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## Decoupling of cascading trophic interactions in a freshwater, benthic food chain

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**Abstract** Food chain theory provides explicit predictions for equilibrium biomasses among trophic levels in food chains of different lengths. Empirical studies on freshwater benthic food chains have typically been performed on chains with up to three levels and in field experiments with limited spatial and temporal scale. Here we use a “natural snapshot experiment” approach to study equilibrium biomass and abundance among trophic levels in natural ponds differing only with respect to fish assemblage structure. Forty-four ponds were surveyed for their density and biomass of fish, snails and periphyton. Ponds were divided into three categories based on fish assemblage: ponds with no fish (two trophic levels), ponds with molluscivorous fish (three trophic levels) and ponds that also had piscivorous fish (four trophic levels). Ponds without fish had a high density and biomass of snails and a low biomass of periphyton, whereas snails were scarce and periphyton biomass was high in ponds with molluscivorous fish. In the presence of piscivores, molluscivore populations consisted of low numbers of large individuals. Snail assemblages in piscivore ponds were characterised by relatively high densities of small-bodied detritivorous species and periphyton biomass was not significantly different from ponds with three trophic levels. Thus, predictions from classic food chain theory were upheld in ponds with up to three trophic levels. In ponds with four trophic levels, however, there was a decoupling of the trophic cascade at the piscivore-molluscivore level. Gape-limited piscivory, predation on snails by molluscivores that have reached an absolute size refuge from predation, and changes in food preferences of the dominant snails are suggested to explain the observed patterns.

**Key words** Interaction strength · Predation · Ponds · Snails · Periphyton

### Introduction

The importance of complex, indirect interactions in freshwater food chains has been recognised in many recent studies. This is especially evident in freshwater pelagic food chains where experimental manipulations of the top trophic levels have often been shown to affect the structure of lower trophic levels through cascading trophic interactions (e.g. Kerfoot and Sih 1987; Carpenter 1988; Gulati et al. 1990; Carpenter and Kitchell 1993). Typically, an increase in piscivore abundance results in a decrease in phytoplankton biomass through a decrease in the density of planktivorous fish species and a concomitant increase in large, cladoceran zooplankton. Strong (1992) suggested that strong effects of cascading interactions are characteristic of species-poor aquatic communities, whereas in more speciose systems the top-down effects are buffered by e.g. a high degree of omnivory and temporal and spatial heterogeneity. However, benthic littoral communities in lakes are typically characterised by high spatial heterogeneity with speciose faunal assemblages where omnivory can be a prominent factor (e.g. Diehl 1992, 1995; Lodge et al. 1994), and yet several recent studies have shown that cascading trophic interactions may have strong effects even in benthic freshwater communities (Power 1990, 1992; Brönmark et al. 1992; Martin et al. 1992; Wootton and Power 1993; Brönmark 1994; Lodge et al. 1994). Several of these studies included interactions between periphytic algae, herbivorous snails and a snail predator (Brönmark et al. 1992; Martin et al. 1992; Brönmark 1994; Lodge et al. 1994).

Snails are an important component of many freshwater benthic food chains, and it has been suggested that predation is the most important factor structuring snail assemblages in permanent lakes and ponds where calcium is not a limiting factor (Lodge et al. 1987). Recently, several studies have shown strong effects of predation on snail density and species composition in ponds and lakes (Weber and Lodge 1990; Merrick et al. 1991; Brönmark et al. 1992; Martin et al. 1992; Brönmark 1994; Lodge et al. 1994). Freshwater snails can have strong effects on

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their major food source, periphytic algae, and affect algal biomass, productivity and species composition (see Brönmark 1989 for a review), and thus predation by a snail predator may indirectly benefit periphytic algae through a decrease in grazing pressure. Predation by specialised molluscivorous sunfishes (Brönmark et al. 1992; Martin et al. 1992) and tench (Brönmark 1994) had indirect positive effects on periphyton through a reduction of herbivorous snails, and similar results were found in an experiment where the density of crayfish was manipulated (Lodge et al. 1994). Thus, these studies showed strong cascading effects in a benthic food chain with three trophic levels (fish/crayfish, snails, algae). Many freshwater systems, however, include a fourth trophic level, piscivorous fish, and although studies on interactions in four-level food chains are commonplace in pelagic systems, only a few studies have addressed the importance of a fourth trophic level in benthic food chains (Power 1990, 1992; Wootton and Power 1993). Thus, further studies on the effect of piscivores on interactions in benthic food chains are needed.

In the above studies on benthic food chains, cascading effects were evaluated by manipulating the density of top predators in enclosure/exclosure field experiments. The use of cages to study mechanisms of interactions between species has clear advantages but also limitations (e.g. Diamond 1986; Frost et al. 1988; Cooper and Barmuta 1993). Results may be confounded by e.g. edge effects, replicates poorly matched for spatial heterogeneity, and changes in the behaviour of organisms in enclosures. These experimental side-effects may increase or outweigh the effect of a manipulation. Furthermore, the duration of experimental studies may also be critical when evaluating the strength of cascading trophic interactions. Although predictions from food chain models (e.g. Oksanen et al. 1981) consider patterns in equilibrium biomass among trophic levels, the importance of cascading trophic interactions in benthic food chains has typically been inferred from strong perturbations of top trophic levels and monitoring of the system over a rather short period post-manipulation (weeks to months, but see Brönmark et al. 1992). On a longer time-scale, changes in the species composition and size structure of prey assemblages together with the plasticity of prey defences and behaviour may decouple the initially strong interactions between top predators and lower trophic levels.

