

DENSITY-DEPENDENT EFFECTS AND THE REGULATION OF CRUCIAN CARP POPULATIONS IN SINGLE-SPECIES PONDS¹

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Abstract. Crucian carp (*Carassius carassius*) is often the only fish species present in small ponds of northern Europe. Such populations are typically at high densities and consist primarily of small, relatively slender, and short-lived fish; populations in multispecies assemblages in lakes display opposite traits. Field and laboratory experiments have implicated predation as an important mechanism structuring crucian populations in multispecies assemblages. To investigate the role(s) of density dependence in structuring pond populations, we manipulated densities of crucians stocked into four sections of a subdivided natural pond in Finland.

Mortality of stocked fish during the 3-mo experiment was low (0–11%) and unrelated to density. Growth rates of crucians were both size and density dependent. Larger fish did not noticeably grow in either high- or low-density sections, but growth of smaller size classes was 22% greater in low-density sections. Lower densities and smaller sizes of zooplankton, especially of inshore cladocerans that are an important food resource for smaller crucians, indicated that resource limitation caused by exploitation competition was an important density-dependent process restricting growth of small fish in high-density sections.

Crucians rely on reserves of glycogen, stored in the liver and muscle, to fuel the over-winter anaerobic metabolism that allows them to maintain populations in ponds where winter hypoxia eliminates other fishes. Liver size was significantly larger and glycogen levels were 82% higher in our low-density pond sections than in high-density sections. At higher, but not lower, densities, relative liver size and glycogen levels decreased with body size; combined with the lack of growth of large fish, this indicates that density-dependent energy limitations contribute to the short life-spans and rarity of large fish that characterize pond populations.

An increase in relative body depth can be induced in crucians by the presence of piscivorous fish, reducing vulnerability to predation. It has been proposed that increased body depth incurs a substantial energy cost during swimming and should be restricted to specific size classes in populations sympatric with predators. However, in our experiment, crucians of all sizes became significantly deeper bodied, which contributed to higher condition factors in low-density vs. high-density sections. This morphological change, occurring in the absence of piscivores, suggests that energy benefits (accumulation of overwintering reserves) can override any proposed costs for this sluggish, but metabolically unique, fish.

Crucian carp successfully reproduced in all sections during the experiment, but growth and recruitment of 0+ fish (young of year) were strongly and negatively related to the numbers of older fish present. The observed density-dependent recruitment was likely caused by starvation-induced mortality and cannibalism; reduced growth observed in 0+ fish would also be expected to cause higher first-winter mortality, reducing further recruitment at higher densities. Density dependence has a variety of regulatory effects on pond populations of crucian carp that contribute to their persistence and resilience.

Key words: *Carassius carassius; competition; density dependence; fish; morphological change; population regulation; recruitment.*

INTRODUCTION

A longstanding debate in ecology concerns the extent to which the density of a population affects its dynam-

ics and contributes to its regulation (Begon and Mortimer 1986). The role of density dependence in population dynamics has been questioned for a number of invertebrate groups (e.g., Strong et al. 1984, Roughgarden et al. 1987, Stiling 1988). In contrast, recent data from natural and experimental populations of sev-

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eral vertebrate groups suggest that parameters such as growth and survival are density dependent (Petranka 1989, Scott 1990, Andrews 1991, Choquenot 1991, Van Buskirk and Smith 1991). Although the persistence of populations within some range of densities suggests regulation via density-dependent agents, without necessarily implying that populations are continually held at some equilibrium level, the productive question seems not to be whether regulation is density dependent or independent, but which population parameters are most sensitive to density, and how strongly and consistently are they affected (VanBuskirk and Smith 1991).

Among fishes, short-term pond and aquaculture experiments (e.g., Johnson and McCrimmon 1967, Hall et al. 1970, Hulata et al. 1982, Fox and Flowers 1990) consistently show density-dependent growth yet generally density-independent survival, although the high densities, short time frames, and focus on older fish that characterize these studies caution against broad generalizations. Still, density-dependent growth in fish should have important demographic consequences (Healy 1980), because fecundity, risk of predation, and starvation, all of which affect recruitment, are usually related to body size (Wootton 1990, Barlow 1992). By growing slowly, juveniles remain vulnerable to size-limited piscivores (including larger conspecifics) for longer periods, increasing their overall risk (Larkin and Smith 1954, Tonn et al. 1986). As well, small, slow-growing juveniles experience higher overwinter mortality (Post and Evans 1989). However, laboratory studies and experiments in small, artificial systems cannot assess the demographic importance of density effects or the conditions under which they occur in nature. It remains unclear if density-dependent population regulation is truly common in fish (Backiel and LeCren 1978, Healy 1980). Greater attention to the recruitment and survival of younger age classes and the use of larger scale field experiments are required, even at a potential cost of limited experimental design and replication (Carpenter 1989, Persson et al. 1993).

Populations of crucian carp, *Carassius carassius*, display a density-related dichotomy in a number of traits, and also possess some unique physiological and morphological attributes that could be sensitive to density and affect population dynamics. Dramatic differences in morphology, size, and age structures are associated with different densities, environmental conditions, and compositions of the coexisting fish assemblages (Piironen and Holopainen 1988, Brönmark and Miner 1992). Because of its unique ability to survive several months in ice-covered anoxic water via anaerobic metabolism of glycogen (Holopainen and Hyvärinen 1985), crucian carp is often the only fish species present in shallow ponds that seasonally experience hypoxia. Stores of glycogen accumulated in the liver and muscle during late summer–fall are therefore crucial for overwinter survival (Hyvärinen et al. 1986). Population

regulation in these single-species “assemblages” have not been studied systematically, although growth and survivorship patterns suggest the operation of density-dependent intraspecific competition; populations are characterized by high densities of small, narrow-bodied, slow-growing, and short-lived fish (Holopainen and Hyvärinen 1985, Piironen and Holopainen 1988).

In contrast to pond populations, multispecies assemblages of larger lakes contain low densities of crucians dominated by large, old, and deep-bodied fish (Bengtsson and Hargeby 1979, Hamrin 1979, Piironen and Holopainen 1988). Whole-lake experiments have implicated size-limited predation as a major influence on these populations, affecting habitat use, growth, and recruitment (Tonn et al. 1989, 1992, Holopainen et al. 1991).

