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PISCIVORY AND RECRUITMENT: MECHANISMS STRUCTURING PREY POPULATIONS IN SMALL LAKES[1]

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Abstract. Detecting mechanisms that structure ecological communities often requires investigations at appropriate spatial and temporal scales. A 15-mo, whole-lake experiment revealed direct and indirect mechanisms by which a fish predator structured its prey population, primarily by affecting recruitment of young-of-the-year (YOY) fish. Piscivorous Eurasian perch (*Perca fluviatilis*) were added to two of four sections of a divided lake in eastern Finland previously stocked with crucian carp (*Carassius carassius*). Although the stocked crucians quickly grew beyond vulnerable sizes, recruitment of their offspring through their 1st yr of life was reduced by 90% in sections with perch. Surviving YOY in predator sections were completely confined to vegetated inshore areas. This restriction to refuges lowered their growth rates in comparison with YOY in predator-free sections, which can further reduce recruitment by prolonging susceptibility to size-limited predation and decreasing energy reserves needed for anaerobic overwintering. In the presence of piscivores, surviving prey subsequently benefit from reduced intraspecific competition, increasing growth rates to achieve large, invulnerable body sizes rapidly. Resulting populations of crucian carp, consisting of relatively few but relatively large individuals, contrast with populations living in the absence of piscivores, which are characterized by high densities of small, stunted individuals. Such divergent population patterns are displayed by a number of prey species in Scandinavia and North America, suggesting that a combination of direct and indirect effects of predation on younger age classes, such as documented for crucian carp, may be common in fish populations of small northern lakes. Detecting these patterns and identifying their underlying mechanisms may often require a combination of extensive and intensive studies.

Key words: Carassius carassius; *crucian carp; Eurasian perch; field experiment; Finland;* Perca fluviatilis; *predation.*

INTRODUCTION

Patterns among fish assemblages, including regularities in species composition, distribution, and abundance, have often been attributed to piscivory (Zaret and Paine 1973, Harvey 1981, Rahel 1984, Robinson and Tonn 1989). For example, in small forest lakes of northern Wisconsin, small-bodied species are often absent from lakes containing piscivores (Tonn and Magnuson 1982), and in northern Europe, some cyprinids form dense, stunted populations in lakes lacking predators but are represented by only a few large-bodied individuals when piscovores are present (Tonn et al. 1990). However, the mechanism(s) by which predation produces these community- and population-level patterns have largely been inferred rather than demonstrated directly (Lyons and Magnuson 1987, DeVries and Stein 1990).

Because piscivorous fishes are typically both size-selective and size-limited predators (Popova 1967, Gillen et al. 1981, Tonn and Paszkowski 1986, Post and Evans 1989*a*), small fish are generally more vulnerable to predation than large fish. Predation might thus be able to directly eliminate small-bodied species from a lake if the local piscivores are capable of consuming all size classes. For large-bodied fishes, complete elimination may be difficult if adults can attain a size refuge from the local predators; nevertheless, piscivorous fish might still be able to regulate populations of larger prey species by controlling the recruitment of young fish.

Piscivores might also influence the survival of small fish and recruitment of young indirectly. Predators can affect habitat use and reduce foraging rates of prey, with the extent of such behavioral responses often depending on prey size (Gilliam and Fraser 1987, Mittelbach and Chesson 1987, Helfman 1989); the affected individuals may grow more slowly and thus remain vulnerable to predation for longer periods (Werner et al. 1983). Predator intimidation might also reduce the energy reserves of small or young fish, increasing their mortality during winter (Post and Evans 1989*b*).