An alternative to experimental manipulations is the "natural snapshot experiment" (Diamond 1986), where a large number of natural systems, in which predator and prey have coexisted for many generations, are surveyed, and then patterns in equilibrium biomass with regard to the studied character can be compared to predictions from theory and/or results from smaller-scale experimental studies.

In this study, we surveyed ponds similar in productivity and superficially differing in only one respect, the composition of the fish assemblage. Given the results from earlier enclosure/exclosure manipulations of benthic freshwater food chains (Power 1990, 1992; Brönmark et al. 1992; Martin et al. 1992; Wootton and Power 1993; Brönmark 1994; Lodge et al. 1994), we expected high densities of snails and a low periphyton biomass in ponds without fish, and low densities of snails and high periphyton biomass in ponds with molluscivorous fish. In addition, predictions from food chain theory and results from experiments in pelagic food chains suggest that including a fourth trophic level, piscivores, should affect lower trophic levels such that molluscivorous fish should decrease in density, snails increase and periphyton decrease.

## Material and methods

Food chain composition was studied in 44 ponds situated near Lund, southern Sweden, in an area with numerous ponds. These ponds occur in an area with a similar geological background (glaciofluvial moraine deposits), and thus any differences in fish or snail densities between ponds should not be due to water chemistry (Table 1); all ponds are eutrophic and hard water.

Fish assemblage composition, snail abundance and periphyton biomass in the ponds were determined during the period 30 July - 17 September 1990. Fish were sampled with two multimesh monofilament nylon gill nets, consisting of panels with mesh sizes of 6, 8, 10, 12.5, 16.5, 22, 30, 40, 55, 75 and 100 mm. The nets were placed in the ponds overnight. In addition, fish associated with the vegetated littoral zone were sampled by electrofishing at 6-8 sites along the perimeter of the pond. The number of individuals and total wet mass of each species were quantified, and 5-10 individuals of representative size classes of each species were placed in a plastic bag, kept on ice and deep-frozen upon arrival in the laboratory. These fish were later analysed for gut content. Invertebrate prey items were identified to the lowest possible taxonomic unit and the presence of vegetation and fish remains in the gut contents was noted.

Benthic invertebrates were sampled with a sweep-net (area = 710 cm<sup>2</sup>, mesh size = 1 mm). Five samples were taken from

**Table 1** Physicochemical characteristics (mean±SD) of ponds with no fish, ponds with molluscivorous fish only and ponds with molluscivores and piscivores

	No fish	Molluscivores	Piscivores
Conductivity (mS/m)	45.5±8.5	60.8±19.5	56.0±11.8
Alkalinity (mEq/l)	2.8±0.7	3.8±1.8	4.4±2.0
pH	7.9±0.5	8.1±0.4	8.0±0.35
Total phosphorus (µg/l)	158±116	442±430	291±431
Total nitrogen (µg/l)	2.1±0.5	2.3±1.7	1.5±0.4
Turbidity (JTU)	5.8±3.6	25.0±62.5	6.1±4.7
Area (m <sup>2</sup> )	817±393	1868±1079	5686±5426
Maximum depth (m)	1.4±0.4	1.9±0.7	2.6±1.0
Mean depth (m)	0.8±0.3	1.1±0.5	1.6±0.6
Number of ponds	5	11	28

each pond at sites chosen haphazardly along the pond perimeter. The water depth at the sampling sites ranged from 0.3 to 1.0 m. At each site, the net was pushed through the vegetation for 1 min. The contents of the net were emptied into a plastic container and preserved in alcohol. The sweep-net samples were later sorted in the laboratory and all snails were identified to species and weighed after drying to constant mass (60°C, 24 h). Only the averages from the five sweep-net samples from each pond were used in the final analyses.

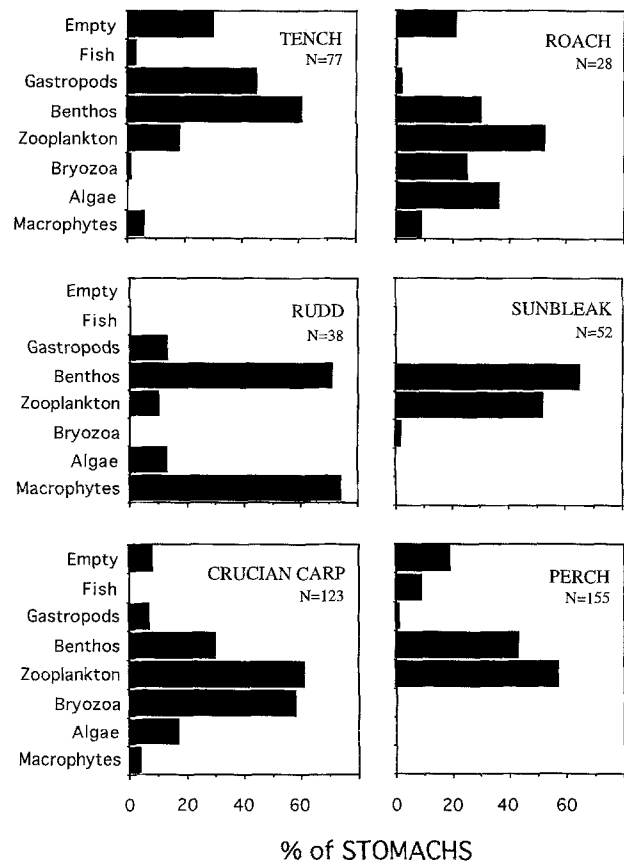
Periphyton were quantified using an artificial substrate (plastic flagging tape). The biomass of periphyton colonising plastic flagging has been shown to closely mirror the biomass of periphyton on natural, submerged macrophytes (Brönmark et al. 1992). On 19 June, three strips of plastic flagging (each strip 80×3 cm) were placed in all ponds, each strip at a different location within the pond. The strips were anchored to the sediment with a screw nut and a small piece of Styrofoam tied to the other end kept them vertical in the water column. All strips were removed from the ponds on 5 September. Strips were transferred individually to a plastic bag, stored on ice and deep-frozen upon arrival in the laboratory. Periphyton were removed from the strips by brushing with a toothbrush and rinsing with water. The volume of the algal suspension was determined and a subsample was filtered onto a preweighed glassfiber filter (Whatman GF/C), dried (60°C, 24 h) and reweighed for determination of periphyton dry mass. The average biomass from the three strips in each pond was used in the analysis.

