

CANNIBALISM AND COMPETITION IN EURASIAN PERCH: POPULATION DYNAMICS OF AN ONTOGENETIC OMNIVORE

LENNART PERSSON,¹ PÄR BYSTRÖM, AND EVA WAHLSTRÖM

Department of Ecology and Environmental Science, Umeå University, S-901 87 Umeå, Sweden

Abstract. In many cannibalistic populations, cannibals share resources with their victims, leading to a size-dependent mixture of cannibalistic and competitive interactions. We analyze the impacts of such interactions on the population dynamics of Eurasian perch (*Perca fluviatilis*) by considering effects of intercohort competition, habitat heterogeneity, habitat selection, and energy gain made by cannibals. Over a six-year period, we measured mortality and recruitment patterns, individual growth, body condition, resource levels, diets, and habitat use as functions of density for an allopatric perch population in a low-productivity lake.

During the course of the study, two major die-offs took place, selectively affecting larger cannibalistic individuals, followed by several years of successful recruitment of young fish. Habitat use of perch ≥ 2 yr old was density dependent, and these fish used only the inshore region at low densities. The appearance of young fish followed the die-offs of cannibalistic perch and their subsequent absence from the offshore area, both of which decreased cannibalism on pelagic recruits. Whereas die-offs of larger perch could not be related to competition with young-of-the-year (YOY) perch, evidence for a competitive impact of YOY perch on Age-1 perch was present due to substantial food overlap. A strong depression in pelagic zooplankton was observed during summer in years with strong recruitment, which resulted in reduced consumption of zooplankton, slow growth, and reduced body condition in Age-1 perch and suggested high mortality of Age-1 perch in autumn. Age-1 perch did not appear to profit substantially from cannibalism on YOY perch because of the short time period that they could efficiently prey on YOY perch. The few larger perch that survived the die-offs gained substantial energy from cannibalism in years with strong recruitments, which increased both growth rates and per capita fecundity.

Size-dependent intercohort competition may have strong impacts on cannibal-victim interactions when victims share resources with cannibals. Furthermore, habitat heterogeneity, combined with habitat selection, may limit the extent to which cannibals have a stabilizing effect on population dynamics. Finally, the energy gained by cannibals may have important consequences on population dynamics as this energy is allocated into new recruits.

Key words: cannibalism; competition; energy gain; growth trajectories; habitat selection; *Perca fluviatilis*; perch fecundity; size structure; starvation.

INTRODUCTION

Historically viewed as an abnormal behavior, it is now well established that cannibalism is a common interaction in ecological communities (Polis 1981, Elgar and Crespi 1992). Cannibalism is known in a wide range of animal phyla from protozoans to vertebrates (e.g., Polis 1981, Smith and Reay 1991, Wadell 1992). Studies of cannibalism have included both evolutionary and ecological processes. The latter have largely focused on two aspects of cannibalism on populations: (1) consequences on variation in population numbers over time and (2) whether cannibalism can function as a “lifeboat” mechanism whereby cannibalistic populations can survive periods of food shortage that would otherwise extirpate noncannibalistic populations (e.g., Van den Bosch et al. 1988, Orr et al. 1990, Hastings and Constantino 1991). With respect to the former, sug-

gested population dynamics of cannibals include a variety of regimes such as equilibrium, periodic cycles, aperiodic cycles, and chaotic dynamics (Diekmann et al. 1986, Hastings and Constantino 1987, Constantino et al. 1997). Cannibalism has been suggested to stabilize population dynamics (Van den Bosch and Gabriel 1997), but this prediction is based on the assumption that cannibals do not gain any energy from cannibalizing. For most cannibalistic systems, this is unrealistic and also contradicts the assumptions of models focused on the lifeboat mechanism. In the latter models, the energetic gain made by adult cannibals is essential to the persistence of the population (Gabriel 1985, Van den Bosch et al. 1988, Cushing 1992).

The extent to which cannibalism influences the dynamics of a given population is likely to depend on the co-occurrence of other factors such as competition from noncannibalistic conspecifics or interspecific competition and predation. Because many cannibals share resources with their victims, the latter may compete with cannibals for this shared resource (Polis 1988,

Manuscript received 26 May 1998; revised 15 January 1999; accepted 15 January 1999; final version received 1 March 1999.

¹ E-mail: Lennart.Persson@animecol.umu.se

Anholt 1994, Wissinger et al. 1996). Polis (1988) suggested that this competition should be an important agent in the evolution of cannibalism whereby cannibals benefit both from feeding on victims and reducing competition for shared resources. In the absence of cannibalism, size-dependent cohort competition for a resource will theoretically generate population oscillations driven by recruits (Persson et al. 1998), a prediction that is supported by empirical data (Hamrin and Persson 1986, McCauley et al. 1988, Townsend et al. 1990). Consequences of the mixture of competitive and predatory interactions between cannibals and victims to population dynamics have yet to be explored both empirically and theoretically.

Cannibalism has been studied most successfully in laboratory, seminatural (tank), or small scale/short term enclosure systems (Mertz 1969, Orr et al. 1990, Wissinger et al. 1996). Studies evaluating the impact of cannibalism on the dynamics of natural populations have generally not been able to separate the impacts of cannibalism and interspecific predation (Johnson et al. 1987, Crowley and Johnson 1992, Claus-Walker et al. 1997). Here, we take advantage of a single-species system to evaluate the impact of cannibalism in a natural system without the complications imposed by mixed-species assemblages and the confounding effects of interspecific interactions. The focus of our study was a single-species population of Eurasian perch (*Perca fluviatilis*), over a six yr period. Perch populations are a suitable study object for field studies of cannibalism because they are often the only fish species in a lake and the only important predators in these populations are conspecifics. Furthermore, interactions among size classes are both predatory and competitive (Alm 1946, 1952, Persson 1988, Persson et al. 1996), making this species a suitable study object for the general issue of how shared resources affect the dynamics between cannibals and victims.

The purpose of our study was to analyze the effects of intercohort predatory and competitive interactions on population dynamics. We focused on three issues. First, we investigated possible mechanisms (fecundity limitation, resource limitation, and cannibalism) that prevented successful recruitment into the population in some years. Second, we investigated the potential for recruits to affect other size (age) cohorts competitively. Third, we investigated the extent to which cannibals profited energetically from cannibalism. Finally, we discuss potential implications for the dynamics of cannibalistic populations where cannibals and victims compete for a shared basic resource.

STUDY SPECIES

Eurasian perch undergo three major ontogenetic niche shifts over their lifetime. Initially, perch feed on pelagic zooplankton (prey size range ~0.3–2 mm). At 30–80 mm, perch shift to macroinvertebrates (size range ~1–30 mm) and finally shift to piscivory at a

size varying between 130 to 180 mm in low-productivity systems (prey size ≥ 12 mm) (Alm 1946, Craig 1978, Persson 1988). Single species populations of perch are common in small boreal lakes and are generally characterized by slow-growing individuals due to high intra- and intercohort competition (Alm 1946, 1952, Sumari 1971). Cannibalism, mainly on young-of-the-year (YOY) and Age-1 individuals, is commonly reported from field studies on perch (Alm 1946, Popova 1978, Van Densen 1994). Corroborating these field observations, experimental studies have demonstrated that large (160–200 mm) perch are efficient predators on small (60–80 mm) perch, whereas individuals slightly larger (90–110 mm) are not susceptible to cannibalism from these piscivores (Eklöv 1992, Eklöv and Diehl 1994). Thus, in these slow-growing populations, risk of cannibalism is largely restricted to individuals during their first year of life. In addition to the upper size limit, there is also a lower limit for prey fish a cannibalistic perch can take as the encounter rate with prey fish is an increasing function of prey fish length (Mittelbach and Persson 1998, Lundvall et al. 1999).

MATERIALS AND METHODS

Lake description

The study was carried out in a small (9.3 ha) oligotrophic lake, Abborrtjärn 3, in central Sweden (64°29' N, 19°26' E) (Persson et al. 1996). The lake is situated in a sandy area and the catchment is covered by slow-growing pine (*Pinus silvestris*) forests with reindeer lichens (*Cladonia rangiferina*) and lingon berries (*Vaccinium vitis-idaea*) as ground cover. The maximum depth of the lake is 12 m, mean depth is 6.3 m, total phosphorus levels vary between 1.6 and 3.1 $\mu\text{g/L}$, and total nitrogen levels vary between 161 and 330 mg/L . The lake has low humic content and sparse vegetation mainly consisting of *Carex rostrata*, *Menyanthes trifoliata*, *Lobelia dortmanna*, and *Nymphaea alba*. Most (69%) of the shoreline is covered with trees that have fallen into the water. The lake is dimictic, with a thermocline at 3–4 m, and lacks surface inlets or outlets. Perch was the only fish species in the lake during 1991–1996. In late autumn 1996 and spring 1997, roach (*Rutilus rutilus*) and artificial vegetation were added to the lake as part of a whole-lake experiment. Data are therefore reported up to the start of the growing season (May) of 1997, when no confounding effect of roach was expected due to low temperatures ($<4^{\circ}\text{C}$) that had persisted since roach were stocked in autumn 1996.

Perch

Perch habitat use.—In 1991, sampling was only carried out once in August with 56×1.5 m survey benthic gill nets (mesh sizes 9.5, 14.5, 18, 24, 29.5, 33, 38, and 46 mm, respectively, each section 7 m long). Two nets were set at 2–3 m and two nets at 5–6 m. Captured fish were measured (to nearest mm) and weighed (to

nearest g). These data were used to generate a size-frequency distribution after correcting for net selectivity using values given in Hamrin (1977).