An impediment to uncovering if and how predation

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operates in structuring populations and assemblages has been the difficulty of conducting appropriately scaled field experiments (Sih et al. 1985). Although suggestive, the short-term, often laboratory-based experiments that have focussed on behavioral responses to predators generally do not demonstrate how such responses modify growth, survival (but see Werner et al. 1983), or reproduction and recruitment, and thus affect prey at the population level. To examine the direct and indirect effects of a size-limited piscivore on the growth, survival, and recruitment of a large-bodied prey, we performed a whole-lake experiment, extending over two reproductive seasons, using Eurasian perch, *Perca fluviatilis,* and crucian carp, *Carassius carassius.*

Crucian carp dominate fish assemblages in small north-European lakes and ponds where winter hypoxia eliminates piscivores and other fish species (Nikolskiy and Shubnikova 1974, Piironen and Holopainen 1988, Paszkowski et al. 1989). By using glycogen reserves, built up during late summer and fall and stored largely in the liver (Hyvärinen et al. 1986, Piironen and Holopainen 1986), crucian carp can overwinter in anoxic water via anaerobic metabolism (Johnston and Bernard 1983, Holopainen and Hyvärinen 1985, Holopainen et al. 1986). In single-species lakes, crucian carp densities can exceed 30 000 individuals/ha, but these populations are dominated by small (4–10 cm total length [TL]; 2–15 g), stunted fish. In lakes containing piscivores (most commonly northern pike, *Esox lucius,* and perch), crucian densities decrease (25–250 individuals/ha) and average individual size can increase by one or more orders of magnitude (15–35 cm, 50–1000 g; Bengtsson and Hargeby 1979, Hamrin 1979, Piironen and Holopainen 1988).

To investigate the role of predation in maintaining these patterns, we stocked crucian carp, with and without piscivorous Eurasian perch, into sections of a lake that had been emptied of fish and partitioned. Although significant treatment effects were detected with the stocked crucians (Holopainen et al. 1992*a*), they grew rapidly in the previously fishless lake and quickly exceeded prey sizes preferentially selected by the predators (Tonn et al. 1992). However, these stocked crucian carp reproduced in all sections of the experimental lake. Here we report on the effects of predation on young-of-the-year fish (YOY), and discuss how these effects can act as important mechanisms structuring prey populations in fish assemblages of small northern lakes.

METHODS

In May 1985, Hermanninlampi, a small (1.5-ha), shallow (maximum depth = 1.6 m), isolated lake in eastern Finland (62°41′ N, 29°41′ E; see Holopainen and Pitkänen 1985 for a more detailed limnological description) was treated with rotenone to remove what was left of the resident crucian carp population of ≈25 000 individuals (Piironen and Holopainen 1988); the population had previously been trapped and fish moved to an adjacent pond. The lake was divided into four sections, referred to as A1 and A2 (predators absent) and P3 and P4 (predators present), with reinforced plastic curtains (see Holopainen et al. 1991*a* for details). Because lake morphometry was irregular, the four sections varied somewhat in size ($\bar{X} \pm 1$ SD = 3719 ± 853 m^2). Submerged macrophytes (mainly *Potamogeton natans*) unevenly covered 25% of the lake; the shoreline was vegetated by emergent grasses and sedges combined with overhanging shrubs.

The lake remained fishless for a year before being restocked. Crucian carp were stocked 30 May–16 June 1986. Stocked crucians came from the original Hermanninlampi population and two from nearby predator-free ponds. Initial size distributions were comparable across sections ($\bar{X}$ = 7.5 cm TL, mode = 6.5 cm, range = 4–15 cm), patterned after populations from ponds lacking predators. Sections A2, P3, and P4 received similar amounts of fish (1455–1489 individuals, 9.5–9.6 kg); as part of an ongoing investigation of intraspecific competition, A1 received 785 fish (5.2 kg). On 10–11 June, 25 and 26 perch (16–26 cm TL, 2.2 kg total in each section) from a nearby lake were added to P3 and P4, respectively; 23 (P3) and 20 (P4) additional perch from the same source were added between 24 June and 13 August.