A watersample was taken from each pond and analysed for pH, alkalinity, turbidity and total phosphorus. Water depth in the ponds was determined along two perpendicular transects crossing the centre of the pond, giving the mean and maximum depth. Pond surface areas were determined from aerial photographs.

## Results

Pike [*Esox lucius* (L.)], crucian carp [*Carassius carassius* (L.)], tench [*Tinca tinca* (L.)], bream [*Abramis brama* (L.)], rudd [*Scardinius erythrophthalmus* (L.)], roach [*Rutilus rutilus* (L.)], sunbleak [*Leucaspis delineatus* (Heckel)], eel [*Anguilla anguilla* (L.)], ten-spined stickleback [*Pungitius pungitius* (L.)], and perch [*Perca fluviatilis* (L.)] were collected in the ponds. Six of these species were captured in sufficient numbers to allow gut content analyses (Fig. 1). These, in combination with literature data and results from a field experiment (C. Brönmark and J.G. Miner, unpublished data), suggested that three of the fish species are potentially important as snail predators, namely tench, crucian carp and rudd, having snails in 45%, 7% and 13% of the guts, respectively. Besides snails, the diets of these species mainly included other benthic invertebrates, zooplankton and, in the case of rudd, plants. Snails comprised <2% of the gut contents in the remaining fish species. Based on gut content analyses, perch >10 cm in total length were considered as potential piscivores, whereas all pike caught were piscivorous.

Ponds were separated into three categories based on fish assemblage structure, i.e. ponds without any fish (No fish), ponds with molluscivorous fish (tench, crucian carp and/or rudd) but without piscivores (Molluscivores) and ponds that also had piscivorous fish (pike and/or perch; Piscivores). A discriminant analysis was performed on water chemistry and pond size variables (Table 1) to see if there were any differences between pond



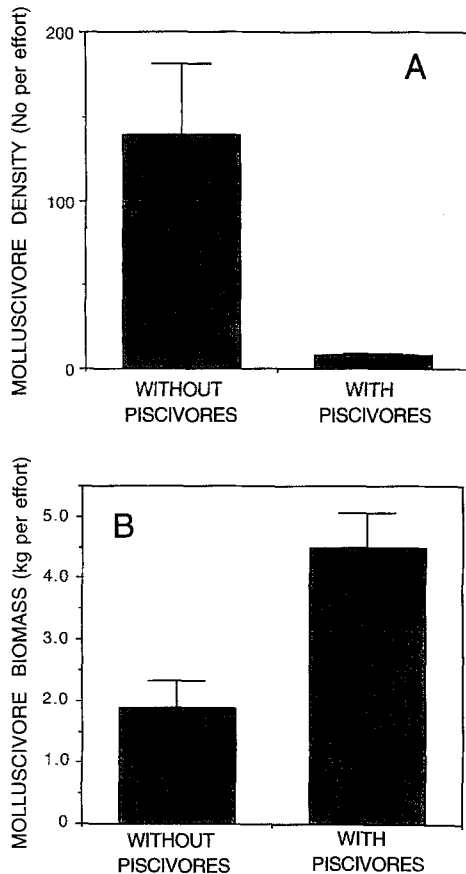
**Fig. 1** Gut contents of the six most abundant fish species in the ponds, expressed as the percentage of guts containing a given food item

**Table 2** Fish biomass (kilograms wet mass per unit effort, mean±SE) in ponds with and without piscivores. Perch >10 cm total length are considered as potential piscivores, based on gut content analysis

Fish species	Molluscivore ponds	Piscivore ponds
Crucian carp	1.63±0.48	0.39±0.13
Tench	0.27±0.13	3.91±0.60
Bream	–	0.11±0.11
Rudd	–	0.22±0.08
Roach	0.05±0.04	0.86±0.14
Sunbleak	0.02±0.01	0.03±0.01
Perch <10 cm	–	0.16±0.11
Perch >10 cm	–	0.40±0.07
Pike	–	1.13±1.30

categories with respect to abiotic characteristics. There was no significant difference ( $P = 0.302$ ) between ponds without fish and Molluscivore ponds, whereas Piscivore ponds were significantly different from No fish ponds ( $P = 0.008$ ) and Molluscivore ponds ( $P = 0.016$ ). Piscivore ponds were deeper (maximum depth,  $P = 0.008$ ; mean depth,  $P = 0.004$ ) and larger (area,  $P = 0.029$ ; Table 1). There was no difference between pond categories with respect to water chemistry variables.