Recent experimental work further indicates that the presence of predators induces morphological change and may be largely responsible for the deeper bodies exhibited by crucians in lake populations (Brönmark and Miner 1992); increasing body depth should decrease vulnerability of crucians to gape-limited predators. Because of the inferred energy costs of a deeper body, which theoretically increases drag during swimming (Webb 1975), it was predicted that crucians should not increase body depth when they are too small to achieve any reduction in vulnerability or in the absence of predators, and should lose this induced morphological defense upon attaining an absolute size refuge from predation (Brönmark and Miner 1992; C. Brönmark, *personal communication*). However, populations of crucians in the presence of predators are typically at lower densities and can respond behaviorally to predators in ways that can increase or decrease growth rates, depending on crucian size and predator densities (Tonn et al. 1989, 1992, Holopainen et al. 1991). The presence of morphological change in a high-food/predator-absent treatment of a laboratory experiment (Brönmark and Miner 1992) suggests that the role(s) of density and resource levels in shaping crucian morphology needs to be addressed further.

Crucian carp are generalist feeders, incorporating a variety of plant, animal, and detrital material into their diets (Prejs 1973, Andersson et al. 1978, Penttinen and Holopainen 1992). Diet differences do exist among size classes, with smaller fish taking larger proportions of zooplankton and larger fish taking more benthic insects. However, no distinct dietary switches occur ontogenetically and diet overlap remains high among size classes, making crucians susceptible to intraspecific competition for food (Hamrin and Persson 1986). A series of laboratory experiments (Paszkowski et al. 1989, 1990) indicated that many small fish can have competitive effects comparable to fewer, but larger, fish; total biomass of conspecifics is a better predictor of competition intensity than either total numbers or average body size.

The boreal ponds that provide the natural habitat

for single-species assemblages of crucian carp are discrete, providing tractable but realistic spatial scales and populations for manipulations; they thus offer an ideal experimental system for examining processes that potentially regulate fish populations. In this study, we manipulated crucian densities in sections of a subdivided pond and assessed the impact of this manipulation on growth and recruitment. We also gathered data on body depth, condition (including amount of overwintering reserves), and resource levels to help identify potential mechanisms behind any density-dependent responses.

METHODS

Study site

The experiment was conducted in Hermanninlampi, a small (1.5 ha), shallow ($z_{\max} = 1.6$ m), isolated pond in eastern Finland (62°41' N, 29°41' E). The bottom substrate is predominantly sand; macrophytes (mainly *Potamogeton natans*) unevenly cover about one-quarter of the area, and grasses, sedges, and small shrubs form the shoreline. A detailed description of Hermanninlampi's limnology is given in Holopainen and Pitkänen (1985).

The premanipulation fish community consisted of a single species, crucian carp; piscivores and other fishes were absent because of severe winter hypoxia. Following a rotenone treatment in 1985 (Piironen and Holopainen 1988), the pond was divided into four sections (referred to here as H1, H2, L1, and L2) using transparent, UV-resistant, reinforced plastic curtains (see Holopainen et al. 1991 for details); the curtain bottom was checked and adjusted by a diver following installation.

In 1986, Hermanninlampi was the site of a predation experiment involving crucian carp in the presence (in L1 and H1) and absence (in L2 and H2) of perch (*Perca fluviatilis*) (Tonn et al. 1992). That experiment ended following ice-out in 1987, when the few surviving predators were removed (their absence was subsequently confirmed by a rotenone treatment in September 1987); densities and size structures of crucian populations were then estimated by removal trapping and mark-recapture methods (Ricker 1975).

Materials and methods

Using the spring 1987 population estimates as starting points, we manipulated crucian populations to create two sections with high densities (H1, H2) and two with low densities of crucians (L1, L2). From late May through mid-June, adult fish (≥ 2 yr) were removed from sections L1 and L2 and added to H1 and H2; as part of an ongoing investigation of size-structure effects, removal of adults from L2 continued until no further fish were caught on consecutive days. One-year-old (1+) fish, hatched during the predation experiment, were not manipulated, so densities of that year class

remained proportionately lower in L1 and H1 (due to the presence of perch in 1986), compared with L2 and H2. Numerical densities in H1 and H2 were estimated by mid-June to be 3 times greater ($\bar{X} = 0.85$ fish/m²) than those in L1 and L2 ($\bar{X} = 0.28$ fish/m²) ($P < .01$, t test); biomass densities were nearly 3.5 times greater in the high-density treatment ($\bar{X} = 5.8$ g/m²) than in the low-density sections ($\bar{X} = 1.7$ g/m²) ($P < .05$, t test).

From 1 to 15 June we fin-clipped adult fish (≥ 2 yr) from sections L1, H1, and H2, sorted by total length (TL) into 1-cm classes, to monitor growth. From each section, a subsample ($n \geq 25$) was weighed, measured for length (TL) and body depth (measured just anterior to the dorsal fin) and sacrificed to determine initial liver mass and glycogen content (Siu et al. 1970).

Following density manipulations, populations were monitored 6 times between 7 July and 18 September. During each sampling 10 traps (5-mm mesh) were set in each section for 48 h in a stratified-random fashion; 5 traps were set inshore (< 2 m from the shoreline) and 5 traps were set offshore (> 10 m from shore). Captured fish were counted, measured (TL), and examined for clipped fins; subsamples of ≈ 50 fish per section were also weighed and measured for body depth. For the first five trappings, all fish were either returned to their home section (the vast majority) or, if removed (for diet analyses, Penttinen and Holopainen 1992), were replaced by similarly sized individuals. Fish from the final trapping were sacrificed to determine final liver mass and glycogen content. On 22 September, rotenone was applied to all sections (see Holopainen and Pitkänen 1985 for methods), and all fish were collected, counted, measured, and weighed separately for each section.

Zooplankton was sampled weekly in each section from three randomly chosen stations, both inshore and offshore. Offshore samples were collected with a 3.5-L vertical tube (0–1 m); for inshore samples, a 1.4-L tube was positioned horizontally at a depth of 20 cm. For each habitat, the three samples were combined, filtered through a 55- μ m mesh net and preserved in 4% formalin. Plankters were counted and sorted into 100- μ m size classes; dry biomass was calculated from carbon masses (Latja and Salonen 1978). Samples for phytoplankton, chlorophyll *a*, and water chemistry analysis were also collected regularly from each section (see Holopainen et al. 1992).