In 1992–1997, fish were sampled with cylindrical plastic traps and fyke nets. In 1992, 60 traps (40×100 cm, mesh sizes 10 and 20 mm, 30 of each mesh size), and in 1993–1997 90 traps (besides the 60 traps used in 1992, 30 traps 25×50 cm, mesh size 5 mm) and 10 fyke nets (mesh size 6 mm) were used. Traps with the two largest mesh sizes mainly captured perch ≥ 2 yr old, whereas the traps with the smallest mesh size and the fyke nets captured perch ≥ 1 yr and also YOY perch in August and September.

Traps were set on four sampling dates (end of May and first weeks in July, August, and September, hereafter May, July, August, and September, respectively) each year. They were set in groups of six (groups of four in 1992), including two traps of each mesh size at 15 different stations of which 10 were inshore stations situated at a depth of 0.5–2 m. The other five stations were set along two vertical profiles, one with two stations and the other with three stations and with both profiles including the maximum depth at that basin. One fyke net was set perpendicular to the shore at every shore station. All sampling gear used were set at 13:00–14:00 and raised at 9:00–10:00 the following day. All captured perch were measured (to nearest millimeter) and weighed (to nearest 0.1 g).

During 1994–1996, larval perch were sampled once a week for five weeks following hatching in early June when they were distributed in the pelagic habitat. Sampling was done with a Bongo trawl attached to a boat. The trawl had a diameter of 60 cm and a length of 4 m and could be adjusted to sample water strata between 0 and 2.0 m (see Byström et al. 1998 for details). In all years, two habitats were sampled, the littoral (trawl depth: 0–0.6 m) and the pelagic (trawl depths: 0.4–1 m and 1.6–2.2 m). At least four hauls of 50–75 m were made per habitat and date. Captured perch larvae were preserved in Lugol's solution. After their shift to the littoral zone, YOY perch were caught by electrofishing along the shore, and in traps and fyke nets in August and September. Larvae were measured to the nearest 0.1 mm (total length) in the laboratory and juveniles to the nearest 1 mm (total length). For juvenile perch, a subsample ($n \geq 30$) was frozen in water on each sampling occasion and stored at -20°C for later stomach and condition analyses. In the laboratory, these fish were measured to nearest 1 mm (total length) and weighed to nearest 0.01 g.

Perch population size.—A large trapping effort was carried out every spring for three weeks to estimate population size of perch ≥ 1 yr old by multiple mark-recapture methods (Youngs and Robson 1978). Perch were marked with blue dye injected with a Pan Jet injector (Hart and Pitcher 1969). Trap catches of perch ≥ 2 yr in May were strongly related to estimates based on mark-recapture (1992–1997, $n = 6$, $r^2 = 0.88$, $F_{1,5}$

$= 29.4$, $P = 0.006$): $\ln(\text{May population estimate}) = 2.5 + 0.955 \ln(\text{May trap capture})$. Based on this regression, population densities of perch ≥ 2 yr in July, August, and September were calculated from trap catches. In spring, Age-1 perch were electrofished from a boat along the shore where they were concentrated. The entire shoreline was covered, dipping the anode of the electrofisher every 3 m. In years when Age-1 perch abundance was too low to allow population estimates based on mark-recapture (1992, 1993, 1994), spring electrofishing and the total number of Age-1 perch captured in traps and fyke nets over the whole sampling season were used as abundance indices. Estimates of YOY perch numbers during the first five weeks after hatching were obtained from quantitative Bongo trawls. Since perch larvae are rarely caught below a depth of 3 m during the pelagic phase (Wang and Eckman 1994), the total number of larvae was calculated using stratified sampling methods by multiplying larvae density estimates for each habitat (strata) with the water volume of each habitat (littoral and pelagic [two depths] habitats).

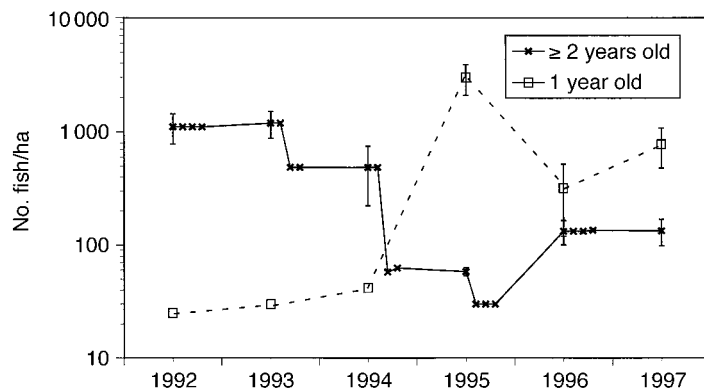
Fish age, mortality, condition, and fecundity.—In August every year, a sample of perch was sacrificed for age analysis. Age and growth of individual fish were determined from opercular bones (Bagenal and Tesch 1978). Annual mortality rate of perch was estimated using age and population estimates (Youngs and Robson 1978).

For YOY and Age-1 perch, condition (K) was defined as $K = 100 \times \text{mass} \times \text{length}^{-3}$ (mass in grams, length in centimeters) (Fulton 1904). The condition factor (K) for YOY perch was only calculated for August and September when the morphological change of perch from larvae to juvenile had been completed. For perch ≥ 2 yr (≥ 100 mm), mass was regressed on body length using a power function, $\text{mass} = a \times \text{length}^b$, as the condition index used for YOY and Age-1 perch was inappropriate due to the large variation in length among individuals. The masses of perch of two different lengths (150 and 200 mm) were then calculated for the different sampling dates.

The perch in the study lake started to spawn before the lake was accessible to sampling in spring, hence, we could not obtain reliable estimates of fecundity based on sampled females. We instead calculated population fecundity based on length-specific fecundity data from Nyberg (1976), who studied perch populations with similar growth patterns and size structures. In the spring of 1997, we directly counted roe strands in the lake and the average number of eggs per strand.

Perch diets.—On every sampling date, stomachs of up to 10 perch from each 20-mm size class >100 mm were flushed for dietary analyses. In 1995 and 1996, stomach contents from 10–20 Age-1 perch were similarly taken at each sample date. In 1995, additional samples were taken every week in June to study the potential presence of cannibalism by Age-1 perch on

FIG. 1. Numbers of Age-1 perch (50–70 mm) and perch ≥ 2 yr old (≥ 80 mm) during the period 1992–1997. Population estimates based on multiple mark-recapture are shown with 95% CL. Population numbers of Age-1 perch in 1992–1994 are based on a regression of population estimates from mark-recapture on numbers captured by trapping in 1995–1997. Numbers of marked 1-yr-old perch were 1000 individuals in 1995, 700 individuals in 1996, and 1000 individuals in 1997. Numbers of marked/recaptured perch ≥ 2 yr were 245/1524 in 1992, 1022/514 in 1993, 275/174 in 1994, 48/146 in 1995, 194/398 in 1996, and 192/138 in 1997.



YOY perch. Stomach contents were frozen for later laboratory analyses. Stomach contents were identified to order, family, or species and lengths of ≤ 10 prey of each group were measured. Lengths were transformed to dry mass using published length-mass relationships for zooplankton (Bottrell et al. 1976) and macroinvertebrates (Persson and Greenberg 1990). Diet data from each sampling date were grouped based on perch size classes (< 100 mm, 101–150 mm, 151–200 mm, > 200 mm). Size classes that contained < 5 stomach samples were discarded from further analyses. All perch, except those sacrificed for age analyses, were released after measurements and stomach-flushing.

Resources

Zooplankton.—Zooplankton were sampled seven or eight times during the growing season in every year at three pelagic stations. Zooplankton were collected with a 100- μ m mesh net (diameter 25 cm) drawn vertically at a speed of ~ 0.5 m/s. One tow was made at each pelagic station from the thermocline (estimated with a thermistor) to the surface. Zooplankton samples were preserved with Lugols solution. In the laboratory, animals were classified by species, counted, and the lengths of 15 individuals (all, if fewer were collected) of each species from each sample were measured in an

inverted microscope. Lengths were transformed to biomass using regressions relating length to dry mass (Dumont et al. 1975, Bottrell et al. 1976).

Macroinvertebrates.—In August 1992, five macroinvertebrate samples were taken with an Ekman dredge (area 630 cm²) at one littoral station at a water depth of 0.5 m. In other years (1993–1996), macroinvertebrate sampling was extended to three littoral stations. Six samples were taken at each station on one date (August) with a core sampler (area 63 cm²). All samples were sieved through a 0.5-mm net, preserved in 70% ethanol, and stained with Rose Bengal. Animals were then classified by taxa and counted. Lengths of all individuals (except chironomids) were measured using an image analysis system (Optilab). Lengths were converted to dry masses using length-mass regressions (Persson and Greenberg 1990). For chironomids, surface area (i.e., the two-dimensional image) was determined and converted to dry mass using an area-mass regression (J. Andersson, *personal communication*). Macroinvertebrates were separated into two groups. One group consisted of organisms living on macrophytes, branches or on other substrates (Hirudinea, Ephemeroptera, Trichoptera, Odonata, Coleoptera, Megaloptera), and which are relatively sensitive to fish predation. The other group (mainly chironomids) consisted of organisms living in the sediment and which are less sensitive to fish predation (see Persson et al. 1996 and references therein).

RESULTS

Population numbers, length, and size-dependent mortality

Over the study period, two distinct phases could be discerned with respect to population numbers of different age/size classes. During the first phase (1991–1993), high numbers (> 1000 individuals/ha) of perch ≥ 2 yr were present, whereas the density of Age-1 perch was very low (Fig. 1, Table 1). Conversely, during the second phase (1994–1997) the density of perch ≥ 2 yr was low whereas that of Age-1 perch was high. This change in population structure over years was associ-

TABLE 1. Total trap and fyke net catches of YOY and Age-1 perch, and population estimates (May) and spring electrofishing capture of Age-1 perch during 1992–1997.