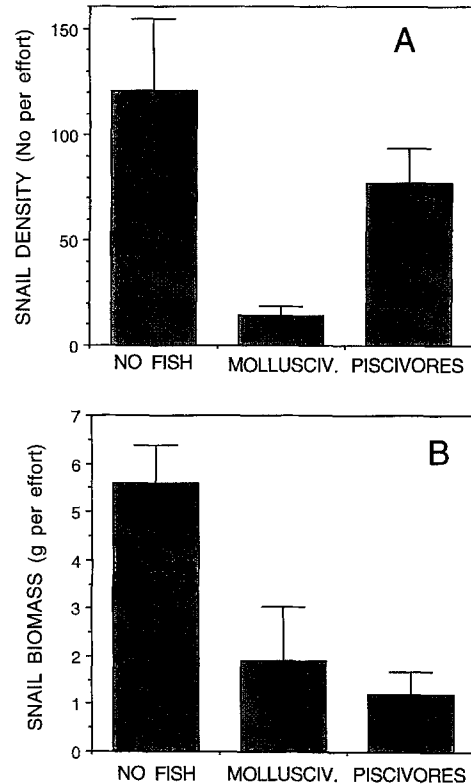
The density of molluscivorous fish was much greater in ponds without piscivores than in ponds with the pi-



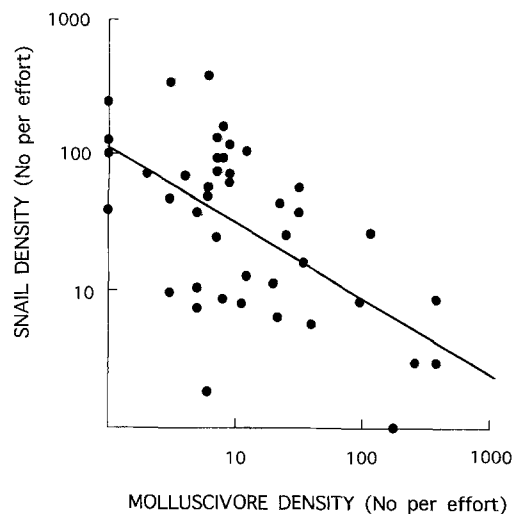
**Fig. 2** Density (number per unit effort) **A** and biomass (kilograms wet mass per unit effort) **B** of molluscivorous fish, including tench, crucian carp and rudd, in ponds with and without piscivores. Vertical bars denote 1 SE

scivorous northern pike and/or perch (Table 2, Fig. 2A, ANOVA  $F = 76.9$ ,  $P < 0.001$ ), whereas total molluscivore biomass was higher in ponds with piscivores (Fig. 2B, ANOVA  $F = 6.5$ ,  $P = 0.015$ ). Molluscivorous fish in the surveyed ponds mainly consisted of crucian carp and tench ( $79 \pm 32\%$  of molluscivore density,  $91 \pm 22\%$  of biomass; mean  $\pm$  SD), with rudd being less important.

Fish assemblage structure had a significant effect on snail density (Fig. 3A; ANOVA  $F = 9.05$ ,  $P = 0.001$ ). Snail densities were high in ponds that lacked molluscivorous fish, whereas in the presence of molluscivores there was a dramatic reduction in snail densities. Snail densities in ponds that had piscivorous fish were higher than in ponds with molluscivores only, and similar to densities in ponds without molluscivores. The differences in snail density between Molluscivore and No fish or Piscivore ponds were significant (Tukey test,  $P = 0.003$ , and  $P = 0.002$ , respectively), whereas there was no significant difference between No fish ponds and Piscivore ponds ( $P = 0.323$ ). The large effect of molluscivores on snail densities was also seen when all the data were combined, resulting in a significant negative relationship between snail density and molluscivore density (Fig. 4, linear regression  $F = 23.4$ ,  $P < 0.001$ ).



**Fig. 3** Density (numbers per sweep-net sample) **A** and biomass (grams dry weight per sweep-net sample) **B** of snails in ponds without fish, ponds with molluscivorous fish and ponds with molluscivores and piscivores. Vertical bars denote 1 SE



**Fig. 4** The relationship between molluscivore density (numbers caught per unit effort) and snail density (numbers per sweep net sample) in surveyed ponds

However, the pattern for snail biomass differed from that for snail densities (Fig. 3B). Snail biomass was significantly higher in ponds without fish than in ponds with molluscivores or in ponds with piscivores (ANOVA,  $F = 9.60$ ,  $P < 0.001$ ; Tukey test  $P = 0.004$  and  $P < 0.001$ , respectively). There was no difference be-

