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Temporal stability in size distributions and growth rates of three *Esox lucius* L. populations. A result of cannibalism?

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The population total length (L_T) structures and individual growth trajectories for three stream living pike *Esox lucius* populations were studied for 7 years. All three populations exhibited small variation in both population L_T structure and individual growth trajectories over time. These dynamics contrasted to the much more variable population L_T structure of perch *Perca fluviatilis* studied previously. The difference in population dynamics between the two species was related to differences in prey:predator size ratios. The pike populations in the more open and larger streams grew to larger sizes, but this difference in life history did not affect population dynamics of pike. It is concluded that (1) cannibalistic population dynamics may be predicted from individual life-history characteristics such as minimum and maximum victim:cannibal size ratios and (2) the cannibal-driven population dynamics observed in pike seems to be robust to variation in environmental conditions (system openness).

Key words: cannibalism; growth rates; pike; population length structure; predation window.

INTRODUCTION

The ability of a predator to capture and handle prey is a function of both the length of the predator and the size of the prey (Christensen, 1996; Hirvonen & Ranta, 1996; Mittelbach & Persson, 1998; Juanes, 2003). Generally, predator and prey interactions are constrained by two limits: an upper and a lower prey and predator size ratio. First, below the minimum size limit predators of a specific length do not encounter victims of a specific length. Second, above the maximum size limit potential victims can avoid being eaten through high escape ability or gape constraints in the predators (Rice *et al.*, 1997; Persson & Crowder, 1998; Claessen *et al.*, 2000; Persson *et al.*, 2000). The size range

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within which predator and prey interactions take place has been termed the 'predation window' (Claessen *et al.*, 2000).

In case of cannibal and victim interactions, cannibal and victims generally share a common resource and are hence engaged in a competitive interaction as well (Polis, 1988; Claessen *et al.*, 2000; Persson *et al.*, 2000). Theoretical analyses of size-dependent cannibalism where cannibals share a common resource with victims show that the size limits allowing victim and cannibal interactions to take place have major implications for population dynamics and cannibal life history (Claessen *et al.*, 2002). If the minimum size limit is high, cannibalism plays only a minor role for cohort interactions and the dynamics is driven by inter-cohort competition where recruiting victims may out-compete their cannibals before the former have reached a size at which they are vulnerable to cannibalism. In contrast, if the minimum size limit is low, cannibals may start to feed on recruiting victims very early on and the dynamics is cannibal driven through the high mortality cannibals impose on victims (Claessen *et al.*, 2002). For intermediate values of the minimum size limit, the dynamics may vary over time between cannibal-driven dynamics and inter-cohort competition with the possibility of very large individuals appearing during the period with cohort competition (Claessen *et al.*, 2002; Persson *et al.*, 2003).

The theoretical predictions of cannibalistic population dynamics in relation to victim:cannibal size ratios advanced by Claessen *et al.* (2002) have recently been supported by a comparison of the growth curves of different year classes of three different cannibalistic fish populations: yellow perch *Perca flavescens* (Mitchill), perch *Perca fluviatilis* L. and pike *Esox lucius* L. (Persson *et al.*, 2004). The purpose of the present study was to extend the generality of these results by including more than one pike population and also present data on temporal variation in population total length (L_T) structures of three different pike populations. Based on prey:predator size ratios, it was hypothesized that the population L_T structures of the pike populations should exhibit relatively little temporal variation. The temporal variation in population L_T structures observed in the three pike populations was contrasted with that observed in a previous study on the population dynamics of perch (Persson *et al.*, 2003). As the different streams varied in the degree of openness to downstream locations and hence potential access to prey resources outside the streams studied, it was investigated whether this affected pike life-history characteristics and population dynamics.

MATERIAL AND METHODS

STUDY SYSTEMS

Pike

The pike study was carried out in three small lotic systems in a plain area of the Venetian region, north-east Italy (11°07′ E; 48°50′ N; Vicenza district). The systems are slow-flowing springs located in a rural area and have a relatively homogeneous morphology (Table I). The sampling stations included the springs and the downstream 100–150 m sections. Yearly average temperature varied between 10·6 and 11·1° C between the three streams [coefficients of variation (CV) between years amounted to

TABLE I. Overall characteristics of the study systems (sampling traits) and fish species presence (+) or absence in the community

Stream	Depth (m) Mean (minimum–maximum)	Width (m) Mean (minimum–maximum)	Cg	Pm	Kp	Ga	Aa	Lz	St*	Lc**
1	0·48 (0·40–0·60)	2·5 (1·2–4·3)	+	+	+	+	+			
2	0·50 (0·30–0·65)	4·3 (4·0–4·7)	+	+	+			+	+	
3	0·53 (0·35–0·70)	5·7 (3·0–8·0)	+	+	+	+	+			+

*Juveniles irregularly introduced by local angling societies.

**Only large individuals (>40 cm L_T) seldom found.

Cg, *Cottus gobio* L.; Pm, *Padogobius martensii* (Günther); Kp, *Knipowitschia punctatissima* (Canestrini); Ga, *Gasterosteus aculeatus aculeatus* L.; Aa, *Anguilla anguilla* (L.); Lz, *Lethenteron zanandreai* (Vladykov); St, *Salmo trutta* L.; Lc, *Leuciscus cephalus* (L.).

0·08–0·17]. The seepage origin of the water gives a relatively stable thermal stability in the area sampled, with small variations between winter and summer means (range 9–14° C). As a consequence, summer temperatures are lower than those found in drainage systems of the same size in the same region, and probably explain the low biomasses of cyprinids in these systems compared to adjacent warmer streams (pers. obs.). Therefore, despite that the streams are relatively productive (conductivity >500 μS m^{-1}), they lack large sized prey fish for adult pike and prey fish consisted, besides pike, mainly of small gobids and cottids (Table I).