During the first sampling, a small leak was discovered offshore between sections L2 and H2 and repaired as completely as possible. In subsequent samplings, we identified (by size and clipped fins) and returned any adult fish from H2 that had crossed into L2; the density of adults thus remained minimal in L2 throughout the experiment. Although we included adult fish obtained in L2 during the September rotenone sampling in our calculations of final densities, we excluded adult fish caught in L2 during the regular trapping periods from

analyses of growth, condition, and reserves because of their unknown residence time. Due to our efforts, the final density in L2 was comparable to that in L1 and remained well below the densities in H1 or H2 (see *Results: Mortality rates and final densities*). Young crucians (0–1 yr) venture offshore infrequently (Tonn et al. 1992); over the six 1987 samplings, such fish comprised 12 and 6% of the catches in sections L2 and H2, respectively (I. J. Holopainen et al., *unpublished data*). Thus, offshore dispersal should have had little effect on our results for fish 0–1 yr; any movement of young fish between L2 and H2 would make our tests of density effects more conservative.

To test for density effects, data from the high- and low-density treatments (means of each section; $N = 2$ for each treatment) during the final trapping or rotenone sampling were usually compared by t tests. For data on growth of adult crucians, only sections L1, H1, and H2 could be analyzed, using ANOVA and Tukey-Kramer multiple comparisons; thus, this analysis tested for differences among those three sections, rather than between high- and low-density treatments. In analyzing density effects on zooplankton food resources, we used repeated-measures ANOVAs, with sample date as the repeated factor; data were \log_e transformed before analysis and the two sections of each treatment were combined. The level of significance for all tests was set at $P < .05$.

RESULTS

Mortality rates and final densities

Because initial numbers of fish ≥ 1 yr were only estimated (from mark–recapture and removal trappings), our assessment of mortality is necessarily approximate. These values indicated that mortality of fish ≥ 1 yr was low in all four sections during the experiment, ranging from 0% (1+ fish in H2) to 10.6% (fish ≥ 2 yr in H1); there were no consistent trends among treatments or age classes. As a result of this low and uniform mortality, final population counts from the September rotenone treatment revealed that density differences between treatments for fish ≥ 1 yr were maintained throughout the summer. Final densities (numerical) were 2.6 times higher in Sections H1 and H2 ($\bar{X} = 0.79$ fish/m²) than in L1 and L2 ($\bar{X} = 0.30$ fish/m²) ($P < .05$, t test). Final differences in biomass density were smaller, but still were 50% higher in H1 and H2 ($\bar{X} = 5.7$ g/m²) than in L1 and L2 ($\bar{X} = 3.8$ g/m²; $P > .10$, t test).

Growth and condition

The convergence of biomass densities across sections despite comparable mortality suggested greater growth among fish in low- vs. high-density sections. This was supported by data from marked size classes and from 1+ fish (Fig. 1). Growth was minimal for the two largest size classes of marked fish and no differences were

observed among sections L1, H1, and H2. For the two smaller size classes, marked crucians in L1 diverged from those in both H1 and H2 by mid-to-late summer and were significantly larger than fish in H1 and H2 at the time of the final removal ($P < .01$, ANOVA and Tukey-Kramer multiple comparisons); in contrast, fish from H1 and H2 did not differ ($P > .05$; Fig. 1A). Final lengths of crucians in L1 averaged 22 and 13% larger than fish in the two high-density sections for the smallest and next smallest size classes of marked fish, respectively.

A similar pattern was observed for 1+ crucians (Fig. 1B); with data from all four sections, differences could be attributed statistically to a treatment (density) rather than a section effect. Final measurements showed that 1+ fish grew significantly larger at low densities vs. high densities ($P < .05$, t test), resulting in a 22% difference in final lengths between fish in low- and high-density sections.

Greater growth suggested that crucians in low-density sections were in better condition than those in high-density sections. Indeed, condition factors ($100 \times \text{mass}/\text{TL}^3$) diverged quickly for fish in high- and low-density sections and differences were maintained throughout the experiment (Fig. 2). During the final sampling, condition factors for fish at low densities were significantly higher than those for fish at high densities ($P < .01$, t test).

Overwintering reserves and morphology

Other biologically important characteristics also indicated that crucians were in better condition in low- than in high-density sections. The crucian liver is a major storage site of glycogen, reserves of which accumulate during late summer and fall for use in anaerobic metabolism over winter (Hyvärinen et al. 1986). At the final sampling, the size of the liver, relative to body mass, was 64% higher in low-density sections ($\bar{X} = 9.8\%$) than at high densities ($\bar{X} = 6.0\%$) ($P < .05$, t test; Fig. 3A). As well, the amount of glycogen in the liver, relative to body mass, was nearly twice as great at low densities ($\bar{X} = 2.6\%$) than at high densities ($\bar{X} = 1.4\%$) (Fig. 3B; $P < .01$, t test; the angular transformation was used prior to testing for both liver and glycogen). Interestingly, relative liver size and glycogen content were negatively related to body size (TL) at high densities (sections combined); slopes were significantly ($P < .001$) less than zero for both relationships. Neither liver ($P > .25$) nor glycogen ($P > .05$) were significantly related to body size in low-density sections.

It has previously been observed that the relative body depth of crucian carp (summarized by the index $100 \times D/\text{TL}$, where D is body depth) varies considerably among populations (Holopainen and Pitkänen 1985, Brönmark and Miner 1992). Although there was no consistent difference initially between treatments in relative body depth (fish in L1 and H1 had deeper