Crucians were monitored regularly from 18 June to 25 September 1986, but with particular intensity during three samplings in July, August, and September. During these samplings, 10 fish traps (0.5 m high, with a 0.3 m lead and 5-mm mesh), able regularly to capture crucians >2 cm, were set in each section for 24 h in a stratified random pattern. Four inshore traps were set directed towards and within 0.5 m of shore and six offshore traps were set >10 m from shore pointing in haphazard directions. Traps were emptied every 3 h to document diel activity and habitat use patterns. Numbers of fish in each trap during each 3-h period were recorded and total lengths were measured for all trapped fish; after examination, fish were returned to their sections. YOY crucians were also caught throughout the summer with hand-held dipnets (2 mm mesh) in shallow water within littoral vegetation.

Concentrated trapping from 15 May to 9 June 1987 assessed the populations (abundance and size/age structure) in all four sections. The 1986 year class, still referred to as YOY for this sampling, was easily distinguished based on length–frequency distributions. Population abundance was determined by the removal trapping (A1, P4) and Schnabel multiple mark–recapture (A2, P3) methods (Ricker 1975). Crucian carp from A1 and P4 were held separately in enclosures during removal trapping and then returned to their respective sections. We also removed all remaining perch, so that the entire lake was rendered predator free. The crucian populations continued to be monitored during summer 1987, allowing us to document abundance and habitat use of juvenile crucians (the 1986 year class and new YOY from 1987) in all sections in the absence of perch. During each of six samplings, July–September 1987, five traps were set inshore and five offshore for 48 h in each section. Rotenone treatment of the entire pond on 22 September 1987 gave us final, quantitative assessments of the abundances of the 1986 and 1987 year classes in each section, with the latter having lived entirely in the absence of perch. Sections 3 and 4 will be referred to as A3 and A4, respectively, when results derived solely from July–September 1987 are discussed, to emphasize the absence of predators from all sections.

RESULTS

Survival of perch

Perch were regularly caught in both predator sections (P3 and P4) throughout the open-water seasons of 1986. At the end of October, just before ice formed on the lake, we caught and removed 4 and 10 perch, respectively, from P3 and P4. Four additional perch were removed from P3 in May 1987, although none were found in P4, indicating that some perch could successfully overwinter in Hermanninlampi, but that winterkill probably eliminated most individuals that remained after the October trapping.

Recruitment of YOY

Spawning of crucian carp was first observed 19 June 1986. Dipnet sampling on 1 July captured YOY, 0.8–2.1 cm TL, in all sections. Initial densities of YOY, based on catch-per-unit-effort on 1 July, were as high or higher in sections with predators (P3 and P4; 17 fish caught) as in predator-free sections (A1 and A2; 9 fish caught). However, beginning with the 24-h sampling of 14–18 July, and continuing with the intensive sampling periods in August and September, at least twice as many YOY were caught in A1 and A2 as in P3 and P4 (Fig. 1A). Population estimates conducted during spring 1987 (Fig. 1B) also indicated substantially fewer YOY in sections that had contained predators (P3, P4). A final quantitative assessment of recruitment of the 1986 year class was provided by the September 1987 rotenone treatment. That sampling showed that the total abundance of the cohort was roughly an order of magnitude greater in sections 1 and 2 than in 4 and 3, respectively (Fig. 1C). This difference in year class strength between treatments was statistically significant ($t = 5.22$, df = 2, $P < .05$; data log-transformed to homogenize variance), despite the minimum number of replicates.

During the summer of 1987, after perch had been eliminated from all sections, crucian carp again spawned in the divided pond, providing a post-treatment temporal comparison with 1986. The September rotenone treatment showed that the 1987 year class was not systematically more abundant in A1 and A2 compared to A3 and A4 ($t = 0.61$, df = 2, $P > .50$; Fig. 1D). Rather, the recruitment pattern in 1987 was strongly and inversely dependent on the density of adult crucians (I. J. Holopainen, W. M. Tonn, and C. A. Paszkowski, *personal observations*), a relationship that was nonexistent when predators were present. The regression between numbers of YOY and adult crucians (both $\log_{10}$-transformed) was significant in 1987 ($r^2 = 0.98$, $P < .01$), but not in 1986 ($r^2 = 0.01$, $P > .75$). Recruitment patterns for the 1986 year class (Fig. 1A–C) were clearly due to the experimental treatment (presence or absence of piscivorous perch during 1986) rather than to any inherent differences in population densities or habitat suitability among sections.