**Table 3** Factor loadings for snail species in ponds with different fish species composition

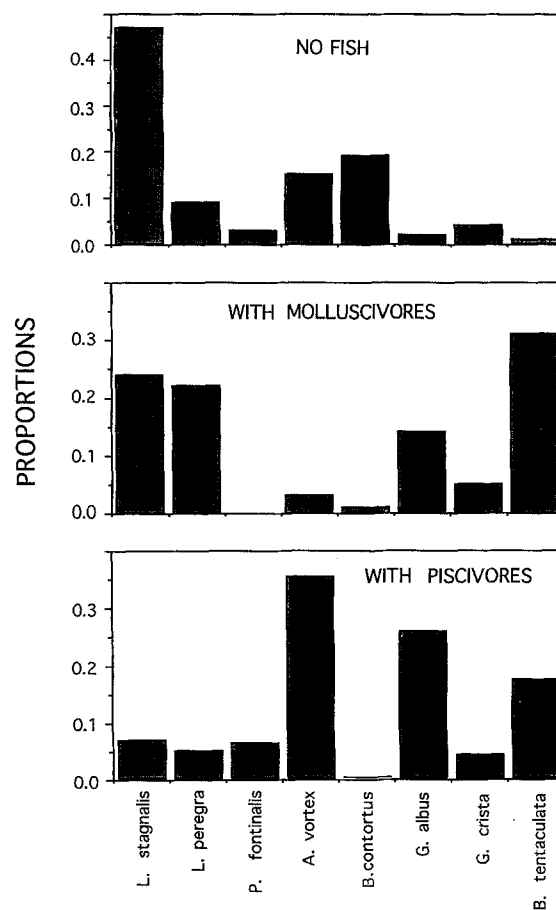
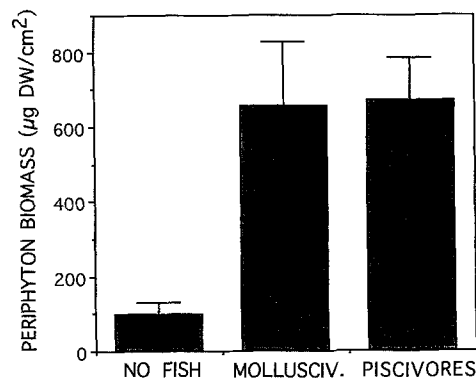
	Principal component	
	1	2
Variance explained	20.7	18.3
Eigenvalue	1.65	1.46
<i>Lymnaea stagnalis</i>	0.66	0.47
<i>Lymnaea peregra</i>	0.14	0.13
<i>Physa fontinalis</i>	-0.47	0.41
<i>Anisus vortex</i>	-0.75	0.40
<i>Bathyomphalus contortus</i>	0.36	0.19
<i>Gyraulus albus</i>	-0.40	-0.72
<i>Gyraulus crista</i>	-0.02	-0.17
<i>Bithynia tentaculata</i>	0.36	-0.55

**Table 4** Comparisons of the principal-component scores for the different pond categories

Pond category	Mean principal-component score	
	axis 1	axis 2
No fish	0.99	1.08
Molluscivores	0.86	-0.28
Piscivores	-0.55	-0.12

tween Molluscivore ponds and Piscivore ponds (Tukey test  $P = 0.71$ ). Thus, the low biomass of snails in the piscivore ponds in relation to the high densities suggests that there is a shift in snail species composition to a dominance of smaller species in the presence of molluscivores. To analyse snail species composition in relation to predator regime (pond category) we performed a principal-components analysis (PCA). Differences among pond categories in principal-component scores were analysed with ANOVA (Tables 3, 4). The first PCA axis separated ponds with piscivores from ponds with either no fish or with molluscivores (Table 4; ANOVA  $F = 22.0$ ,  $P < 0.001$ ; Tukey test  $P < 0.001$ ), whereas No fish ponds were significantly different from the two other pond categories along the second principal-components axis (ANOVA  $F = 4.91$ ,  $P = 0.01$ ; Tukey test  $P < 0.05$ ). Thus, ponds with no fish were dominated by *Lymnaea stagnalis* (L.), whereas both pond categories with molluscivores had relatively more *Gyraulus albus* (Müller) and *Bithynia tentaculata* (L.) (Fig. 5). Further, in ponds where molluscivores coexisted with piscivores, *Anisus vortex* (L.) dominated.

The biomass of periphyton on artificial substrate differed between pond categories (Fig. 6). Artificial substrates in ponds without fish had significantly less periphyton than in ponds with fish (ANOVA  $F = 6.01$ ,  $P = 0.006$ ; Tukey test  $P < 0.01$ ). There was no difference in periphyton biomass between ponds with molluscivores only and ponds that also had piscivores (Tukey test  $P = 0.99$ ).

**Fig. 5** Relative snail species composition in ponds without fish, ponds with molluscivorous fish and ponds with both molluscivores and piscivores**Fig. 6** Periphyton biomass [ $\mu\text{g}$  dry weight (DW)/ $\text{cm}^2$ ] on artificial substrates in ponds without fish, ponds with molluscivorous fish and ponds with both molluscivores and piscivores. Vertical bars denote 1 SE

## Discussion

The presence of piscivores in these ponds had a dramatic effect on populations of molluscivorous fish. Ponds with piscivores had a low density of molluscivores although the molluscivore biomass was high, whereas in ponds

without piscivores, the density of molluscivores was high but the biomass low. The dominant molluscivores in the surveyed ponds were tench and crucian carp, species whose population densities and size structures are greatly affected by the presence of piscivores (Piironen and Holopainen 1988; Brönmark et al. 1995). In the surveyed ponds, populations of both species were dominated by small individuals at high densities in the absence of piscivores, whereas in ponds with piscivorous pike and/or perch, populations of crucian carp and tench were sparse and consisted almost exclusively of large-bodied individuals (Brönmark et al. 1995), resulting in a large total biomass. Field experiments have demonstrated that size-limited predation is responsible for the population structure of crucian carp in ponds with piscivores (Tonn et al. 1989, 1991; Holopainen et al. 1991; Brönmark and Miner 1992), whereas the high-density crucian carp populations in ponds without piscivores are limited by intraspecific competition (Paszkowski et al. 1990; Tonn et al. 1994). The evidence for tench is less extensive, but results from whole-pond experiments where pike density was manipulated indicate that piscivory can effectively reduce density and change the size structure of tench populations as well (C. Brönmark and J.G. Miner, unpublished data).