Year	YOY, total capture	Age-1		
		Population estimate ($\bar{X} \pm 95\%$ CL)	Spring electrofishing	Total capture
1992	†	†	0	†
1993	0	†	0	3
1994	742	†	†	4
1995	1238	32 000 \pm 8600	481	542
1996	515	3000 \pm 1900	52	42
1997	...	7800 \pm 2100	547	...

† No sampling.

‡ Too few fish caught to allow population estimate based on mark-recapture.

ated with changes in body condition, growth rates, habitat use, and diet that will be considered below after having treated the changes in population numbers for three major age classes: YOY perch, Age-1 perch, and perch ≥ 2 yr.

In spring of 1992 and 1993, no Age-1 perch were captured by electrofishing, indicating a low survival of YOY perch born in 1991 and 1992 (Table 1). Trap/fyke net captures of Age-1 perch were also very low in 1992 and 1993 (Table 1). No trap/fyke net catches of YOY perch were obtained in August and September 1993. The population density of perch ≥ 2 yr (≥ 80 mm) in the spring of 1992 was estimated at 1100 ± 330 individuals/ha (mean \pm 95% CL) and remained the same in spring of 1993 (Fig. 1). The mean size of these perch increased from 157 mm in May 1992 to 160 mm in May 1993 as individuals in the dominant year classes increased in size (Fig. 2). Between July and August 1993, a major decrease in the population size of perch ≥ 2 yr to 490 individuals/ha took place (Fig. 1). Estimates of age specific mortality rates show that the mortality from 1993 to 1994 was restricted to perch ≥ 5 years old (size ≥ 151 mm) (Table 2). Between July and August 1994, a further decrease in abundance of these perch to 60 individuals/ha took place. This mortality was also age (size) dependent, although all age classes suffered a high mortality in this year (Table 2).

Coinciding with the drop in density of perch ≥ 2 yr, high numbers of YOY perch were captured in 1994 (Table 1). Correspondingly, a large number of Age-1 perch was present in spring of 1995 (Table 1, Figs. 1 and 2), which totally dominated the perch population (97% of total population) (Fig. 2). The population size structure of perch ≥ 2 yr (≥ 80 mm) in May 1995 was bimodal, consisting of one group with a peak value of 143 mm and one group of individuals with a peak value of 228 mm (Fig. 2). The trapping data in summer 1995 suggested a further decrease in abundance of perch ≥ 2 yr. In 1996, the population of perch ≥ 2 yr increased to >110 individuals/ha owing to a strong 1994 year class (the number of perch ≥ 151 mm (≥ 3 yr) only amounted to 20 individuals/ha) (Figs. 1 and 2). In 1997, population abundance was estimated at 130 individuals/ha. As a result of individual growth, the size distribution of these perch shifted towards larger sizes (Fig. 2).

High numbers of YOY perch were also trapped in 1995 and 1996. In 1994 and 1995, the numbers of YOY perch during the pelagic phase (from June to early July) did not decrease over time, although the absence of a significant decrease in 1995 was a result of a low estimate 14 d after hatching (1994: $r^2 = 0.23$, $F_{1,4} = 2.20$, $P = 0.23$; 1995: $r^2 = 0.34$, $F_{1,4} = 1.57$, $P = 0.30$) (Fig. 3). In 1996, the number of YOY perch decreased during the pelagic phase ($r^2 = 0.75$, $F_{1,4} = 9.0$, $P = 0.058$). Because of low catches, mortality rates from Age-0 to Age-1 were only estimated for the 1994–1997 period.

This mortality was lower in spring of 1995 than in 1996 and 1997 (Table 2).

The numbers of Age-1 perch in 1996 and 1997 were lower than in 1995, but still much higher than during 1992–1994 (Table 1, Figs. 1 and 2). Almost all captures were made during May–August, in 1995; only 1 out of 542 captured Age-1 perch was caught in September (in 1996, 1 out of 42). After starting out unimodal in May and July, size distributions of Age-1 perch developed towards bimodality in both 1995 and 1996 (Fig. 4). As a result, the variation in size between individuals (coefficient of variation) increased from May and July to August (1995, May/July: 8.2–9.8, August: 31.2; 1996, May/July: 8.9–11.7, August: 37.0). Annual mortality between Age 1 and Age 2 was 97% in 1996 and 98% in 1997 (Table 2). This mortality, which primarily affected small Age-1 perch, tended to be higher than that of YOY perch from 30 d of age to Age-1 in all years (t test, $t_3 = 2.23$, $P = 0.11$). Mortality decreased substantially to 30% between Age 2 and Age 3.

Growth rates, condition, and population fecundity

1984–1991 year classes.—The perch in Abborrtjärn 3 consisted of slow growing individuals when we started our study in 1991 (Fig. 5). Growth typically levelled off at a size of 150 mm (5–6 yr) and very few individuals were >200 mm. Back-calculated rates before 1992 and observed growth rates for 1992 suggested similar growth rates for the 1984–1992 period. In 1994, growth rates of the few remaining perch age 3–5 yr accelerated dramatically coinciding with high trap captures of YOY perch (Table 1, Fig. 5). The high growth rates of these year classes persisted through 1995 and 1996.

The length–mass relationship of perch 150 and 200 mm showed only minor seasonal variation in 1992 (Fig. 6). In 1993, a decrease in condition was observed in the summer for 200 mm perch, whereas the condition of 150 mm perch was similar to 1992 (t test, change 1992–1993, 150 mm perch $t_6 = 0.14$, $P = 0.90$, 200 mm perch, $t_6 = 3.05$, $P = 0.023$). In May and July 1994, condition was low for both 150 and 200 mm perch (Fig. 6). However, in August and September, condition increased substantially for the few surviving perch ≥ 2 yr (change from May–July to August–September, t test, 150 mm perch, $t_2 = 7.07$, $P = 0.019$, 200 mm perch, $t_2 = 6.26$, $P = 0.025$). Condition of perch 150 and 200 mm thereafter remained high in 1995 and 1996. Both the decrease in condition in 1993 (mainly affecting 200 mm perch) and in 1994 (affecting both 150 and 200 mm perch) was associated with an increased mortality rate in 1993 (of perch ≥ 5 yr) and 1994 (of all perch ≥ 2 yr) (Table 2).

1994–1996 year-classes.—Sufficient numbers of YOY and Age-1 perch to estimate growth and condition were present only in 1994–1996. In 1994, YOY perch averaged 54.5 ± 5.1 mm at the end of the growing season, 43.7 ± 3.8 mm in 1995, and 50.5 ± 3.8 mm

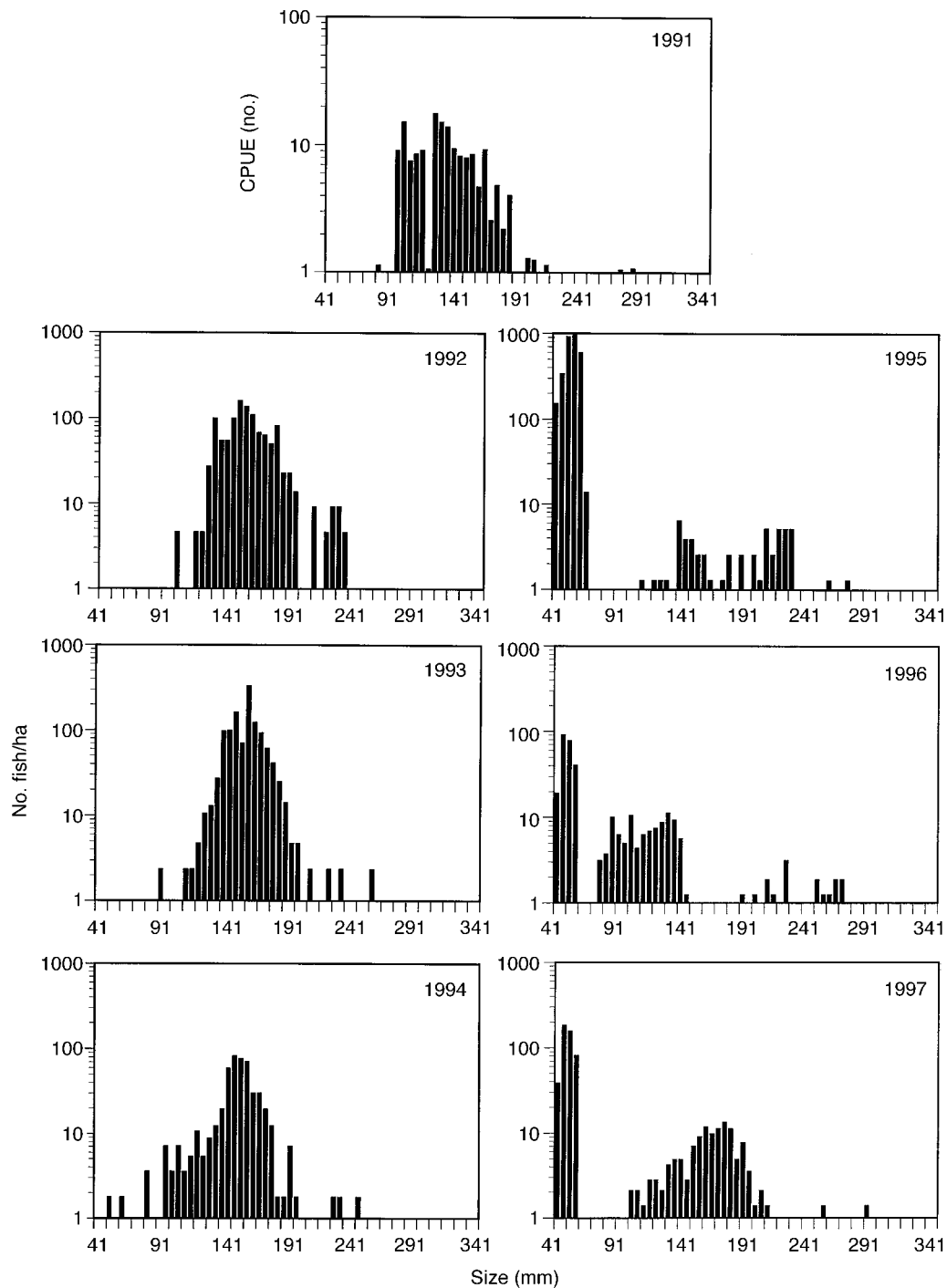


FIG. 2. Size distributions of perch from 1991 to 1997. For 1991, the catch per unit effort of different size classes is given, whereas for 1992–1997, absolute numbers of fish per hectare of different size classes are given. Note the logarithmic scale of y-axis.

in 1996 (means \pm 95% CL). In all years, condition decreased between August and September (t test, $t_{45-90} = 3.24\text{--}7.48$, $P = 0.0001\text{--}0.002$) (Table 3). This decrease in condition was smaller in 1994 than in 1995 and 1996, corresponding to the larger size of YOY

perch in 1994 (ANOVA, post hoc tests, Bonferroni adjusted, 1994 versus 1995/96, $P = 0.004\text{--}0.013$, 1995 vs. 1996, $P = 1.0$).