Growth and habitat use

Besides being fewer in number, YOY crucians also grew less in sections with perch than in sections without piscivores. When YOY were first caught in 1986 (1 July), total length was comparable across sections (one-way ANOVA; $F_{3,22} = 1.88$, $P > .10$). However, by August and September 24-h samplings, size distributions showed that growth was significantly reduced among YOY in P3 and P4 (Fig. 2). Such was not the case in 1987 when growth of YOY, like recruitment, was density dependent (I. J. Holopainen, W. M. Tonn, and C. A. Paszkowski, *personal observations*).

The reduced growth in 1986 appeared linked to changes in habitat use of YOY crucians in the presence of piscivores. Crucian carp are primarily inhabitants of vegetated littoral zones, although some individuals are typically encountered offshore, with this latter tendency increasing with body size (Tonn et al. 1989). Although inshore occurrence was generally stronger among YOY than among stocked fish during 1986 (test of independence, $G = 253.6$, df = 1, $P \ll .001$), the presence of perch intensified the inshore preference of YOY crucians to the extreme. Not a single YOY was trapped offshore during 24-h samplings in P3 and P4, compared with an average of 14% offshore in A1 and A2 (Fig. 3A). The possibility that these differences in habitat use between sections might have occurred regardless of the presence or absence of piscivores was not supported by the results of 1987 trappings, after perch removal. From July to September 1987, small crucians (<6.5 cm), from the 1986 and 1987 year classes, were as likely to be offshore in A3 and A4 as in A1 and A2 (Fig. 3B). Overall, 8.7% were offshore in A3 and A4 compared with 8.9% in A1 and A2.

DISCUSSION

Perca spp. and other fish piscivores are size-limited predators (Popova 1967, Tonn and Paszkowski 1986, Hart and Hamrin 1990). Under laboratory conditions, perch consistently prey most heavily on the smallest size classes of crucian carp available when presented with prey as small as 3 cm (Tonn et al. 1992). YOY fishes are especially vulnerable to direct effects of such