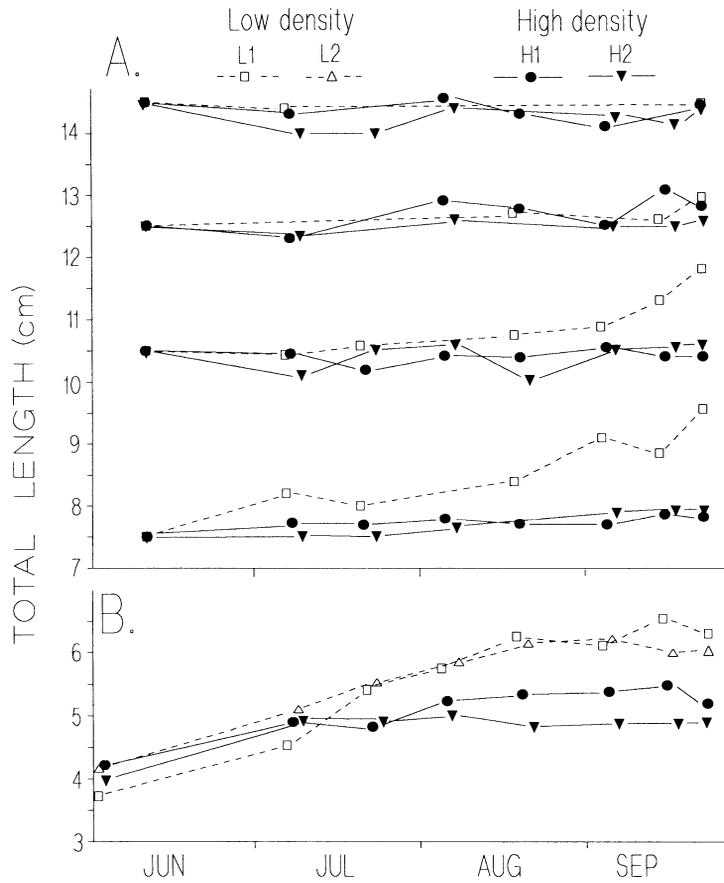


FIG. 1. (A) Growth of four marked size classes of crucian carp stocked into three sections (L1, H1, H2) of Hermanninlampi, during the experiment. No fish of these size classes were stocked into section L2. (B) Growth of yearling (1+ yr old) crucian carp in all four sections.

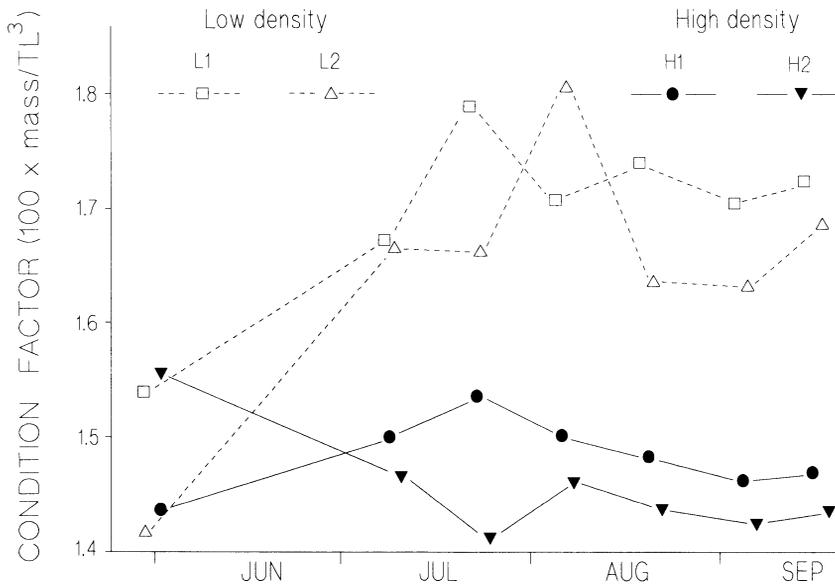


FIG. 2. Mean condition factors of crucian carp (>0+ yr old) in the four sections of Hermanninlampi during the experiment.

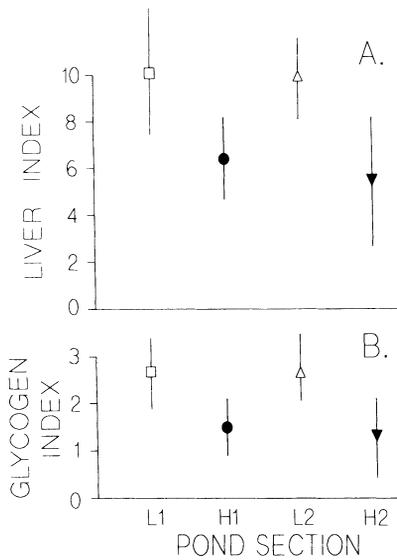


FIG. 3. (A) Indices of liver size ($100 \times$ liver mass/body mass) for crucian carp ($>0+$ yr old) in the four sections of Hermanninlampi at the end of the experiment (means \pm 1 SD). (B) Indices of liver glycogen ($100 \times$ glycogen mass/body mass) for crucian carp ($>0+$ yr old) in the four sections (means \pm 1 SD). Open symbols indicate low-density sections (L1, L2); solid symbols are high-density sections (H1, H2).

bodies than those in L2 and H2), populations quickly diverged by treatment (Fig. 4). During the final sampling, fish from low-density populations had significantly deeper bodies than fish held at high densities ($P < .05$, t test). This overall pattern held true for both 1+ and older (≥ 2 yr) crucians.

Recruitment of 0+ fish

Young-of-the-year fish (0+) were first observed (and captured with hand nets within inshore vegetation) in L1 and H1 during 24–26 June and in L2 and H2 during the next period of inshore netting (8–13 July). Because such netting was qualitative in nature, recruitment of these fish could not be reliably determined until the rotenone sampling of 22 September.

Total counts at that time showed that recruitment of 0+ fish in a given section was strongly and negatively correlated to the numbers of older fish ($\geq 1+$) present ($r = -0.994$, $P < .01$; Fig. 5). As a result, age compositions of the high- and low-density sections differed substantially. Overall, 0+ fish constituted 26.4% of the populations in low-density sections but only 6.2% in high-density sections. Because of these recruitment differences, numerical densities in low-density sections had begun to converge upon those in high-density sections (see *Results: Mortality rates and final densities*).

Consistent with earlier results for 1+ crucians and the smaller marked size classes of older fish (Fig. 1), 0+ fish were significantly larger in the low-density sections ($\bar{X} = 3.0$ cm) vs. the high-density sections ($\bar{X} = 2.6$ cm) ($P < .01$; t test).

