside the vegetation in the piscivore treatment. This notion is strengthened by the gradual decline in the proportion of 0+ roach staying in the open water during the day in the presence of piscivores. The same behavioral response was shown for juvenile roach in an experimental study by Persson and Eklöv (1995). In a field study, Hall et al. (1979) showed that golden shiner (*Notemigonus crysoleucas*), another cyprinid fish, also aggregated close to dense vegetation during the day, only foraging in open water during dawn and dusk, and they suggested that this was probably a predator-avoidance behavior. Even though roach are primarily visual foragers in light conditions, they may change to nonaimed feeding during darkness (Van den Berg et al. 1994), and, in our study, single fish activity occurred during night both in the presence and absence of piscivores. Our observations corroborate results from a field study that showed that juvenile roach feed actively as single fish during the night even in the presence of piscivores (Brabrand and Faafeng 1993).

Just as macrophytes may serve as a refuge for 0+ roach against piscivore predation, recent studies have shown that the nonlethal presence of fish may cause *Daphnia* to move into the vegetation (Lauridsen and Lodge 1996); thus, macrophytes may serve as a daytime refuge for zooplankton groups performing diel migrations between vegetation and open water (Timms and Moss 1984; Lauridsen et al. 1996). In our study, we observed (Table 2, Fig. 5) this general diel migration pattern in *Daphnia* and *Bosmina*—partly supporting studies performed in Danish eutrophic lakes (Lauridsen and Buenk 1996; Lauridsen et al. 1996)—whereas *Ceriodaphnia* density did not increase in open water during the night. Thus, it seems that, in our study, zooplankton avoid the high-predation-pressure habitat of open water during the day and aggregate in the vegetation. The general cladoceran distribution patterns observed in both treatments, we believe, is driven by a combination of factors, including both behavioral shifts (because of the continuous presence of 0+ roach) and selective foraging by 0+ roach. The cladocerans, *Daphnia* and *Bosmina,* showed decreasing densities outside the refuge (open water during the day) but showed remaining high or increasing densities in the vegetation. This ability to maintain high density suggests that refuges in the vegetation allowed for reproduction and, thereby, a buildup of cladoceran populations even in the presence of a high predation pressure.

As was discussed above, 0+ roach showed two different antipredator behaviors during the season, and we argue that both behaviors led to a lower daytime predation pressure on zooplankton in open water during the treatment periods. These periods of lowered predation pressure in open water did not, however, lead to overall higher enclosure densities in the piscivore compared with the no-piscivore treatment. This may be explained by both the short duration of the treatment and by the foraging limitations of small roach. Small roach (<25 mm) are gape-limited foragers with an optimal prey size of less than 1mm (Wanzenböck 1995), and roach feeding rates are also known to decrease in structural complexity (Winfield 1986; Christensen and Persson 1993; Schriver et al. 1995; Manatunge et al. 2000). Thus, we do not find it likely that foraging by small roach in early summer affected the density of large *Daphnia*, nor that foraging inside the vegetation in late summer affected total cladoceran density substantially during the treatment periods.

We argue that the difference in *Daphnia* distribution between treatments observed in our study was not a result of consumption but of linked behavioral interactions. When piscivores were added, *Daphnia* responded to the change in the predation pressure by 0+ fish by optimizing their habitat use spatially. When 0+ roach changed their daytime behavior because of the presence of piscivorous perch, *Daphnia* apparently perceived a lower predation risk in open water and migrated out from the vegetation into the preferred habitat of open water. During early summer, this behavioral response seemed to involve primarily large *Daphnia,* which is in concert with earlier findings that large *Daphnia* show a stronger response (in diel vertical migration) than small *Daphnia* to fish kairomones (data from Loose 1992 presented in De Meester et al. 1999). *Bosmina* and *Ceriodaphnia* did not change their daytime habitat in the presence of piscivores, which suggests considerable differences in behavioral responses to predators among zooplankton genera. Some zooplankton groups may respond to a combination of actual predation risk and competitive interactions (Stich and Lampert 1981; Vanni 1986), whereas other groups may not respond behaviorally at all.