In 1995, Age-1 perch did not increase in length from May to July (Fig. 4). However, their condition did in-

TABLE 2. Annual mortality of different age classes of perch in 1992–1997.

Age	1992/ 1993	1993/ 1994	1994/ 1995	1995/ 1996	1996/ 1997
0–1	0.80†	0.99†	0.97†
1–2	0.97	0.98
2–3	0.08
3–4	0.02	0.02	0.68
4–5	0.33	0.02	0.72	0.60	0‡
5–≥6	0.21	0.96	0.94	0.76	0‡

Note: For YOY to Age-3, sufficient numbers to estimate mortality rates are only present from the 1994 year class.

† Mortality from 30 d of age was 0.82–0.90 in 1994/1995–1996/1997.

‡ The same mortality has been assumed because age classes could not be separated based on length (see Fig. 2).

crease (from 0.77 to 0.89, t test, $t_{91} = 2.67$, $P = 0.009$). From July to August, Age-1 perch increased in length (Fig. 4). A similar seasonal development of size distribution was observed in 1996 with the condition of Age-1 perch increasing between May (0.83) and July (1.04) (t test, $t_{33} = 3.05$, $P = 0.005$). Perch hatched in 1993 did not grow faster than previous year classes during their first three years. Once they had reached 120 mm, however, their growth rate was much higher than that of other year classes (Fig. 5).

Population fecundity was highest in 1992 and 1993, decreased substantially in 1994, and reached a minimum in 1995, after which the population fecundity started to increase again in 1996 (Table 4). Population fecundity was thus inversely related to the number of YOY perch present in late summer. The number of eggs in 1997, calculated from mass specific fecundity data from the literature, was similar to that from direct counts of roe strands.

Habitat use and diet

Perch ≥80 mm (≥2 yr old).—Habitat use of perch ≥2 yr old varied considerably over time in relation to the changes in population numbers described above. In 1992 and early 1993, most perch were captured offshore (the high inshore capture on the first sampling of 1992 was due to spawning activity) (Fig. 7A). Perch offshore were larger than those inshore (Mann-Whitney U test, $P = 0.002$). In August 1993, inshore use increased from <34% to 70% which coincided with a 50% decrease in the overall number of these older perch (Figs. 3 and 7A). The density inshore did not decrease in 1993, hence this decrease in the population resulted from a decrease in offshore fish. In 1994, a further drop in trap catches took place that again mainly affected offshore catches. The proportion of perch ≥80 mm (≥2 years old) trapped inshore was negatively related to their own density and the density at which they restricted their habitat use to the inshore area was distinct (at a trap catch of 0.8 perch/trap) ($r^2 = 0.61$, $F_{1,17} = 9.6$, $P = 0.007$) (Fig. 7B). In 1995, very few perch >100 mm were captured and all were captured inshore.

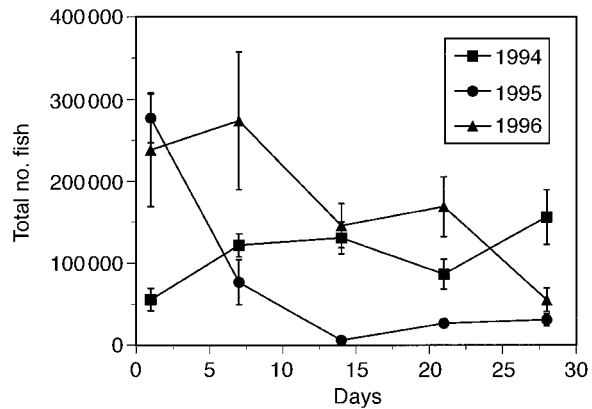


FIG. 3. Numbers (mean \pm 1 SE) of YOY perch from hatching to day 30 in 1994–1996. The first sampling in 1994 was done when larvae were still hatching. Captures at each sampling date varied between 130 and 422 individuals in 1994, between 10 and 242 in 1995, and between 80 and 220 in 1996.

The number of perch captured offshore increased in 1996, associated with the increase in the numbers of perch ≥ 2 yr (Figs. 1 and 7A).

Perch 101–150 mm (age 3–5) had a higher proportion of pelagic zooplankton in their diet in 1992 and the first half of 1993 than in 1994–1996 (Fig. 8). Zooplankton played a smaller role in the diet of 151–200 mm (≥ 5 yr old) perch, but the temporal pattern in the

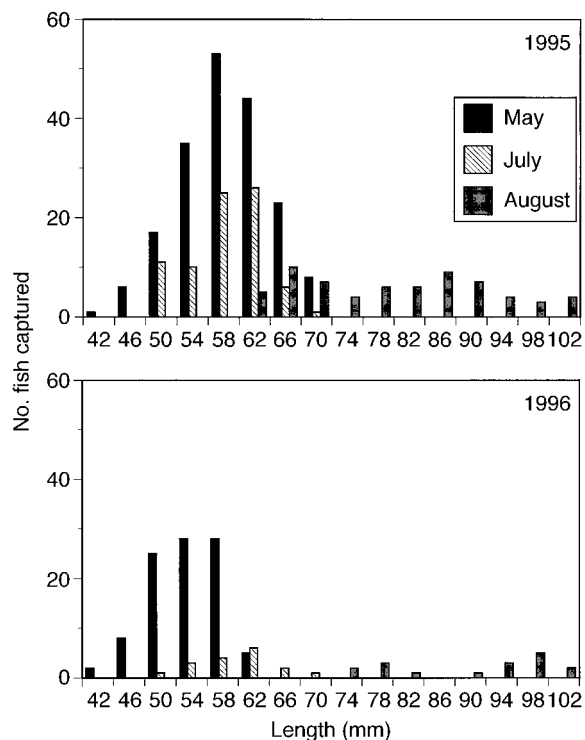
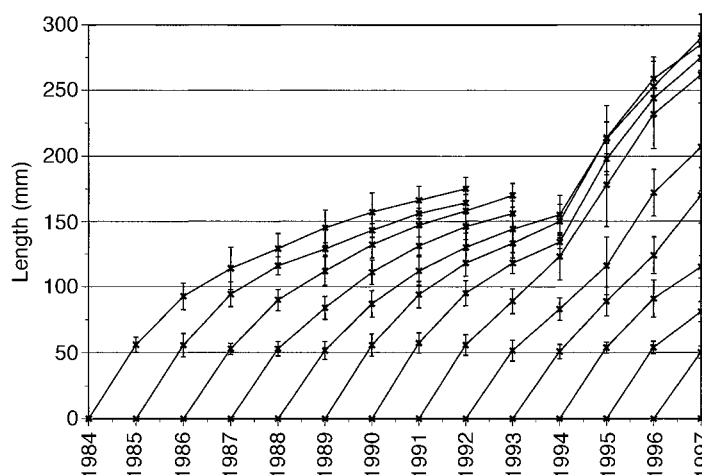


FIG. 4. Size distributions of Age-1 perch in May, July, and August of 1995 and 1996.

FIG. 5. Growth rates (mean \pm 1 SD) of different age cohorts of perch from 1985 to 1997. Growth trajectories for different year classes were based on sample sizes of 7–33 individuals.



importance of zooplankton was qualitatively similar to that of 101–150 mm perch. For perch >200 mm, zooplankton were all but absent in the diet. Little or no cannibalism was recorded in 1992 and 1993 (Fig. 8). Intense cannibalism on YOY perch by the few remaining large perch was observed in August and September 1994, 1995, and 1996, coinciding with high numbers of YOY perch along the shore.

YOY perch.—Perch lay their roe along the shore of lakes. In the years with data (1994–1996), YOY perch moved to the pelagic area after hatching, returning to the inshore area during the first week of July. The diet of YOY perch was dominated by zooplankton in July just after the inshore shift. In 1994, zooplankton still dominated diets in August, whereas macroinvertebrates, mainly small chironomids and small Ephemeroptera, were dominant prey in August 1995 and 1996 (Fig. 9).

Age-1 perch (60–100 mm).—All Age-1 perch were

captured inshore on all sampling dates during 1993–1996 (sampling of Age-1 perch in 1992 was restricted to spring electrofishing, Table 2). In early June of 1995 and 1996, almost half of the diet consisted of zooplankton (Fig. 9). In July 1995 and 1996, macroinvertebrates dominated, and formed the entire diet of Age-1 perch in August. In contrast to YOY perch, predator-sensitive prey in the diet were dominated by Trichoptera, Odonata, and Coleoptera larvae. The length of predator-sensitive macroinvertebrate prey in the diet was positively related to Age-1 perch size in August (1995: $F_{1,9} = 10.9$, $P = 0.011$; 1996: $F_{1,9} = 10.1$, $P = 0.013$). Cannibalism was observed among Age-1 perch, but was restricted to a two week period in June and never exceeded 10% of their diet.