Crucian diets and effects of fish density on zooplankton

The diets of all sizes of crucian carp consisted of zooplankton (especially Cladocera), benthic/littoral chydorid cladocerans, chironomid larvae, and detritus, in proportions that varied ontogenetically (Penttinen and Holopainen 1992). Planktonic microcrustaceans comprised $>50\%$ (by carbon mass) of the diets of 0+

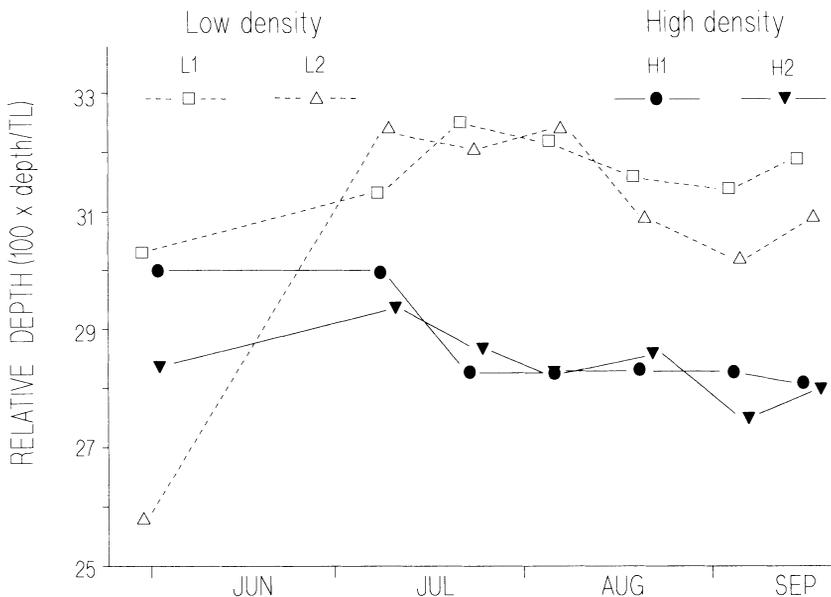


FIG. 4. Mean relative body depths of crucian carp ($>0+$ yr old) in the four sections of Hermanninlampi during the experiment.

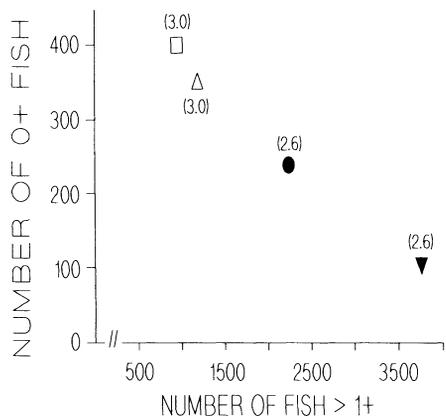


FIG. 5. Stock-recruit relation (number of 0+ yr old fish vs. number of fish $\geq 1+$ yr old) for crucian carp in the four sections of Hermanninlampi at the end of the experiment. Symbols are as in Fig. 1; open symbols are low-density sections (L1, L2) and solid symbols are high-density sections (H1, H2). Numbers within parentheses are mean total lengths (cm) of 0+ yr old fish at the end of the experiment.

crucians and 15–20% of the diets of older fish. Zooplankton eaten by crucians were $>200 \mu\text{m}$, with cladocerans $>400 \mu\text{m}$ (especially *Bosmina*) occurring most frequently (O.-P. Penttinen and I. J. Holopainen, unpublished data).

Density of crucians clearly affected their zooplankton food resource; effects tended to be strongest in the inshore habitat, where 74–88% of all crucians, and higher percentages of smaller fish, were captured during samplings (see also Holopainen et al. 1992). Offshore, zooplankton biomass was 30% higher in low-density sections ($\bar{X} = 194.5 \text{ mg/m}^3$) than in high-density sections ($\bar{X} = 149.5 \text{ mg/m}^3$; $F_{1,7} = 11.9$, $P = .003$; repeated-measures ANOVA). Zooplankton biomass inshore was 2.7 times greater in low-density ($\bar{X} = 169.5 \text{ mg/m}^3$) vs. high-density sections ($\bar{X} = 46.0 \text{ mg/m}^3$; $F_{1,7} = 73.5$, $P < .001$). Cladocerans were significantly ($P < .005$) reduced at high crucian densities both inshore and offshore; copepods and rotifers also tended to be lower in the high fish density treatment, but differences were significant ($P < .01$) only inshore. A higher proportion of large ($>400 \mu\text{m}$) *Bosmina longispina*, the most abundant cladoceran, occurred in low-density compared with high-density sections ($P < .01$; chi-square test); the largest individuals ($>600 \mu\text{m}$) were restricted to low-density sections. Densities of other taxa were not consistently high enough among sections or habitats to permit similar size analyses. High-density sections also had higher concentrations of chlorophyll *a*, higher algal biomass, higher algal richness, and lower Secchi disc transparency than low-density sections (Holopainen et al. 1992).

DISCUSSION

Among fishes, two major density-dependent effects have been suggested as potential influences on popu-

lation dynamics, decreased growth, and increased mortality (Backiel and LeCren 1978). The former is more commonly documented, especially among older age classes, which are, in turn, more commonly studied. The latter, which could be caused directly (via starvation) or indirectly, through decreased growth, is thought to be most important among young fish, and thus might affect recruitment. Our whole-lake experiment demonstrated that under natural densities and realistic environmental conditions, pond populations of crucian carp are affected by both density-dependent growth and recruitment; additional effects, on morphology and accumulation of glycogen, linked to the unique biology of crucians, can combine with growth and recruitment to influence demography and contribute to the regulation of these populations.

Growth of individual fish is highly plastic and dependent on resource levels (e.g., Rask 1983); not surprisingly, density-dependent growth in fish has most often been associated with per capita food availability. Both intra- and intercohort competition may occur, depending on the degree of spatial or diet overlap within or among age classes (Persson 1983, Hamrin and Persson 1986). Our data suggested that competition for limited food resources was the mechanism behind reduced growth and poorer condition of crucians in high-density sections. Resource overlap was high among size classes of crucians and growth suppression was strongest among smaller size classes, which are at an exploitative disadvantage compared with larger fish (Paszkowski et al. 1989, 1990). The biomass of zooplankton, the most important food of small crucians, was significantly reduced in high-density sections, especially in inshore areas where most small crucians were found. Significantly lower proportions of large ($>400 \mu\text{m}$) *Bosmina*, the most important cladoceran in the plankton and in crucian diets (Penttinen and Holopainen 1992), were found in high- vs. low-density sections, indicating that size-selective planktivory was intense in the former. Such relations between fish biomass and their zooplankton prey, coupled with effects on growth and condition, indicate intense density-dependent exploitation competition (Persson et al. 1993). The effects on growth and condition corroborate patterns suggested by earlier field studies (Holopainen and Pitkänen 1985, Piironen and Holopainen 1988) and smaller scale laboratory experiments (Paszkowski et al. 1989, 1990), demonstrating that density dependence can rapidly produce these effects under conditions and at scales meaningful to crucian populations in single-species assemblages.