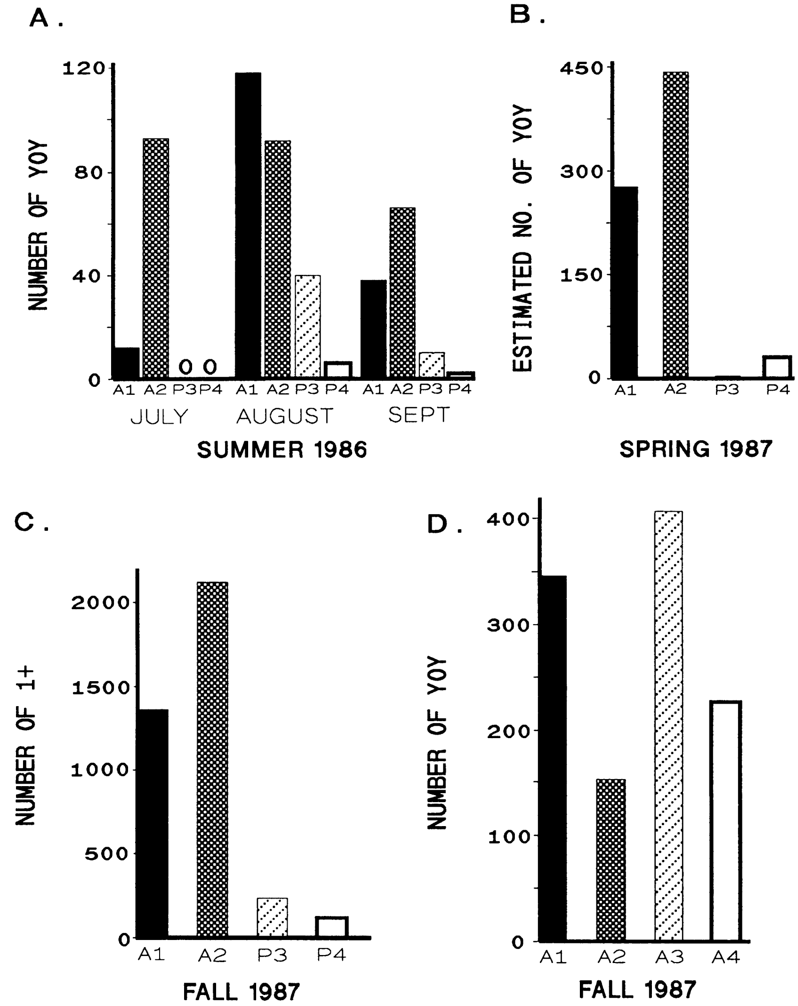

FIG. 1. (A) Number of young-of-year (YOY) crucian carp caught in four sections of Hermanninlampi (A1 and A2: predators absent; P3 and P4: predators present) during three 24-h samplings in 1986. Trapping effort was equal in all sections during all three samplings. (B) Estimated number of YOY crucian carp in each section, based on population estimates resulting from 2–8 d of removal trapping (A1 and P4) or mark–recapture sampling (A2 and P3) during May–June 1987. (C) Total number of crucian carp from the 1986 year class obtained in each section during final trappings and following rotenone treatment in September 1987. (D) Total number of YOY crucian carp (1987 year class) obtained in each section during final trappings and following rotenone treatment in September 1987.

predation. Because of their small size, they are available as food to a wide range of size-limited piscivores (Post and Prankevicius 1987). In addition, their sensory and motor systems can be incompletely developed, making them easier to capture than older fish (Yates 1983, Magurran 1986, Fernald 1988). In Hermanninlampi, YOY were always smaller than stocked crucians and the direct effect of predation on YOY numbers was both rapid and large.

However, perch of the sizes used in our study are physically capable of eating crucian carp up to 12 cm, although vulnerability drops off significantly for fish >8 cm (Tonn et al. 1992). Thus, because half of the populations in P3 and P4 were initially <8 cm, we had expected, and were initially surprised not to find, significant direct predation mortality among the stocked fish. In an earlier field experiment, pond sections having the highest densities of predators (perch and pike) exhibited the lowest survival of stocked crucians, 6–8 cm TL (Tonn et al. 1989). The relatively low densities of perch used in the present experiment and the larger spatial scale of Hermanninlampi, even when compared to the earlier experimental pond, may have contributed to the limited direct impact on the stocked fish. However, we suggest that the early growth of these crucians following their introduction into the fishless pond, combined with the appearance of YOY within 2 wk of the addition of perch, was primarily responsible for the reduced direct impact on the stocked crucians. In our earlier pond experiment crucian carp did not spawn, so the smallest available prey were always among the stocked fish.