Resource levels

Seasonal patterns of zooplankton abundance differed between years of high YOY survival (1994–1996) and low YOY survival (1992–1993) (Fig. 10). In 1994–1996, zooplankton biomass decreased dramatically in July, which coincided with the inshore shift by YOY. In contrast, zooplankton biomass decreased only slightly (1993) or even increased (1992) over the summer (repeated-measures ANOVA, date \times year interaction 1992–1993 vs. 1994–1996, $F_{5,15} = 12.23$, $P = 0.003$). The main difference between 1992 and 1993 was the increase in *Ceriodaphnia* biomass in the autumn of

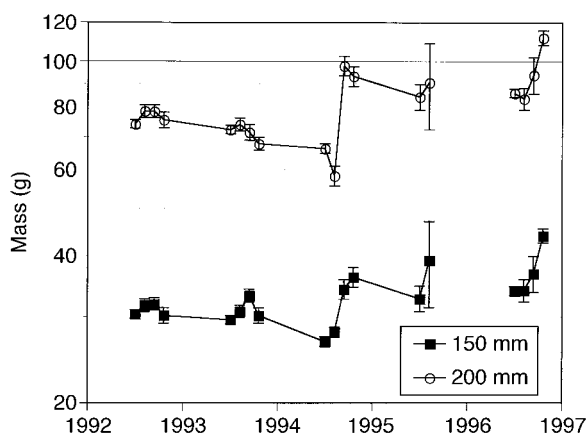


FIG. 6. Mass (mean \pm 95% CL) of a 150-mm and 200-mm perch on different dates in 1992–1996 based on mass-length regressions. In July and September 1995, too few (<5) fish were captured to make regressions meaningful.

TABLE 3. Variation in the condition factor K (mean \pm 1 SE) for YOY perch between August and September 1994–1996, after perch had completely transformed into juveniles.

Year	August		September	
	K	n	K	n
1994	1.04 \pm 0.01	36	0.97 \pm 0.02	11
1995	0.93 \pm 0.01	63	0.85 \pm 0.02	29
1996	1.02 \pm 0.02	21	0.87 \pm 0.01	30

TABLE 4. Population fecundity (mean \pm 95% CL) of the perch population in 1992–1997 based on population estimates, size distributions, and regressions of fecundity vs. body length (from Nyberg 1976).

Year	Regression estimates of population fecundity ($\times 10^{-6}$)
1992	7.6 ± 2.2
1993	6.8 ± 1.8
1994	1.6 ± 0.86
1995	0.6 ± 0.2
1996	1.1 ± 0.33
1997	1.5 ± 0.34

Note: In 1997 direct counts of egg numbers produced 1.4 ± 0.40 ($\times 10^6$) eggs.

1992 and the persistence of *Holepedium* over the growing season in 1993.

The abundance of predator-sensitive macroinvertebrates did not change between 1992 and 1993, when the first major die-off of perch ≥ 150 mm took place. Thereafter, the abundance of predator-sensitive invertebrates increased, which resulted in a negative relationship between their abundance and perch biomass among years ($r^2 = 0.67$, $F_{1,4} = 8.95$, $P = 0.058$; Fig. 11). No relationship was found between the biomass of inshore chironomids and perch ($r^2 = 0.0003$, $F_{1,4} = 0.0008$, $P = 0.98$).

DISCUSSION

Resource limitation, fecundity, and habitat-dependent cannibalism as mechanisms affecting recruitment

The lack of successful recruitment in 1991–1993 and the presence of successful recruitment (i.e., YOY perch appearing in large numbers along the shore in July and August and as Age-1 the following spring) in 1994–1996 can be related to three potential mechanisms: population fecundity, resource limitation, and cannibalism. A fecundity limitation hypothesis is at odds with higher

reproductive outputs in 1992 and 1993 than in 1994–1996 (many roe strands were also observed in 1992–1993, L. Persson, *personal observation*). Similarly, other studies on perch population fecundity find that egg production in any given year is more than sufficient to allow strong year classes (Alm 1946, 1952, Le Cren 1962, Nyberg 1976). This becomes apparent considering that one 200-mm female may produce 6000 eggs, whereas a maximum of 300 000 perch larvae were observed in any one year. Thus 50 females of this size would be enough to produce the highest number of offsprings observed in 1994–1996.

That resource limitation prevented successful recruitment in 1992 and 1993 is neither supported by our data nor by experimental evidence. First, this hypothesis is at odds with the development of the zooplankton community over the growing season in different years. In particular, the presence of *Holopedium* throughout 1993 suggests relatively limited predation pressure on zooplankton in this year compared to 1994–1996 (Stenson 1973, Tessier 1986, Rodriguez et al. 1993). Second, maintenance requirements of YOY perch larvae, in terms of zooplankton density (1.1–1.5 $\mu\text{g/L}$) (Byström and García-Berthou 1999), are far below observed densities at any time period in 1992 and 1993. Correspondingly, pelagic enclosure experiments in Abborrtjärn, using high densities of YOY perch that depleted zooplankton to $<4\%$ of those observed in 1992 and 1993, showed no evidence of starvation mortality in perch larvae or juveniles (Byström et al. 1998, Byström and García-Berthou 1999).

Fecundity and resource limitation are thus both unlikely explanations for the absence of successful recruitment in 1991–1993. In contrast, cannibalism is consistent with the lack of successful recruitment in 1991–1993 (see also Alm 1952). This explanation is admittedly based on negative inference, as no sampling was done during the period (June), that most of the

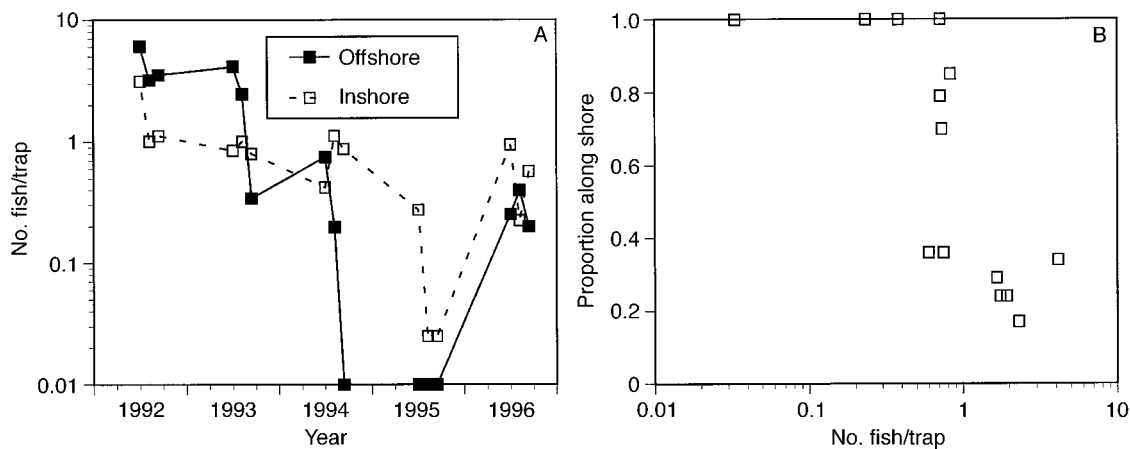


FIG. 7. (A) Numbers of perch ≥ 2 yr old (≥ 100 mm) captured inshore and offshore in May, July, August, and September 1992–1996. (B) Proportion of perch ≥ 2 yr old (≥ 100 mm) captured inshore in relation to their own density (based on trap catches). In (A), zero captures (offshore in 1995 and 1996) have been given a value of 0.01 because of the log scale used.

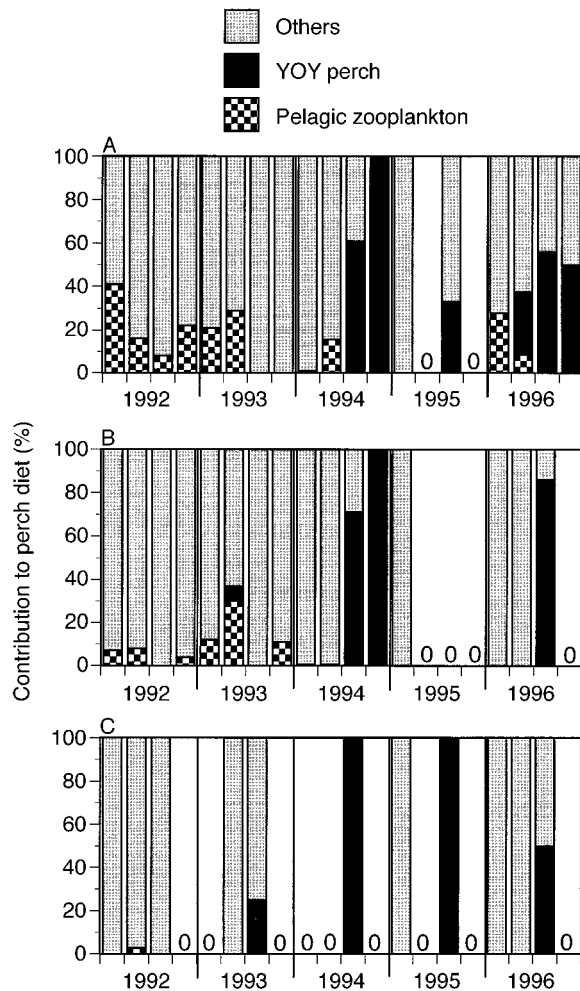


FIG. 8. Seasonal variation in the percentage contribution of zooplankton, perch, and other prey items to the diet of three size classes of perch >100 mm in 1992–1996: (A) perch 101–150 mm, (B) perch 151–200 mm, (C) perch >200 mm. Other prey include macroinvertebrates and benthic microcrustaceans. A zero indicates that <5 stomachs were sampled.

cannibalism is hypothesised to have taken place. Nevertheless, several lines of evidence suggest it as a dominant mechanism. First, experimental studies show that perch of the sizes forming the main part of the perch population in 1991–1993, prey efficiently on small perch larvae (Lundvall et al. 1999), and are capable of inflicting substantial mortality on perch larvae during their pelagic phase. Next, the appearance of the strong YOY cohort in 1994 and its survival to Age-1 appear related to two factors that reduced cannibalism: a decrease in numbers of Age-2 and older perch and their restriction to the inshore region. Although Age-1 perch inflicted mortality on YOY perch in 1995 and 1996 when densities of Age-1 perch were high, our diet data suggested that the mortality impact was confined to a short (14 d) period in June. This is consistent with experimental results showing that vulnerability to Age-

1 perch decreases rapidly with larval size (Lundvall et al. 1999). Furthermore, Age-1 perch were only captured inshore in 1994–1996, which is likely to have further decreased their impact on YOY perch.