Ponds with piscivores were larger and deeper than ponds without fish or with molluscivorous fish. Piscivores, such as pike and perch, are sensitive to the low-oxygen conditions that may prevail in shallow, eutrophic ponds covered by ice during winter, whereas tench and, especially, crucian carp can survive very low oxygen levels (e.g. Doudoroff and Shumway 1970). Crucian carp have physiological adaptations for anaerobic metabolism under low temperatures (Holopainen and Hyvärinen 1985) and this allows them to survive the almost completely anoxic conditions during winter kill conditions that may commonly occur in shallow ponds during harsh winters.

Molluscivorous fish had a strong effect on snails in accordance with earlier studies showing that predators, such as fish and crayfish, can have strong direct effects on the density and species composition of freshwater snail assemblages (Brown and DeVries 1985; Merrick et al. 1991; Brönmark et al. 1992; Martin et al. 1992; Osenberg et al. 1992; Brönmark 1994; Lodge et al. 1994). The relative dominance of snail species changed in response to predation pressure in these ponds. In the absence of molluscivorous fish, the snail assemblage was dominated by the large, relatively thinshelled species *L. stagnalis*, whereas in the presence of molluscivorous fish, there was a shift in dominance towards smaller, more thick-shelled species such as *G. albus* and *B. tentaculata*. Foraging experiments in the laboratory have shown that both crucian carp and tench are sizeselective and prefer thinshelled species such as *Lymnaea* over thickshelled species such as *Bithynia* (W.M. Tonn, C.A. Paszkowski and C. Brönmark, unpublished work). Studies on other molluscivores have shown that they are size and/or species selective (Stein et al. 1984; Osenberg and

Mittelbach 1989; Klosiewski 1991), and thus predation by molluscivorous fish or crayfish may alter the species composition in freshwater snail assemblages towards small, thick-shelled species (Brown and DeVries 1985; Klosiewski 1991; Lodge et al. 1994). Predation may also have indirect effects, for example by reducing the density of a competitively dominant species, allowing other species to increase in density. Predation by lake trout controls densities of *Lymnaea elodes* (Say) in arctic lakes (Merrick et al. 1991), and it was suggested that a reduction in density of the competitively dominant *L. elodes* allows a fugitive species, *Valvata lewisi* (Currier), to increase to high population densities (Hershey 1990).

Addition of a fourth trophic level, the piscivores, was predicted to decrease the predation pressure on snails, and thus in ponds with piscivores, the density of snails would be higher than in ponds with molluscivores only. Indeed, snail densities in piscivore ponds were higher than in ponds with molluscivores. Furthermore, food chain models may also predict the relative ranking of snail abundances in two-versus four-level systems. Oksanen et al. (1981) predicted that the number of trophic levels increases as a function of productivity. However, in this study, productivity is similar among ponds, whereas the number of trophic levels differs. Thus, predictions for two- and three-level systems could be extended into the productivity region which supports four-level systems (see e.g. Fig. 1 in Mittelbach et al. 1988), resulting in the prediction that snails should be most abundant in two-level systems, least abundant in three-level systems and intermediate in systems with four trophic levels. The ranking of snail abundances among pond categories is in accordance with these predictions (Fig. 3), although differences between ponds without molluscivores and ponds with piscivores (two vs. four-levels) were not significant. Snail biomass, however, was not higher in ponds with piscivores than in ponds with only molluscivores. In piscivore ponds, the relative importance of larger species such as lymneids and *Bithynia* decreased further and the small *A. vortex* and *G. albus* dominated. Small numbers of large-bodied tench and crucian carp coexisted with piscivores and the predation pressure from these may be intense enough to control the densities of large species.

A number of studies in both streams and lakes have shown that snails are dominant grazers of periphytic algae and can reduce standing crops and change species composition of the periphytic layer (e.g. Brönmark 1989; McCormick and Stevenson 1989; Swamikannu and Hoagland 1989; Barnese et al. 1990). Recently, manipulations of molluscivore density have been shown to indirectly affect periphytic algae. Enclosure/exclosure experiments in the field have shown that molluscivorous sunfishes (Brönmark et al. 1992; Martin et al. 1992) and tench (Brönmark 1994) reduce the density of snails, indirectly increasing the biomass of periphytic algae. A positive, indirect effect on periphyton through decreased grazing pressure by snails was also shown in a study of the more omnivorous crayfish, *Orconectes rusticus*

(Lodge et al. 1994), which also feeds on macrophytes and periphyton. In the present study, we predicted that the periphyton biomass on an artificial substrate should be highest in molluscivore ponds (three-level systems), intermediate in piscivore ponds (four-level) and lowest in ponds without fish (two-level). Periphyton biomass was indeed much higher in ponds with fish where snail densities were low than in ponds without fish and with high snail densities. However, the higher density of snails in ponds with piscivores did not result in reduced periphyton biomass as compared to molluscivore ponds. This is probably due to the low biomass of snails in the piscivore ponds, i.e. a dominance of small species. In a recent review of factors affecting removal rates of periphyton by grazers, it was shown that grazer body mass was the most important determinant of periphyton removal rates (Cattaneo and Mousseau 1995). However, Vermaat (1994) showed that mass specific periphyton removal rates differed between snail species. Grazing rates of *B. tentaculata*, which was one of the dominating species in ponds with molluscivores, were only 10% of *Lymnaea peregra* grazing rates. Further, lymneid snails prefer algae and have a high cellulase activity and assimilation efficiency of algal food items, whereas planorbids, such as *Anisus* and *Gyraulus*, have low cellulase activity and are mainly detritivores (Calow and Calow 1975). A shift in snail species composition from species which have high grazing rates on periphytic algae to species which are less efficient grazers or are mainly detritivorous should reduce the grazing pressure on periphytic algae.