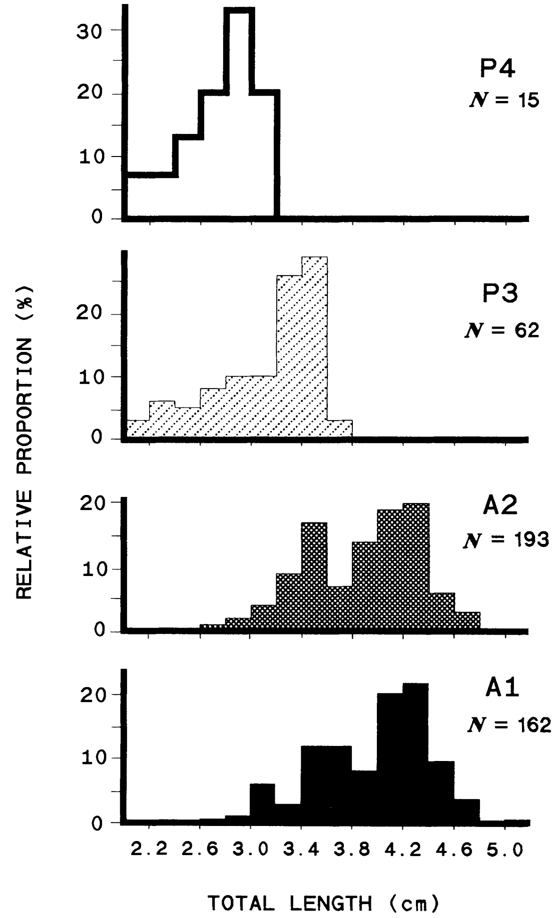

FIG. 2. Length–frequency distributions of YOY crucian carp among four sections of Hermanninlampi (A1 and A2: predators absent; P3 and P4: predators present) during 24-h samplings in August–September 1986. Except for A1 and A2 ($P > .05$), distributions differ from each other at the $P < .001$ level (Kolmogorov-Smirnov test).

Although there was no evidence of large-scale predation mortality during 1986 among stocked crucian carp, the presence of perch did have measurable indirect effects on fish in sections P3 and P4, especially smaller (< 10 cm) individuals (Holopainen et al. 1992*a*). These short-term behavioral responses of stocked crucians, similar to those reported for other prey species responding to predation risk (reviewed in Ydenberg and Dill 1986, Mittelbach and Chesson 1987, Sih 1987), also appeared to have long-term consequences regarding growth and survival. Because of their similarity to the responses of YOY, these indirect effects on stocked fish are helpful in interpreting impacts of predation risk on YOY.

A striking behavioral response involved habitat use. Offshore prey, e.g., planktonic microcrustaceans, are important food resources for crucians (Holopainen et al. 1992*b*, Penttinen and Holopainen 1992), but the offshore foraging zone was underutilized by small stocked fish in P3 and P4 because of the presence of predators. Smaller crucians in P3 and P4 were both less active and more concentrated in the shallow, vegetated, inshore areas compared with those in A1 and A2 (Holopainen et al. 1992*a*). In sections without perch, use of the offshore habitat peaked during the day, with fish moving inshore at night; the same pattern was also exhibited by larger crucians (> 10 cm) in P3 and P4. However, the few small stocked crucians that ventured offshore in P3 and P4 did so only at night, when visual foraging would be impaired (Holopainen et al. 1992*a*). We believe that the inshore habitat restriction of small crucians, as well as their depressed activity and altered diel patterns, were behind the reduced food intake observed for these fish in sections containing perch (Penttinen 1990). Small fish in P3 and P4 also grew less and accumulated fewer glycogen reserves than small fish in A1 and A2 (Holopainen et al. 1992*a*), presumably because of their reduced food intake. It seems likely that these effects on habitat use, growth, and accumulation of overwintering reserves among small stocked cru-