The observed density-dependent habitat selection in cannibalistic perch has implications for whether cannibalism tends to stabilize population dynamics or not (Hastings and Constantino 1987, Hopper et al. 1996, Claus-Walker et al. 1997). Our data provide evidence of strong population fluctuations in perch and the relationship between adult perch density, offshore habitat use, and recruitment of YOY perch suggests that habitat heterogeneity, in combination with habitat selection in cannibals, may limit the extent to which cannibalism is a stabilizing factor for population dynamics. Cannibals restrict their habitat use when at low numbers, and the two factors will combine to decrease their ability to control recruitment pulses of victims. This contrasts with current thinking suggesting that habitat heterogeneity promotes stability (Stenseth 1980, Abrams 1988).

Small scale experiments generally show that can-

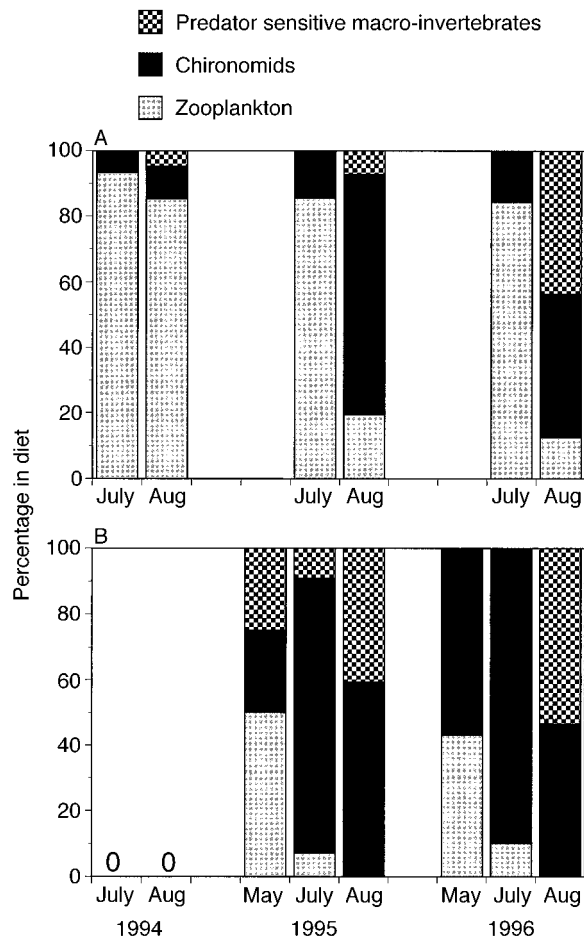


FIG. 9. The diet of (A) YOY perch in July and August 1994–1996 and (B) Age-1 perch in May, July, and August 1995 and 1996. A zero indicates that <5 stomachs were sampled.

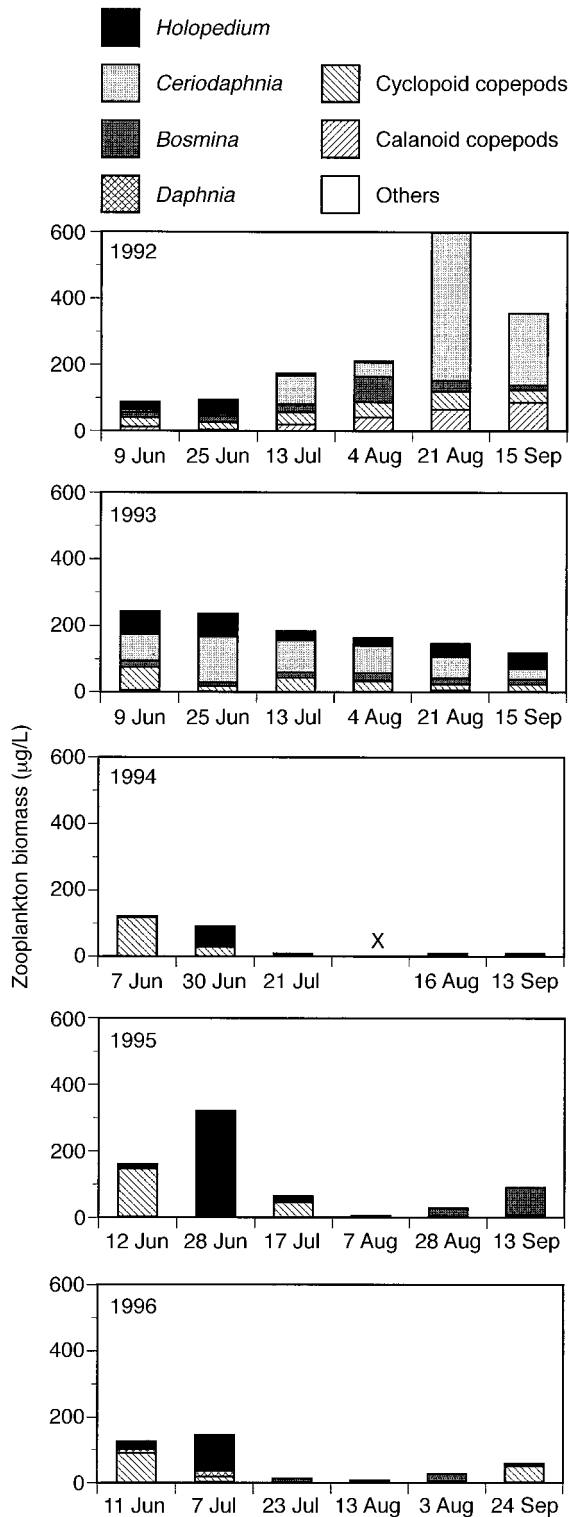


FIG. 10. Seasonal development of zooplankton biomass during 1992–1996. X = no sample.

nibalism is density and resource dependent, and that the presence of alternative prey will reduce its impact (Johansson 1991, Hopper et al. 1996, Wagner and Wise 1996). We found that high zooplankton biomass (alternate prey), offshore habitat use, high numbers of perch 120–190 mm (which were substantially zooplanktivorous), and poor recruitment of perch all co-occurred in 1992 and 1993. This suggests that in environments with large-scale heterogeneity, effects of alternative resources on cannibalism may vary and depend on the degree of habitat overlap of conspecifics and alternative prey.

Mortality patterns and intercohort competition

Two major die-offs among perch ≥ 100 mm (1993, 1994) were both followed by strong recruitment. The first die-off was associated with an overall decrease in body condition and a restricted habitat use to the in-shore region. This die-off cannot be related to decreased resource availability per se because: (1) the biomass of the more predator-sensitive large cladoceran *Holopedium* (Stenson 1973, Tessier 1986, Rodríguez et al. 1993) increased in 1993, and (2) the abundance of littoral macroinvertebrates was similar in 1992 and 1993. The increase in the mean size of perch from 1992 to 1993 implies that average per capita metabolic demands of perch increased. Furthermore, the foraging efficiency of perch on even large zooplankton decreases above a perch size of 90 mm (Persson 1987). Thus, perch were likely less able to exploit the pelagic resource in 1993 (vs. 1992). Both increased metabolic demands and decreased foraging rates on zooplankton would increase metabolic stress in perch after the energy expenditure associated with spawning, especially for larger individuals.

The second die-off (1994) coincided with the presence of a strong cohort of YOY. However, because larger perch had already restricted their habitat use to

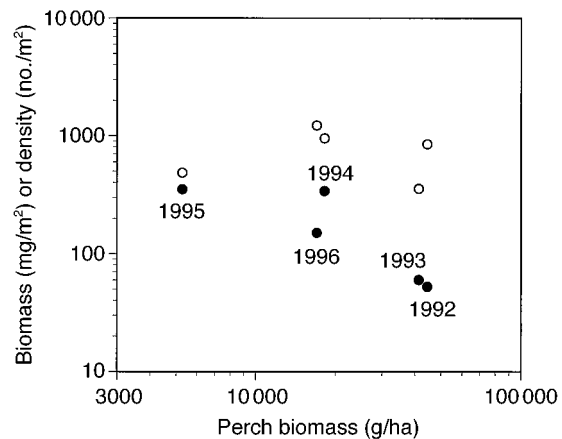


FIG. 11. Density of predator-sensitive macroinvertebrates (closed circles; number/m²) and biomass of chironomids (open circles; mg/m²) at littoral stations vs. perch biomass in 1992–1996.

the shore area and fed entirely on macroinvertebrates in 1993, it is questionable whether competition from YOY perch was involved. Also, our data suggest that the larger perch were already in poor condition in May, before YOY perch hatched. In contrast, there are several lines of evidence suggesting a competitive effect of YOY on Age-1 perch. These include: (1) substantial food overlap between YOY and Age-1 perch, (2) reduced consumption of zooplankton in July by Age-1 perch in response to a depleted zooplankton resource, (3) a substantially submaximum growth rate of Age-1 perch (based on Lessmark 1983), (4) reduced body condition in small Age-1 perch in August, and (5) very low captures of Age-1 perch in September, indicating a substantial drop in numbers (also supported by the high mortality from Age-1 to Age-2).