The patterns among trophic levels in food chains with up to three levels displayed in this survey of natural systems, where predator and prey have coexisted for many generations, are in general agreement with the predictions from food chain theory and earlier experiments. Molluscivorous fish reduced snail densities and had an indirect positive effect on periphyton. However, patterns among trophic levels in ponds with four trophic levels were not fully consistent with the theory and results from earlier field experiments. Piscivores reduced molluscivore density to have a positive effect on snail densities but not on snail biomass, and the primary producers, periphytic algae, were not affected by the addition of a fourth trophic level. Manipulations of food chains with four trophic levels in pelagic freshwater systems have often shown that piscivores impose strong cascading effects all the way down to the primary producers, phytoplankton (e.g. Carpenter and Kitchell 1993). With benthic freshwater food chains, only one study has so far manipulated the density of secondary predators (Power 1990). In a stream, steelhead salmon and roach reduced fish fry and invertebrate predators, resulting in an increase in herbivorous midge larvae and a reduction in the biomass of filamentous algae. Many factors, including e.g. omnivory, spatial and temporal heterogeneity, and efficient prey defence adaptations may decouple predator-prey dynamics and affect the strength of indirect interactions in food chains (Strong 1992; Neill 1994). Furthermore, changes in the size structure of prey popula-

tions may affect predation intensity. For example, large, deep-bodied planktivores may enjoy an absolute size refuge from predation by gape-limited piscivores, resulting in a population of planktivores dominated by large individuals (Hambright et al. 1991; Hambright 1994). The continued ingestion of zooplankton by these larger individuals could uncouple trophic interactions in the pelagic food chain, i.e. reduce the efficiency of transfer of cascading effects from piscivores to phytoplankton. In the surveyed ponds, we believe that low abundances of molluscivores that have reached an absolute size refuge from predation by piscivores reduced densities of large, efficient, periphyton-grazing snail species, resulting in a snail assemblage dominated by small, thick-shelled, mainly detritivorous snail species. Hence, decoupling of the trophic cascade at the piscivore-molluscivore level resulted in patterns of biomass distribution among trophic levels that deviate from predictions from classic food chain theory. Gape-limited predation, prey defence adaptations and grazer food choice may all contribute to reducing the interaction strength in this benthic freshwater food chain.

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## References

- Barnese LE, Lowe R, Hunter RD (1990) Comparative grazing efficiency of pulmonate and prosobranch snails. *J North Am Benthol Soc* 9: 35–44
- Brönmark C (1989) Interactions between epiphytes, macrophytes and freshwater snails: a review. *J Molluscan Stud* 55: 299–311
- Brönmark C (1994) Effects of tench and perch on interactions in a freshwater, benthic food chain. *Ecology* 75: 1818–1824
- Brönmark C, Miner JG (1992) Predator-induced phenotypical change in body morphology in crucian carp. *Science* 258: 1348–1350
- Brönmark C, Klosiewski SP, Stein RA (1992) Indirect effects of predation in a freshwater, benthic food chain. *Ecology* 73: 1662–1674
- Brönmark C, Paszkowski CA, Tonn WM, Hargeby A (1995) Predation as a determinant of size structure in populations of crucian carp (*Carassius carassius*) and tench (*Tinca tinca*). *Ecology of Freshwater Fish* 4: 85–92
- Brown KM, DeVries DR (1985) Predation and the distribution and abundance of a pulmonate pond snail. *Oecologia* 66: 93–99
- Calow P, Calow LJ (1975) Cellulase activity and niche separation in freshwater gastropods. *Nature* 255: 478–480
- Carpenter SR (ed) (1988) Complex interactions in lake communities. Springer, Berlin Heidelberg New York
- Carpenter SR, Kitchell JF (eds) (1993) The trophic cascade in lakes. Cambridge University Press, Cambridge
- Cattaneo A, Mousseau B (1995) Empirical analysis of the removal rate of periphyton by grazers. *Oecologia* 103: 249–254
- Cooper SC, Barmuta LA (1993) Field experiments in biomonitoring. In: Rosenberg DM, Resh VH (eds) Freshwater biomonitoring and benthic macroinvertebrates. Chapman and Hall, New York, pp 399–441