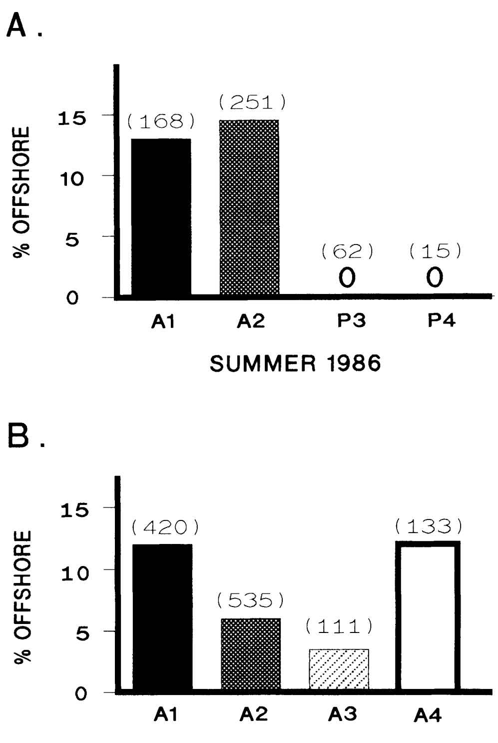

FIG. 3. Percentage of YOY crucian carp captured in offshore traps during 24-h samplings in four sections of Hermanninlampi during 1986 (A) and percentage of YOY and 1+ crucian carp (<6.5 cm) captured offshore during 48-h samplings in 1987 (B). Histogram bars show means of three (A) or six (B) samplings; data were arcsine transformed for calculation of means. Numbers in parentheses above each bar are the total number of YOY obtained in the section during all samplings.

cians during 1986 contributed to the higher mortality of stocked fish in P3 and P4 vs. A1 and A2 that was determined from population estimates performed the following spring (1987).

In contrast to fish <10 cm, larger size classes of the stocked fish, which were essentially invulnerable to predation, grew significantly better in P3 and P4 and had similar levels of glycogen reserves, when compared with large crucians in A1 and A2 (Holopainen et al. 1992*a*). Improved growth in the presence of predators, attributed to reduced competition for offshore resources from their smaller, more intimidated conspecifics, was also observed in large, invulnerable size classes of bluegill, *Lepomis macrochirus* (Werner et al. 1983).

Like the small stocked fish, YOY crucians altered their habitat use in the presence of perch, although the response of YOY in P3 and P4 was even more extreme than stocked fish; not a single YOY fish was captured outside of the highly structured, shallow-water inshore habitat during 1986. The distribution of young crucians in 1987, following the removal of perch, confirmed that the extreme habitat use pattern observed in 1986 was due to the presence of predators rather than any differences in habitat quality among sections.

Restriction to a relatively small refuge area will increase the ecological density experienced by the confined fish, which can reduce food intake and growth among crucians by increasing intraspecific competition (Holopainen and Pitkänen 1985, Paszkowski et al. 1990, I. J. Holopainen, W. M. Tonn and C. A. Paszkowski, *personal observations*). YOY fish restricted to inshore refugia would also be denied access to planktonic microcrustaceans, which are especially important resources for young crucians (Penttinen and Holopainen 1992). In contrast, YOY in A1 and A2 could, and did, leave the inshore habitat in 1986 and, like the smaller stocked fish, grew better than their counterparts in P3 and P4.

The translation of predator-induced habitat shifts into reduced growth can, of course, negatively affect survival of YOY. Because perch prey more heavily on smaller crucians than larger ones, YOY with lower growth rates would be more vulnerable, and vulnerable for a longer period of time, than faster growing conspecifics (Werner et al. 1983, Tonn et al. 1986). Furthermore, small fish generally possess fewer reserves than large fish and are more likely to exhaust them over winter when feeding is depressed (Post and Evans 1989*b*). Because predation risk reduced feeding in smaller stocked crucian carp in P3 and P4, they were less capable of accumulating glycogen reserves, needed for maintenance and overwinter survival in hypoxic conditions, than fish in A1 and A2 that enjoyed higher feeding rates. As a result, small stocked fish in P3 and P4, and likely the similarly slow-growing YOY, were more vulnerable to exhaustion of their glycogen stores than fish in predator-free sections. Although the accumulation and use of glycogen for anaerobiosis is a special adaptation of crucian carp, we suggest that increased overwinter mortality via reserve exhaustion might be an important, indirect effect of piscivores on recruitment in other prey populations of northern lakes.