Long-term demographic consequences of persistent reduced growth could include delayed maturation and reduced fecundity, since both are typically size related in fish (Mills 1991, Barlow 1992); however, direct field demonstrations of these effects are either lacking or inconsistent (Healy 1980). A more immediate and, for crucian carp in ponds, probably more important con-

sequence of intense, density-dependent exploitation competition for food is the reduction in reserves of glycogen needed for anaerobic overwintering in hypoxic waters (Holopainen and Hyvärinen 1984). Although size-related exhaustion of stored energy reserves can contribute to overwinter mortality in 0+ fish of other species (Post and Evans 1989), density-dependent effects on overwintering reserves in crucians could also strongly affect older fish. Larger size classes displayed zero growth in both high- and low-density treatments, but depression of reserve accumulation at high densities was strongest among larger crucians. Larger fish have a greater absolute requirement for energy reserves; thus, lower reserves would likely contribute to higher overwinter mortality rates among larger crucians at high densities, which is consistent with the documented patterns of short life-spans and few large fish in high-density populations (Holopainen and Pitkänen 1985, Piironen and Holopainen 1988). Strong effects of resource limitation among large, older fish have also been documented elsewhere (e.g., Mittelbach 1983, Hamrin and Persson 1986) and proposed as a mechanism for stunting among some fish populations (Persson 1987).

In low-density sections, crucians not only grew more and built up more reserves, but their body depths also increased; body depths of fish in high-density sections either did not change or decreased. Increased body depth occurred among all sizes of fish ≥ 1 yr (0+ fish were not measured), even among larger fish that did not grow in length. It has long been known that body shape of crucian carp differs between "lake" and "pond" populations, with the former consisting of large, deep-bodied fish and the latter having shorter, more slender individuals (Berg 1964, Muus and Dahlström 1978). Although transplant studies have shown that differences are not genetic (Ekström 1838, cited in Brönmark and Miner 1992), only recently have the dynamics of morphological change been documented. The suggestion that lower intraspecific densities, higher resource levels, and the more benign physical conditions facing lake populations contribute to body depth differences appeared to receive support from Holopainen and Pitkänen (1985), who documented an increase in body depth in crucians transplanted from a dense pond population into a similar pond that had been emptied of fish with rotenone. After 4 mo, relative depth of the introduced crucians increased 31%; growth of these fish was also very high, implying high per capita resource levels.

Recent experiments by Brönmark and Miner (1992), however, indicate that the presence of piscivorous fish, which typically co-occur with crucian carp in lakes (Tonn et al. 1990), can induce increased body depths in crucians as an antipredator response, independent of resource levels. Body depths at the start of our experiment were consistent with this; initial depths in sections L1 and H1 were considerably greater than in

other sections, particularly L2. Crucians from the former two sections had co-occurred with piscivorous perch in the previous year (Tonn et al. 1992), whereas fish from L2 and H2 had not been previously exposed to predators. However, after removal of the remaining predators and establishment of the density treatments in June, body depths diverged significantly in a pattern that matched the contemporary density treatment but was independent of any earlier exposure to piscivorous fish. Brönmark and Miner (1992) suggested that because increased body depth should incur a substantial energy cost via increased drag (Webb 1975), crucians should not increase body depth when predation is not a threat. The increased depth we documented for fish in the low-density sections, despite the absence of predators, is inconsistent with this hypothesis. An alternative might be that under conditions of high per capita resource levels, the development of a deep body results in additional storage of glycogen in white muscle and allows for a large liver.

The increase in body depth that we observed at low densities was independent of body size. The predation hypothesis would suggest that because a deeper body would still not provide a morphological refuge for small fish, their energy should be focussed on simply growing longer (C. Brönmark, *personal communication*). However, we have found that small crucians are almost exclusively restricted to the inshore habitat and grow less in the presence of predators than sympatric large fish or small fish occurring without predators (Holopainen et al. 1991, Tonn et al. 1992). Clearly, body shape in crucian carp is a complex phenomenon that can involve predators, per capita resource levels, and crucian size.

The other major density-dependent effect that we measured was a significantly negative stock-recruit relationship. Because young were observed only shortly after experimental densities were established, fecundity was not likely affected by our manipulation, indicating that the survival rate of 0+ fish was lower in high-density sections. Our data, and other observations, suggest that a combination of starvation and cannibalism was responsible. Growth depression was observed among 0+ crucians in high-density sections, where their main food resource, zooplankton, was reduced. Larval fish are especially sensitive to food supplies (Mills 1991), and smaller larvae, with their extremely limited energy reserves, are more susceptible to starvation-induced mortality than are larger fish (Li and Mathias 1987). Density-dependent food limitation also contributed to higher larval mortality in dace (*Leuciscus leuciscus*), another European cyprinid (Mills 1982), and has been implicated similarly elsewhere (Miller et al. 1988).

We have documented a significant capability for cannibalism in crucian carp in laboratory trials (I. J. Holopainen, *unpublished data*). Crucians as small as 1.8 cm readily consumed 0.8-cm larvae, even in the presence

of alternative prey (planktonic microcrustacea). Crucians are fractional spawners, having up to three spawning periods between May and August (Piironen and Holopainen 1988); thus, 0+ crucians from the first spawning, as well as older fish, would be able to eat fry from later spawnings. Crucians as large as 2 cm were consumed by fish 7–8 cm; only by 3.5–4.0 cm did crucians appear to achieve a size refuge from conspecific predators. Crucians will also cannibalize eggs. Cannibalism should increase directly with adult density; however, an indirect density-dependent mechanism is also likely, involving growth suppression of 0+ fish followed by increased mortality via size-dependent cannibalism. Small crucians are concentrated inshore and it was in the inshore areas of high-density sections where zooplankton resources were most severely reduced. Because smaller fish are more vulnerable to cannibals, growth depression in 0+ fish at high densities would increase their mortality, both because slow-growing fish are smaller at a given age and because the period of greatest vulnerability is extended (Post and Prankevicus 1987, Rice et al. 1987).

By the end of our 3-mo experiment, populations of the two treatments had begun to converge in structure (numbers and biomass), due to the relatively strong growth and recruitment in low-density sections. Although other short-term studies have frequently demonstrated effects of density on growth of individual fish, few have observed such a striking stock-recruit relation (Wootton 1990). The relevance and importance of the responses we measured to the long-term dynamics of pond populations of crucians is strongly supported both by recent studies of other planktivores and by our extensive and longer term studies of crucians in ponds.