- Diamond J (1986) Laboratory experiments, field experiments, and natural experiments. In: Diamond J, Case TJ (eds) Community ecology. Harper and Row, New York, pp 3–22
- Diehl S (1992) Fish predation and benthic community structure: the role of omnivory and habitat complexity. *Ecology* 73: 1646–1661
- Diehl S (1995) Direct and indirect effects of omnivory in a littoral lake community. *Ecology* 76: 1727–1740
- Doudoroff P, Shumway DL (1970) Dissolved oxygen requirements of freshwater fishes. FAO Fish Techn Paper No 86
- Frost TM, DeAngelis DL, Bartell SM, Hall DJ, Hurlbert SH (1988) Scale in the design and interpretation of aquatic community research. In: Carpenter SR (ed) Complex interactions in lake communities. Springer, Berlin Heidelberg New York, pp 229–258
- Gulati RD, Lammens EHRR, Meijer ML, Donk E van (1990) Bio-manipulation: tool for management. (Developments in hydrobiology, vol 61) Kluwer, Dordrecht
- Hambright KD (1994) Morphological constraints in the piscivore-planktivore interaction: implications for the trophic cascade hypothesis. *Limnol Oceanogr* 39: 897–912
- Hambright KD, Drenner RW, McComas SR, Hairston NG Jr (1991) Gape-limited piscivores, planktivore size refuges, and the trophic cascade hypothesis. *Arch Hydrobiol* 121: 389–404
- Hershey AE (1990) Snail populations in arctic lakes: competition mediated by predation? *Oecologia* 82: 26–32
- Holopainen IJ, Hyvärinen H (1985) Ecology and physiology of crucian carp [*Carassius carassius* (L)] in small Finnish ponds with anoxic conditions in winter. *Verh Int Ver Limnol* 22: 2566–2570
- Holopainen IJ, Tonn WM, Paszkowski CA (1991) Ecological responses of crucian carp populations to predation by perch in a manipulated pond. *Verh Int Ver Limnol* 24: 2412–2417
- Kerfoot WC, Sih A (eds) (1987) Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, Pa
- Klosiewski SP (1991) Selective predation by pumpkinseed sunfish and its influence on snail assemblage structure. PhD dissertation, Ohio State University
- Lodge DM, Brown KM, Klosiewski SP, Stein RA, Covich AP, Leathers BK, Brönmark C (1987) Distribution of freshwater snails: spatial scale and the relative importance of physico-chemical and biotic factors. *Am Malacol Bull* 5: 73–84
- Lodge DM, Kershner MW, Aloï J (1994) Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. *Ecology* 75: 1265–1281
- Martin TH, Crowder LB, Dumas CF, Burkholder JM (1992) Indirect effects of fish on macrophytes in Bays Mountain Lake: evidence for a littoral trophic cascade. *Oecologia* 89: 476–481
- McCormick PV, Stevenson RJ (1989) Effects of snail grazing on benthic algal community structure in different nutrient environments. *J North Am Benthol Soc* 8: 162–172
- Merrick GW, Hershey AE, McDonald ME (1991) Lake trout (*Salvelinus namaycush*) control of snail density and size distribution in an arctic lake. *Can J Fish Aquat Sci* 48: 498–502
- Mittelbach GG, Osenberg CW, Leibold MA (1988) Trophic relations and ontogenetic niche shifts in aquatic ecosystems. In: Ebenman B, Persson L (eds) Size-structured populations. Springer, Berlin Heidelberg New York, pp 219–235
- Neill WE (1994) Spatial and temporal scaling and the organization of limnetic communities. In: Giller PS, Hildrew AG, Raffaelli DG (eds) Aquatic ecology: scale, pattern and process. Blackwell, Oxford, pp 189–231
- Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation ecosystems in gradients of primary productivity. *Am Nat* 118: 240–261
- Osenberg CW, Mittelbach GG (1989) The effects of body size on the predator-prey interaction between pumpkinseed sunfish and gastropods. *Ecol Monogr* 59: 405–432
- Osenberg CW, Mittelbach GG, Wainwright PC (1992) Two-stage life histories in fish: the interaction between juvenile competition and adult performance. *Ecology* 73: 255–267
- Paszkowski CA, Tonn WM, Piironen J, Holopainen IJ (1990) Behavioural and population-level aspects of intraspecific competition in crucian carp. *Ann Zool Fenn* 27: 77–85
- Piironen J, Holopainen IJ (1988) Length structure and reproductive potential of crucian carp [*Carassius carassius* (L)] populations in some small forest ponds. *Ann Zool Fenn* 25: 203–208
- Power ME (1990) Effects of fish in river food webs. *Science* 250: 811–814
- Power ME (1992) Habitat heterogeneity and the functional significance of fish in river food webs. *Ecology* 73: 1675–1688
- Stein RA, Goodman CG, Marshall EA (1984) Using time and energetic measures of cost in estimating prey value for fish predators. *Ecology* 65: 702–715
- Strong DR (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73: 747–754
- Swamikannu X, Hoagland KD (1989) Effects of snail grazing on the diversity and structure of a periphyton community in a eutrophic pond. *Can J Fish Aquat Sci* 46: 1698–1704
- Tonn WM, Paszkowski CA, Holopainen IJ (1989) Responses of crucian carp populations to differential predation pressure in a manipulated pond. *Can J Zool* 67: 2841–2849
- Tonn WM, Paszkowski CA, Holopainen IJ (1991) Selective piscivory by perch: effects of predator size, prey size, and prey species. *Verh Int Ver Limnol* 24: 2406–2411
- Tonn WM, Holopainen I, Paszkowski CA (1994) Density-dependent effects and the regulation of crucian carp populations in single-species ponds. *Ecology* 75: 824–834
- Vermaat JE (1994) Periphyton removal by freshwater micrograzers. In: Vierssen W van (ed) Lake Veluwe, a macrophyte-dominated system under eutrophication stress. Kluwer, Dordrecht, pp 213–249
- Weber LM, Lodge DM (1990) Periphyton food and crayfish predators: relative roles in determining snail distribution. *Oecologia* 82: 33–39
- Wootton JT, Power ME (1993) Productivity, consumers, and the structure of a river food chain. *Proc Natl Acad Sci USA* 90: 1384–1387