Our experiment demonstrates that the presence of a fish predator results directly and indirectly in extremely poor recruitment among YOY of a prey species. We suggest that it is via these recruitment impacts that piscivorous fish can regulate co-occurring populations of the large-bodied crucian carp, contributing to the regularly observed dichotomy in crucian carp population structure in northern Europe (Nikolskiy and Shubnikova 1974, Hamrin 1979, Holopainen and Pitkänen 1985, Piironen and Holopainen 1988). In small, shallow, isolated lakes, which regularly experience winter hypoxia, predators cannot persist and fish assemblages become dominated (often exclusively so) by crucian carp (Tonn et al. 1990). Populations in such lakes can reach very high densities, but because of intense intraspecific competition, are characterized by small, slow-growing, and short-lived individuals (Holopainen and Pitkänen 1985, Piironen and Holopainen 1988, Paszkowski et al. 1990). In lakes where predators can persist, they can minimize crucian carp recruitment. However, consistent with our experimental results in Hermanninlampi, age-structures indicate that some YOY do survive, at least every few years, to maintain the population (Bengtsson and Hargeby 1979). Because of high growth potential under reduced intraspecific competition (Persson 1974, Holopainen and Pitkänen 1985), the few surviving crucian carp can quickly outgrow their vulnerability to predators, ultimately achieving large body sizes (>35 cm) over a long lifespan (>20 yr); (Bengtsson and Hargeby 1979, Hamrin 1979). A similar dichotomy in population structure is seen in another cyprinid, tench (*Tinca tinca*), which in Swedish lakes often co-occur with crucian carp in the presence and absence of predators (Bengtsson and Hargeby 1979, C. Brönmark, *personal communication*).

In environmentally similar small lakes in North America, cyprinid and other prey species are frequently absent from lakes containing piscivores (e.g., Harvey 1981, Robinson and Tonn 1989); their exclusion can probably be credited to direct predation because these small-bodied prey lack the size refuge possessed by European cyprinids (Tonn et al. 1990). A North American exception may be the central mudminnow (*Umbra limi*), which frequently co-occurs with yellow perch (*P. flavescens*) and displays both a high degree of tolerance to winter hypoxia (Klinger et al. 1982, Magnuson et al. 1983) and parallel patterns of density and size structure in lakes with and without perch, as observed for crucian carp (Tonn 1985, Tonn and Paszkowski 1986). Mudminnows are smaller and therefore potentially more vulnerable to fish piscivores than crucian carp, but because of the stunted nature of yellow perch populations and the occasional winterkill of adult perch in these small dystrophic lakes, limited or sporadic recruitment of mudminnows can occur, allowing coexistence of mudminnows and perch (Tonn and Paszkowski 1986). Our work thus indicates a strong similarity in the suite of ecological mechanisms, including winterkill and the effect of *Perca* and other predators on recruitment of young, that structure populations of fugitive fish species in small forest lakes of northern Europe and central North America, contributing to similarities in fish assemblage structure in small Holarctic lakes (Tonn et al. 1990).

Studies of the crucian carp–Eurasian perch system illustrate the advantages of a pluralistic approach, conducted at a variety of spatial and temporal scales and with appropriate size and age structures, when documenting mechanisms structuring populations and communities. Our current understanding of how piscivory contributes to population and community patterns in small-lake ecosystems has resulted from a combination of extensive lake surveys, small-scale experiments, and large-scale field manipulations.

Whole-lake experiments using ecologically realistic treatments, often used successfully by ecosystem ecologists (e.g., Likens 1985, Carpenter et al. 1987, Schindler 1988), are especially suited for identifying population-level phenomena not observable at smaller scales. However, to accommodate the needs of the larger scales and appropriate population structures used in field experiments, ecologists will often have to accept a smaller number of experimental units; although duplication is unlikely to provide sufficient replication for traditional statistical analyses in most whole-system experiments (Carpenter 1989), the strength of the impacts and the fact that responses in both P3 and P4 consistently differed from A1 and A2 when predators were present (1986), but not when they were absent (1987), support our interpretation that effects of piscivory on recruitment are important in structuring fish assemblages of small lakes.

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