A survey of pond populations of crucians (Piironen and Holopainen 1988) revealed a remarkable degree of structural similarity among populations occurring in the absence of predators; size structures were dominated by a single mode, primarily of fish 5–10 cm, with few fish >15 cm. This similarity among pond populations, and the initial stages of convergence we observed between treatments, suggests a high degree of persistence and resilience of these predator-free populations and no evidence of alternate stable population states (see also Persson et al. 1993). The resilience of these populations is further supported by the rapid response of the pre-1985 population in Hermanninlampi, following an earlier manipulation. In July 1982, Hermanninlampi was treated with rotenone and found to contain a population of 44 000 crucians (\bar{X} length = 6 cm; \bar{X} mass = 3 g; Holopainen and Pitkänen 1985); the pond was restocked subsequently (October 1982) with only 280 fish. Within 2 yr (May 1985), the population had rebounded to 25 000, and closely approached its original size structure (\bar{X} length = 5.2 cm; \bar{X} mass = 2.1 g; Piironen and Holopainen 1988). Growth and recruitment were very high in 1983, when density was very low, and both decreased as density increased

in 1984. A similar rapid convergence towards pre-manipulation population structures was observed in another European planktivore, roach (*Rutilus rutilus*), following population reductions (Persson et al. 1993); the rapid response was similarly attributed to strong density-dependent growth and recruitment of young fish, caused by density-dependent interactions between the planktivores and zooplankton. Regulation via density effects on recruitment have also been documented for populations of other freshwater planktivores (Hamrin and Persson 1986, Townsend and Perrow 1989).

Although our experiment ended in the fall, our results concerning growth, accumulation of reserves, and perhaps morphology, combined with the unique biology of crucians, suggest that density-dependent overwinter mortality also contributes to the regulation of pond populations of crucians. The density-dependent growth of 0+ crucians we observed suggests that size-dependent overwinter mortality of young fish could be important for crucians, as in other temperate freshwater fishes (Hunt 1969, Toney and Coble 1979, Post and Evans 1989). Density-dependent overwinter mortality due to a shortage of accumulated reserves of glycogen is also implicated as the mechanism behind the consistent lack of older, larger fish observed in pond populations (Piironen and Holopainen 1988). Density-dependent factors clearly affect several physiological and demographic parameters of crucian carp that strongly influence the long-term dynamics of pond populations and contribute to the stable population structure that characterizes this unique species.

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LITERATURE CITED

- Andersson, G., H. Berggren, G. Cronberg, and C. Gelin. 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. *Hydrobiologia* 59: 7–15.
- Andrews, R. M. 1991. Population stability of a tropical lizard. *Ecology* 72:1204–1217.
- Backiel, T., and E. D. LeCren. 1978. Some density relationships for fish population parameters. Pages 279–302 in S. D. Gerking, editor. *Ecology of freshwater fish production*. Blackwell Scientific, Oxford, England.
- Barlow, J. 1992. Nonlinear and logistic growth in experimental populations of guppies. *Ecology* 73:941–950.
- Begon, M., and M. Mortimer. 1986. *Population ecology: a unified study of animals and plants*. Sinauer, Sunderland, Massachusetts, USA.
- Bengtsson, T., and A. Hargeby. 1979. Fiskundersökningar i Tåkern 1979. Rapport till Statens Naturvårdsverk, Avdelningen för biologi, Universitetet i Linköping, Linköping, Sweden.