We may only speculate about how the behavioral cascade induced by the presence of piscivores would affect the outcome of the trophic cascade in a lake. If pelagic piscivores and small (0+) planktivores dominate the fish community, large zooplankton will be able to move out from the refuge when pelagic piscivores prevents small planktivores from foraging in open water. In this case, large zooplankton will probably have a higher total density than if piscivores were absent, because the predation pressure will be lower in their preferred habitat. In an even more complex food web, behavioral cascades may further complicate the outcome of the trophic cascade.

In conclusion, by applying horizontal echo sounding techniques to an experimental setup, we were able to show that the behavioral responses of 0+ fish in the presence of a caged pelagic piscivore, releases *Daphnia* from the risk of predation outside the refuge, and enables them to migrate back to their possibly preferred habitat also during daytime. Thus, a main conclusion from our study is that the concept of cascading trophic interactions, based solely on direct consumption links, has to be complemented with a cascading behavioral interaction concept, because many of the predicted direct interactions obviously never occur because of behavioral adjustments among prey at different levels (Fig. 1).

References

Abrams, P. A., B. A. Menge, G. G. Mittelbach, D. Spiller, and P. Yodiz. 1996. The role of indirect effects in food webs, p. 371–395. *In* G. A. Polis and K. O. Winemiller [eds.], Food webs. Integration of patterns and dynamics. Chapmann & Hall.

Brabrand, Å., and B. Faafeng. 1993. Habitat shift in roach (*Rutilus rutilus*) induced by pikeperch (*Stizostedion lucioperca*) introduction: Predation risk versus pelagic behavior. Oecologia **95:** 38–46.

Brönmark, C., and J. Miner. 1992. Predator-induced phenotypic changes in body morphology in Crucian carp. Science **258:** 1348–1350.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience **35:** 634–639.

Christensen, B. 1996. Predator foraging capabilities and prey antipredator behaviors: Pre- versus postcapture constraints on size-dependent predator prey interactions. Oikos **76:** 368–380.

———, and L. Persson. 1993. Species-specific antipredatorbehaviours: Effects on prey choice in different habitats. Behav. Ecol. Sociobiol. **32:** 1–9.

De Meester, L., P. Dawidowicz, E. van Gool, and C. J. Loose. 1999. Ecology and evolution of predator-induced behavior of zooplankton: Depth selection behaviour and diel vertical migration, p. 161–176. *In* R. Tollrian and D. C. Harvell [eds.], The ecology and evolution of inducible defenses. Princeton Univ. Press.

Eklöv, P., and S. Diehl. 1994. Piscivore efficiency and refuging prey: The importance of predator search mode. Oecologia **98:** 344–353.

Hall, D. J., and others. 1979. Diel foraging behavior and prey selection in the golden shiner (*Notemigonus crysoleucas*). J. Fish. Res. Board Can. **36:** 1029–1039.

Hansson, L.-A. 1992. The role of food chain composition and nutrient availability in shaping algal biomass development. Ecology **73:** 241–247.

———. 2000. Synergistic effects of food web dynamic and induced behavioural responses in aquatic ecosystems. Ecology **81:** 842–851.

Hargeby, A., G. Andersson, I. Blindow, and S. Johansson. 1994. Trophic web structure in a shallow eutrophic lake during dominance shift from phytoplankton to submerged macrophytes. Hydrobiology **279/280:** 83–90.

Irving, P. W., and A. E. Magurran. 1997. Context-dependent fright reactions in captive European minnows: The importance of naturalness in laboratory experiments. Anim. Behav. **53:** 1193–1201.

Krause, J., S. P. Loader, J. McDermott, and D. Ruxton. 1998. Refuge use by fish as a function of body length–related metabolic expenditure and predation risk. Proc. R. Soc. Lond. B **265:** 2373–2379.

Kubecka, J. 1996. Use of horizontal dual-beam sonar for fish surveys in shallow waters, p. 165–178. *In* I. G. Cowx [ed.], Stock assessment in inland fisheries. Blackwell Scientific.

Lauridsen, T. L., and I. Buenk. 1996. Diel changes in the horizontal distribution of zooplankton in the littoral zone of two shallow eutrophic lakes. Arch. Hydrobiol. **137:** 161–176.

———, and D. M. Lodge. 1996. Avoidance by *Daphnia magna* of fish and macrophytes: Chemical cues and predator mediated use of macrophyte habitat. Limnol. Oceanogr. **4:** 794—798.