Outcomes of competitive interactions between individuals of different sizes are essentially the result of the individual's capacity to ingest food (based on attack rate and handling time) and its metabolic rate, both of which increase with body size (Werner 1988, Lundberg and Persson 1993, Persson et al. 1998). Experiments on fish show that the minimum resource requirements (i.e., resource density at which energy intake rate equals metabolic rate) increases monotonically with body size. Smaller individuals will hence be at a competitive advantage with respect to exploitative competition (Persson and Crowder 1998, Persson et al. 1998, Byström and García-Berthou 1999). The higher mortality of Age-1 perch (vs. YOY) during 1994–1996, despite substantial mortality of YOY perch due to cannibalism, is consistent with this expectation. The bimodal size distribution of Age-1 perch observed in August 1995 and 1996 was associated with larger size classes feeding more on larger macroinvertebrates not consumed by YOY, suggesting that they escaped from competition with YOY through a diet shift. Smaller individuals, unable to make the diet shift, were subjected to strong competition from YOY perch when the latter moved to the inshore in July.

In the absence of cannibalism, size-dependent interactions between cohorts have produced strongly oscillating population dynamics in both theoretical models and in field populations, with recruits being stronger competitors than larger individuals due to the lower per capita metabolic demands of recruits (Hamrin and Persson 1986, McCauley et al. 1996, Persson et al. 1998). Despite the presence of cannibalism, a strong element of such asymmetrical dynamics was present in the interactions between YOY and Age-1 perch. The importance of this component for overall dynamics is indicated by the lack of increase in the number of perch ≥ 2 yr in the spring of 1997, despite strong recruitment in 1995, as a result of the high mortality in Age-1 perch. Thus, in the asymmetrical interactions between YOY and Age-1-perch involving both cannibalism and competition, our data suggest that the competitive asymmetry had a stronger impact than the cannibalistic

asymmetry. Correspondingly, growth trajectories of the 1993 and 1994 cohorts suggest that perch cohorts did not profit substantially from cannibalism before an age of 3 yr.

Energy gain by cannibals

The energy gained by cannibalism has been suggested to be an important element in cannibal-victim interactions, in addition to a reduction in resource competition (Polis 1988, Dong and Polis 1992). Our study provides substantial evidence for the presence of an energetic gain during some periods. In years with low recruitment (1991–1993), large perch (140–170 mm) did not benefit much, in terms of increased growth, from cannibalism, which likely occurred when victims were small and relatively unprofitable. In contrast, growth rates of the few remaining larger perch (130–150 mm) increased dramatically during 1994–1997 when there was substantial cannibalism throughout the season by these size cohorts on YOY perch. As a result, there were two asymptotic lengths of perch, depending on densities of older (≥ 2 yr) perch. In years of high densities (up to 1994), the asymptotic size was ~ 180 mm whereas at low densities (from 1994), the asymptotic size exceeded 300 mm as a result of a “double asymptotic” growth trajectory (cf. Fig. 5). Similar double asymptotic growth trajectories have been observed in other fish populations and have also been correlated with strong year classes of YOY perch (Le Cren 1992). The importance of victim size for growth is indicated in the growth trajectories of Age-1 perch in 1995 and 1996, when cannibalism only occurred when victims were small (June). Growth rates of these perch did not differ from other Age-1 cohorts; indeed an increased growth related to cannibalism was not observed until Age-4 when the period of cannibalism was extended into July.

Our data suggest that the energy gained by the few large cannibals in 1994–1997 had substantial effects on population dynamics. Although these cannibals were few, their per capita fecundity increased as a result of accelerated growth allowing substantial recruitment to take place in 1995–1997. As suggested above, these recruitment events, in turn, affected the survival of Age-1 perch through competition from YOY perch. This effect on cannibal fecundity and long-term population dynamics has hardly been considered previously, largely since theoretical studies have assumed that cannibalism gives no energy return to the cannibal (Diekmann et al. 1986, Dennis et al. 1997, Van den Bosch and Gabriel 1997). The energy gained by cannibals can theoretically increase population persistence, but population dynamics per se were not considered (Van den Bosch et al. 1988, Cushing 1992, Henson 1997). Interestingly, a recent model of cannibalistic populations with competing victims and including energy gained by cannibals generated the shift between different growth trajectories presented here.

Moreover, this modelling study also supports our general interpretations about the mechanisms (cannibalism and intercohort competition) driving the system (Claessen et al. 2000).

In conclusion, the interactions among perch involve both competitive and cannibalistic processes. High adult perch densities, in combination with an extended offshore habitat use is suggested to prevent successful recruitment through cannibalism. Habitat heterogeneity, in combination with density-dependent habitat use in cannibals, is suggested to limit the extent to which cannibalism has a stabilizing effect on population dynamics. We also suggest that the energy gained from cannibalism will have substantial effects on reproductive output and thereby population dynamics. Investigating the impact of the mortality induced on recruits and the energy gained by cannibals is an interesting task for future modelling efforts. In doing this, physiologically structured models should be a most appropriate tool, because of the straightforward way that energy gains at the individual level can be analyzed at the population level (cf. De Roos et al. 1990, Persson et al. 1998, Claessen et al. 2000).

ACKNOWLEDGMENTS

This study was supported by grants from the Swedish Natural Science Research Council and the Swedish Council for Forestry and Agricultural Sciences which are gratefully acknowledged. We thank Jens Andersson, Eva Maria Diehl, Sebastian Diehl, Joakim Hjelm, Jens Karlsson, Ann Lingerbrandt, David Lundwall, Johan Lövgren, Per Nilsson, Anders Persson, Kristina Samuelsson, Lena Staffans, Rickard Svanbäck, Roger Wallin, and Erika Westman for field and laboratory assistance during different phases of the study. We also thank the Åman Fishery Cooperative for access to the study lake. Most valuable comments on previous drafts of this manuscript were given by David Claessen, André De Roos, Frank Johansson, Bill Tonn, and four anonymous reviewers.

LITERATURE CITED

- Abrams, P. A. 1988. Resource productivity–consumer species diversity: simple models of competition in spatially heterogeneous environments. *Ecology* **69**:1418–1433.
- Alm, G. 1946. Reasons for the occurrence of stunted fish populations with special reference to perch. Report from the Institute of Freshwater Research, Drottningholm **25**:1–146.
- Alm, G. 1952. Year class fluctuations and span of life of perch. Report from the Institute of Freshwater Research, Drottningholm **40**:17–38.
- Anholt, B. R. 1994. Cannibalism and early instar survival in a larval damselfly. *Oecologia* **99**:60–65.
- Bagenal, T. B., and F. W. Tesch. 1978. Age and growth. Pages 101–136 in T. Bagenal, editor. *Methods for assessment of fish production in fresh waters*, IBP Handbook Number 3. Blackwell Scientific Publications, Oxford, UK.
- Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierik, A. Herzig, A. Hillbrich-Ilkowska, H. Kurasawa, P. Larsson, and T. Weglenska. 1976. A review of some problems in zooplankton production studies. *Norwegian Journal of Zoology* **24**:419–456.
- Byström, P., and E. García-Berthou. 1999. Density dependent growth and stage-specific competitive interactions in young fish. *Oikos* **86**:217–232.
- Byström, P., L. Persson, and E. Wahlström. 1998. Competing predators and prey: juvenile bottlenecks in whole lake experiments. *Ecology* **79**:2153–2167.
- Claessen, D., A. M. De Roos, and L. Persson. 2000. Giants and dwarfs—cannibalism and competition in size-structured populations. *American Naturalist*, in press.
- Claus-Walker, D. B., P. H. Crowley, and F. Johansson. 1997. Fish predation, cannibalism, and the larval development in the dragonfly *Epiplatys cynosura*. *Canadian Journal of Zoology* **75**:687–696.
- Constantino, R. F., R. A. Desharnais, J. M. Cushing, and B. Dennis. 1997. Chaotic dynamics in insect populations. *Science* **275**:389–391.
- Craig, J. F. 1978. A study of the food and feeding of perch, *Perca fluviatilis* L., in Windermere. *Freshwater Biology* **8**:59–68.
- Crowley, P. H., and D. M. Johnson. 1992. Variability and stability of a dragonfly assemblage. *Oecologia* **90**:260–269.
- Cushing, J. M. 1992. A size-structured model for cannibalism. *Theoretical Population Biology* **42**:347–361.
- Dennis, B., R. A. Desharnais, J. M. Cushing, and R. F. Constantino. 1997. Transitions in population dynamics: equilibria to periodic cycles to aperiodic cycles. *Journal of Animal Ecology* **66**:704–729.
- De Roos, A. M., J. A. J. Metz, E. Evers, and A. Leipoldt. 1990. A size dependent predator-prey interaction: who pursues whom? *Journal of Mathematical Biology* **28**:609–643.
- Diekmann, O., R. M. Nisbet, W. S. C. Gurney, and F. van den Bosch. 1986. Simple mathematical models for cannibalism: a critique and a new approach. *Mathematical Biosciences* **78**:21–46.
- Dong, Q., and G. A. Polis. 1992. The dynamics of cannibalistic populations: a foraging perspective. Pages 13–37 in M. A. Elgar and B. J. Crespi, editors. *Cannibalism—ecology and evolution among diverse taxa*. Oxford Science Publications, Oxford, UK.
- Dumont, H. J., I. Van de Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of cladocera, copepoda and rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia* **19**:75–97.
- Eklöv, P. 1992. Group foraging versus solitary foraging efficiency in piscivorous predators: the perch, *Perca fluviatilis*, and pike, *Esox lucius*, patterns. *Animal Behaviour* **44**:313–326.
- Eklöv, P., and S. Diehl. 1994. Piscivore efficiency and refuging prey: the importance of predator search mode. *Oecologia* **98**:344–353.
- Elgar, M. A., and B. J. Crespi. 1992. Ecology and evolution of cannibalism. Pages 1–12 in M. A. Elgar and B. J. Crespi, editors. *Cannibalism—ecology and evolution among diverse taxa*. Oxford Science Publications, Oxford, UK.
- Fulton, C. W. 1904. The rate of growth of fishes. *Fisheries Board of Scotland Annual Report* **22** (Part 3):141–241.
- Gabriel, W. 1985. Overcoming food limitation by cannibalism: a model study of cyclopoid copepods. *Archiv für Hydrobiologie* **21**:373–381.
- Hamrin, S. F. 1977. The pelagic fish fauna in southern and northern Lake Bolmen 1970–1976 and an attempt to estimate its relative density. Report, University of Lund, Lund, Sweden.
- Hamrin, S. F., and L. Persson. 1986. Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish. *Oikos* **47**:223–232.
- Hart, P. J. B., and T. J. Pitcher. 1969. Field trials of fish marking using a Jet Inoculator. *Journal of Fish Biology* **1**:383–385.
- Hastings, A., and R. F. Constantino. 1987. Cannibalistic egg–larvae interactions in *Tribolium*: an explanation for the oscillations in population numbers. *American Naturalist* **130**:36–52.
- Hastings, A., and R. F. Constantino. 1991. Oscillations in