- Berg, L. S. 1964. Freshwater fishes of the USSR and adjacent countries. Volume 2. Israel Program of Scientific Translation, Jerusalem, Israel.
- Brönmark, C., and J. G. Miner. 1992. Predator-induced phenotypical change in body morphology in crucian carp. *Science* **258**:1348-1350.
- Carpenter, S. R. 1989. Replication and treatment strength in whole-lake experiments. *Ecology* **70**:453-463.
- Choquenot, D. 1991. Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. *Ecology* **72**:805-813.
- Fox, M. G., and D. D. Flowers. 1990. Effects of fish density on growth, survival, and food consumption by juvenile walleyes in rearing ponds. *Transactions of the American Fisheries Society* **119**:112-121.
- Hall, D. J., W. E. Cooper, and E. E. Werner. 1970. An experimental approach to the production dynamics of freshwater animal communities. *Limnology and Oceanography* **15**:839-928.
- Hamrin, S. F. 1979. Biomass of tench, perch, crucian carp and pike in a small eutrophic lake in southern Sweden. *Jyväskylän Yliopiston Biologian Laitoksen Tiedonantoja* **19**:57-67.
- Hamrin, S. F., and L. Persson. 1986. Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish species. *Oikos* **47**:223-232.
- Healy, M. C. 1980. Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* **37**:255-267.
- Holopainen, I. J., and H. Hyvärinen. 1985. Ecology and physiology of crucian carp (*Carassius carassius* (L.)) in small Finnish ponds with anoxic conditions in winter. *Proceedings of the International Association of Theoretical and Applied Limnology* **22**:2566-2570.
- Holopainen, I. J., and A. K. Pitkänen. 1985. Population size and structure of crucian carp (*Carassius carassius* (L.)) in two small, natural ponds in Eastern Finland. *Annales Zoologici Fennici* **22**:397-406.
- Holopainen, I. J., W. M. Tonn, and C. A. Paszkowski. 1991. Ecological responses of crucian carp populations to predation by perch in a manipulated pond. *Proceedings of the International Association of Theoretical and Applied Limnology* **24**:2412-2417.
- Holopainen, I. J., W. M. Tonn, and C. A. Paszkowski. 1992. Effects of fish density on planktonic communities and water quality in a manipulated forest pond. *Hydrobiologia* **243/244**:311-321.
- Hulata, G., R. Moav, and G. Wohlfarth. 1982. Effects of crowding and availability of food on growth rates of fry in the European and Chinese races of the common carp. *Journal of Fish Biology* **20**:323-327.
- Hunt, R. 1969. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. *Journal of the Fisheries Research Board of Canada* **26**:1473-1483.
- Hyvärinen, H., I. J. Holopainen, and J. Piironen. 1986. Anaerobic wintering of crucian carp (*Carassius carassius* L.). I. Annual dynamics of glycogen reserves in nature. *Comparative Biochemistry and Physiology* **82A**:797-803.
- Johnson, M. G., and H. R. McCrimmon. 1967. Survival, growth and reproduction of largemouth bass in southern Ontario ponds. *Progressive Fish-Culturist* **29**:216-221.
- Larkin, P. A., and S. B. Smith. 1954. Some effects of introduction of the redeye shiner (*Richardsonius balteatus*) on the Kamloops trout (*Salmo gairdneri kamloops*) in Paul Lake, British Columbia. *Transactions of the American Fisheries Society* **83**:161-175.
- Latja, R., and K. Salonen. 1978. Carbon analysis for the determination of individual biomasses of planktonic animals. *Proceedings of the International Association of Theoretical and Applied Limnology* **20**:2556-2560.
- Li, S., and J. Mathias. 1987. The critical period of high mortality of larval fish—a discussion based on current research. *Chinese Journal of Oceanography and Limnology* **5**:81-96.
- Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* **45**:1657-1670.
- Mills, C. A. 1982. Factors affecting the survival of dace, *Leuciscus leuciscus* (L.), in the early post-hatching period. *Journal of Fish Biology* **20**:645-655.
- . 1991. Reproduction and life history. Pages 456-482 in I. J. Winfield and J. S. Nelson, editors. *Cyprinid fishes: systematics, biology and exploitation*. Chapman & Hall, London, England.
- Mittelbach, G. G. 1983. Optimal foraging and growth in bluegills. *Oecologia* (Berlin) **59**:157-162.
- Muus, B. J., and P. Dahlström. 1978. Freshwater fishes of Britain and Europe. Collins, London, England.
- Paszowski, C. A., W. M. Tonn, and I. J. Holopainen. 1989. An experimental study of body size and food size relations in crucian carp, *Carassius carassius*. *Environmental Biology of Fishes* **24**:275-286.
- Paszowski, C. A., W. M. Tonn, J. Piironen, and I. J. Holopainen. 1990. Behavioral and population-level aspects of intraspecific competition in crucian carp. *Annales Zoologici Fennici* **27**:77-85.
- Penttinen, O.-P., and I. J. Holopainen. 1992. Annual feeding activity and ontogenetic shift in diet of crucian carp. *Environmental Biology of Fishes* **33**:215-221.
- Persson, L. 1983. Food consumption and competition between age classes in a perch *Perca fluviatilis* population in a shallow eutrophic lake. *Oikos* **40**:197-207.
- . 1987. The effects of resource availability and distribution on size class interactions in perch, *Perca fluviatilis*. *Oikos* **48**:148-160.
- Persson, L., L. Johansson, G. Andersson, S. Diehl, and S. F. Hamrin. 1993. Density dependent interactions in lake ecosystems: whole lake perturbation experiments. *Oikos* **66**:193-208.
- Petranka, J. W. 1989. Density-dependent growth and survival of larval *Ambystoma*: evidence from whole-pond manipulations. *Ecology* **70**:1752-1767.
- Piironen, J., and I. J. Holopainen. 1988. Length structure and reproductive potential of crucian carp (*Carassius carassius* (L.)) populations in some small forest ponds. *Annales Zoologici Fennici* **25**:203-208.
- Post, J. R., and D. O. Evans. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. *Canadian Journal of Fisheries and Aquatic Sciences* **46**:1958-1968.
- Post, J. R., and A. B. Prankevicius. 1987. Size-selective mortality in young-of-the-year yellow perch (*Perca flavescens*): evidence from otolith microstructure. *Canadian Journal of Fisheries and Aquatic Sciences* **44**:1840-1847.
- Prejs, A. 1973. Experimentally increased fish stock in the pond type Lake Warniak. IV. Feeding of introduced and autochthonous non-predatory fish. *Ekologia Polska* **21**:465-503.
- Rask, M. 1983. Differences in growth of perch (*Perca fluviatilis* L.) in two small forest lakes. *Hydrobiologia* **101**:139-144.
- Rice, J. A., L. B. Crowder, and M. E. Holey. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. *Transactions of the American Fisheries Society* **116**:703-718.

- Ricker, W. E. 1975. Computation and interpretation of biological statistics on fish populations. *Bulletin of the Fisheries Research Board of Canada* **191**.
- Roughgarden, J., S. D. Gaines, and S. W. Pacala. 1987. Supply side ecology: the role of physical transport processes. Pages 491–518 in J. H. R. Gee and P. S. Giller, editors. *Organization of communities: past and present*. Blackwell Scientific, Oxford, England.
- Scott, D. E. 1990. Effects of larval density in *Ambystoma opacum*: an experiment in large-scale field enclosures. *Ecology* **71**:296–306.
- Siu, L., J. C. Russel, and A. W. Taylor. 1970. Determination of glycogen in small tissue samples. *Journal of Experimental Physiology* **28**:234–236.
- Stiling, P. D. 1988. Density-dependent processes and key factors in insect populations. *Journal of Animal Ecology* **57**:581–593.
- Strong, D. R., J. H. Lawton, and T. R. E. Southwood. 1984. *Insects on plants: community patterns and mechanisms*. Blackwell Scientific, Oxford, England.
- Toneys, M. L., and D. W. Coble. 1979. Size-related, first winter mortality of freshwater fishes. *Transactions of the American Fisheries Society* **108**:415–419.
- Tonn, W. M., J. J. Magnuson, M. Rask, and J. Toivonen. 1990. Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes. *American Naturalist* **136**:345–375.
- Tonn, W. M., C. A. Paszkowski, and I. J. Holopainen. 1989. Responses of crucian carp populations to differential predation pressure in a manipulated pond. *Canadian Journal of Zoology* **67**:2841–2849.
- Tonn, W. M., C. A. Paszkowski, and I. J. Holopainen. 1992. Piscivory and recruitment: mechanisms structuring prey populations in small lakes. *Ecology* **73**:951–958.
- Tonn, W. M., C. A. Paszkowski, and T. C. Moermond. 1986. Competition in *Umbra-Perca* fish assemblages: experimental and field evidence. *Oecologia (Berlin)* **69**:126–133.
- Townsend, C. R., and M. R. Perrow. 1989. Eutrophication may produce population cycles in roach, *Rutilus rutilus* (L.), by two contrasting mechanisms. *Journal of Fish Biology* **34**:161–164.
- Van Buskirk, J., and D. C. Smith. 1991. Density-dependent population regulation in a salamander. *Ecology* **72**:1747–1756.
- Webb, P. W. 1975. Hydrodynamics and energetics of fish propulsion. *Bulletin of the Fisheries Research Board of Canada* **190**:1–159.
- Wootton, R. J. 1990. *Ecology of teleost fishes*. Chapman & Hall, London, England.