———, L. J. Pedersen, E. Jeppesen, and M. Søndergaard. 1996. The importance of macrophyte bed size for cladoceran composition and horizontal migration in a shallow lake. J. Plankton Res. **18:** 2283–2294.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Can. J. Zool. **68:** 619–640.

Manatunge, J., T. Aseada, and T. Priyadarshana. 2000. The influence of structural complexity on fish-zooplankton interactions: A study using artificial submereged macrophytes. Environ. Biol. Fish. **58:** 425–438.

Mazumder, A. 1994. Patterns of algal biomass in dominant odd- vs. even-link lake ecosystems. Ecology **75:** 1141–1149.

Miller, T. E., and W. C. Kerfoot. 1987. Redefining indirect effects, p. 33–37. *In* W. C. Kerfoot and S. Sih [eds.], Predation: Direct and indirect impacts on aquatic communities. Univ. Press of New England.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends Ecol. Evol. **14:** 483–488.

Peacor, S. D., and E. E. Werner. 1997. Trait-mediated indirect interactions in a simple aquatic food web. Ecology **78:** 1146–1156.

Persson, L. 1999. Trophic cascades: Abiding heterogeneity and the trophic level concept at the end of the road. Oikos **85:** 385–397.

———, and P. Eklöv. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. Ecology **76:** 70–81.

Pitcher, T. J., and J. K. Parrish. 1993. Functions of shoaling behaviour in teleosts, p. 363–439. *In* T. J. Pitcher [ed.], Behaviour of teleost fishes. Chapman and Hall.

Romare, P. 2001. An evaluation of horizontal echo sounding as a method for behavioral studies of 0+ fish in field experiments. J. Fish Biol. **58:** 1512–1523.

Schriver, P., J. Bøgstrand, E. Jeppesen, and M. Søndergaard. 1995. Impact of submerged macrophytes on fish-zooplankton–

phytoplankton interactions: Large-scale enclosure experiments in a shallow eutrophic lake. Freshw. Biol. **33:** 255–270.

SIH, A., G. ENGLUND, AND D. WOOSTER. 1998. Emergent impacts of multiple predators on prey. Trends Ecol. Evol. **13:** 350–355.

STICH, H. B., AND W. LAMPERT. 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. Nature **293:** 396–396.

TIMMS, R. M., AND B. MOSS. 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing in the presence of zooplanktivorous fish in a shallow wetland ecosystem. Limnol. Oceanogr. **29:** 472–486.

TURNER, A. M., AND G. G. MITTELBACH. 1990. Predator avoidance and community structure: Interaction among piscivores, planktivores, and plankton. Ecology **71:** 2241–2254.

VAN DEN BERG, C., J. G. M., VAN DEN BOOGAART F. A. SIBBING, AND J. W. M. OSSE. 1994. Zooplankton feeding in common bream (*Abramis brama*), white bream (*Blicca bjoerkna*) and roach (*Rutilus rutilus*): Experiments, models and energy intake. Neth. J. Zool. **44:** 15–42.

VANNI, M. J. 1986. Competition in zooplankton communities: Suppression of small species by *Daphnia pulex.* Limnol. Oceanogr. **31:** 1039–1056.

WANZENBÖCK, J. 1995. Changing handling times during feeding and consequences for prey size selection of 0+ zooplanktivorous fish. Oecologia **104:** 372–378.

WERNER, E. E., AND J. F. GILLIAM. 1984. The ontogenetic niche and species interactions in size-structured populations. Anim. Rev. Ecol. Syst. **15:** 393–425.

WINFIELD, I. J. 1986. The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Rutilus rutilus,* rudd, *Scardinius erythrophtalmus,* and perch, *Perca fluviatilis.* J. Fish. Biol. Suppl. A **29:** 37–48.

WOOTTON, J. T. 1993. Indirect effects and habitat use in an intertidal community—interaction chains and interaction modifications. Am. Nat. **141:** 71–89.

———. 1994. The nature and consequences of indirect effects in ecological communities. Annu. Rev. Ecol. Syst. **25:** 443–466.

Received: 7 August 2002
Accepted: 17 March 2003
Amended: 13 April 2003