- population numbers: age-dependent cannibalism. *Journal of Animal Ecology* **60**:471–482.
- Henson, S. M. 1997. Cannibalism can be beneficial even when its mean yield is less than one. *Theoretical Population Biology* **51**:108–117.
- Hopper, K. R., P. H. Crowley, and D. Kielman. 1996. Density dependence, hatching synchrony, and within-cohort cannibalism in young dragonfly larvae. *Ecology* **77**:191–200.
- Johansson, F. 1991. Foraging models in an assemblage of odonate larvae—effects of prey and interference. *Hydrobiologia* **209**:79–87.
- Johnson, D. M., C. L. Pierce, T. H. Martin, C. N. Watson, R. E. Bohanan, and P. H. Crowley. 1987. Prey depletion by odonate larvae: combining evidence from multiple field experiments. *Ecology* **68**:1459–1465.
- Le Cren, E. D. 1962. The efficiency of reproduction and recruitment in freshwater fish. Pages 283–296 in E. D. Le Cren and M. W. Holdgate, editors. *The exploitation of natural animal populations*. Blackwell, Oxford, UK.
- Le Cren, E. D. 1992. Exceptionally big individual perch (*Perca fluviatilis* L.) and their growth. *Journal of Fish Biology* **40**:599–625.
- Lessmark, O. 1983. Competition between perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in South Swedish lakes. Dissertation, University of Lund, Lund, Sweden.
- Lundberg, S., and L. Persson. 1993. Optimal body size and resource density. *Journal of Theoretical Biology* **164**:163–180.
- Lundvall, D., R. Svanbäck, L. Persson, and P. Byström. 1999. Size-dependent predation—the interaction between predator foraging capacity and prey avoidance ability. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:1285–1292.
- McCauley, E., E. E. Murdoch, and S. Watson. 1988. Simple models and variation in plankton densities among lakes. *American Naturalist* **132**:383–403.
- McCauley, E., R. M. Nisbet, A. M. De Roos, E. E. Murdoch, and W. S. C. Gurney. 1996. Structured models of herbivorous zooplankton. *Ecological Monographs* **66**:479–501.
- Mertz, D. B. 1969. Age-distribution and abundance in populations of floor beetles. I. Experimental studies. *Ecological Monographs* **39**:1–31.
- Mittelbach, G. G., and L. Persson. 1998. The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:1454–1465.
- Nyberg, P. 1976. Production and food consumption of perch in two Swedish forest lakes. Dissertation, University of Uppsala, Uppsala, Sweden.
- Orr, B. L., W. W. Murdoch, and J. R. Bence. 1990. Population regulation, convergence, and cannibalism in *Notonecta* (Hemiptera). *Ecology* **71**:68–82.
- Persson, L. 1987. The effects of resource availability and distribution on resource utilization in perch (*Perca fluviatilis*). *Oikos* **48**:148–160.
- Persson, L. 1988. Asymmetries in competitive and predatory interactions in fish populations. Pages 203–218 in B. Ebenman and L. Persson, editors. *Size-structured populations: ecology and evolution*. Springer, Heidelberg, Germany.
- Persson, L., J. Andersson, E. Wahlström, and P. Eklöv. 1996. Size-specific interactions in whole-lake systems—predator gape limitation and prey growth rate and mortality. *Ecology* **77**:900–911.
- Persson, L., and L. B. Crowder. 1998. Fish-habitat interactions mediated via ontogenetic niche shifts. Pages 3–23 in E. Jeppesen, M. Søndergaard, M. Søndergaard, and K. Christoffersen, editors. *The structuring role of submerged macrophytes in lakes*. Springer Verlag, New York, New York, USA.
- Persson, L., and L. A. Greenberg. 1990. Optimal foraging and habitat shift of perch (*Perca fluviatilis*) in a resource gradient. *Ecology* **71**:1699–1713.
- Persson, L., K. Leonardsson, A. M. de Roos, M. Gyllenberg, and B. Christensen. 1998. Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theoretical Population Biology* **54**:270–293.
- Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics* **12**:225–251.
- Polis, G. A. 1988. Exploitation competition and the evolution of interference, cannibalism, and intraguild predation in age/size-structured populations. Pages 185–202 in B. Ebenman and L. Persson, editors. *Size-structured populations—ecology and evolution*. Springer-Verlag, Berlin, Germany.
- Popova, O. A. 1978. The role of predaceous fish in ecosystems. Pages 215–249 in S. D. Gerking, editor. *Ecology of freshwater fish production*. Blackwell Scientific Publications, Oxford, UK.
- Rodríguez, M. A. P., P. Magnan, and S. Lacasse. 1993. Fish species composition and lake abiotic variables in relation to the abundance and size structure of cladoceran zooplankton. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:638–647.
- Smith, C., and P. Reay. 1991. Cannibalism in teleost fish. *Reviews in Fish Biology and Fisheries* **1**:41–64.
- Stenseth, N. C. 1980. Spatial heterogeneity and population stability: some evolutionary consequences. *Oikos* **35**:165–184.
- Senson, J. A. E. 1973. On predation and *Holopedium gibberum* (Zaddach) distribution. *Limnology and Oceanography* **18**:1005–1010.
- Sumari, O. 1971. Structure of the perch populations of some ponds in Finland. *Annales Zoologici Fennici* **8**:406–421.
- Tessier, A. J. 1986. Comparative population regulation if two planktonic cladocera (*Holopedium gibberum* and *Daphnia catawba*). *Ecology* **67**:285–302.
- Townsend, C. R., W. J. Sutherland, and M. R. Perrow. 1990. A modelling investigation of population cycles in the fish *Rutilus rutilus*. *Journal of Animal Ecology* **59**:469–485.
- Wadell, D. R. 1992. Cannibalism in lower eukaryotes. Pages 85–101 in M. A. Elgar and B. J. Crespi, editors. *Cannibalism—ecology and evolution among diverse taxa*. Oxford Science Publications, Oxford, UK.
- Wagner, J. D., and D. H. Wise. 1996. Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. *Ecology* **77**:639–652.
- Van den Bosch, F., A. M. De Roos, and W. Gabriel. 1988. Cannibalism as a life boat mechanism. *Journal of Mathematical Biology* **26**:619–633.
- Van den Bosch, F., and W. Gabriel. 1997. Cannibalism in an age-structured predator-prey system. *Bulletin of Mathematical Biology* **59**:551–567.
- Van Densen, W. L. T. 1994. Predator enhancement in freshwater fish communities. Pages 102–119 in I. G. Cowx, editor. *Rehabilitation of freshwater fisheries*. Fishing News Books, Blackwell Scientific Publications, Oxford, UK.
- Wadell, D. R. 1992. Cannibalism in lower eukaryotes. Pages 85–101 in M. A. Elgar and B. J. Crespi, editors. *Cannibalism—ecology and evolution among diverse taxa*. Oxford Science Publications, Oxford, UK.
- Wang, N., and R. Eckman. 1994. Distribution of perch (*Perca fluviatilis* L.) during their first year of life in Lake Constance. *Hydrobiologia* **277**:135–143.
- Werner, E. E. 1988. Size, scaling and the evolution of life. Pages 60–81 in B. Ebenman and L. Persson, editors. *Size-structured populations—ecology and evolution*. Springer-Verlag, Berlin, Germany.
- Wissinger, S. A., G. B. Sparks, G. L. Rouse, W. S. Brown, and H. Steltzer. 1996. Intraguild predation and cannibalism among larvae of detritivorous caddisflies in subalpine wetlands. *Ecology* **77**:2421–2430.
- Youngs, W. D., and D. S. Robson. 1978. Estimation of population number and mortality rates. Pages 137–154 in T. Bagenal, editor. *Methods for assessment of fish production in fresh waters*, IBP Handbook Number 3. Blackwell Scientific Publications, Oxford, UK.