The bottom of the streams was composed mainly by fine sediments (sand and mud) and covered for 70–80% by dense strands of aquatic macropytes (*Ranunculus* sp., *Elodea* sp., *Myriophillum* sp., *Apium nodiflorum* and *Lemmna trisulca*). Two of the systems (streams 2 and 3) were wider (Table I) and were also well connected with larger systems downstream, allowing pike to move between habitats. In contrast, one stream (stream 1) lacked an adequate downstream connection for fishes as large as pike because of zones of extreme shallowness.

Perch

The field data for perch come from a long-term study of a perch population in a small (9·3 ha) low productive lake, Abborrtjärn 3, situated in the middle of Sweden (64°29′ N; 19°26′ E) (Persson *et al.*, 2000).

SAMPLING

The three streams were sampled once a year between 1985 and 1992 during the pike spawning season (February to April). Stream 2 was not sampled in 1985 but was sampled in 1993. For logistic reasons, stream 3 was only sampled in October in 1989. No data are available for any of the three streams for 1990. Pike were sampled by electrofishing on a linear transect of *c.* 150 m. Captured pike were measured (L_T) to the nearest mm and weighed to the nearest 0·1 g before being released. A sub-sample of individuals from each population was tagged with numbered T bar tags. The sampling during the spawning season allowed determination of the sex of pike individuals by external examination of the genital papilla (Crossman & Casselman, 1987).

A description of methods for estimating perch L_T distributions from the system used to compare with pike has been given previously (Persson *et al.*, 2000, 2003).

PIKE DIETS AND PIKE AND PERCH GROWTH

A sub-sample of pike individuals from the three streams was sacrificed for analysis of stomach content. In order to reduce this source of mortality to a minimum, only a few individuals per sampling date were sacrificed and data for different years were therefore pooled. To increase sample size, data from sampling dates outside the spawning season in 1985–1993 were included in the analysis. Stomach contents were analysed under a dissecting microscope and food resources were classified into one of the following three categories: invertebrates only, pike and other prey fishes (with or without invertebrates). It should be noted that this classification underestimates the importance of invertebrates in the diet of pike as stomachs that contained a mixture of fishes and invertebrates were classified as piscivorous.

Pike age was assessed from scale examination to avoid sacrificing the individuals. For each individual, four to six scales were taken and placed in an alcohol solution and then cleaned and dried. A dissecting microscope was used for the examination of scales. The scales were submerged in water and observed at × 30–40 magnification. The true annuli were characterized by a gradual change from the broad opaque summer growth zone to a narrow transparent winter zone, which ended relatively abruptly with a sharp line of discontinuity to the next summer zone. Two independent readings were made by the same reader. When the results differed, two additional readings were made. If there was still a disagreement between readings, the sample was rejected. A valuable validation of age determination was obtained by comparing scale readings conducted on the same tagged individuals in different years (*i.e.* between known time intervals). Growth curves were modelled using the von Bertalanffy growth equation $L_t = L_\infty\left\{1 - e^{[-k(t-t_0)]}\right\}$, where L_t is the length at time t, L_∞ is the asymptote, k is the rate at which growth approaches L_∞ and t_0 is the time when the fish had zero size (Bagenal & Tesch, 1978).

Age and growth of perch from the system used to compare with the three pike populations were determined by backcalculating L_T of the fish in time using opercular bones (Persson *et al.*, 2003).

SIZE-DEPENDENT PREY FISH USE BY PERCH AND PIKE

A comparison of prey size of different sized pike and perch was based on data from two lakes (Lakes Abborrtjärn 1 and 2) in middle Sweden. Any observed differences between the two species would not be due to different environmental conditions as pike and perch coexist there. The lakes are described by Persson *et al.* (1996, 1999). For perch, all existing data from the two lakes over the time period 1992–2002 were used (partly given by Byström *et al.*, 2003) complemented with experimental data (Lundvall *et al.*, 1999). For pike, at least 20 fish varying in size between 50 and 600 mm L_T was sampled in each of the two lakes every week from the end of May to the end of August in 2002. Stomach contents of the sampled pike were analysed under a dissection microscope and identified to order, family or species and 10 prey of each group (all if 10 in stomach) were measured. For the perch and pike eaten, data on mass and L_T regressions were used (unpubl. data). Based on the diet data on piscivory, a lower and an upper boundary for piscivory was drawn (Claessen *et al.*, 2000).

STATISTICAL ANALYSIS

Kolmogorov–Smirnov tests were used to compare the size frequency distributions of pike for a given station among different sampling dates (Zar, 1984). For each station, each sampling date was compared to the average distribution and to all the other sampling dates, for a total of 28 tests for each station. Kolmogorov–Smirnov tests were also used to compare each size distribution of perch to the average distribution and to all the other sampling dates, for a total of 55 tests for the period 1991–2001.

RESULTS

PISCIVORY WINDOWS OF PIKE AND PERCH

The diet of pike from Lakes Abborrtjärn 1 and 2 was dominated by larger macroinvertebrates. Piscivory in pike involved both cannibalism and predation on perch. Piscivory in perch consisted entirely of cannibalism (Persson *et al.*, 1999; Byström *et al.*, 2003). A comparison between pike and perch showed that the minimum size ratio was lower (0·03) for pike than for perch (0·05) (*t*-test, ln transformed data, one-tailed test, $n = 4$, $P = 0{\cdot}01$), whereas the upper size ratio was higher (0·55) for pike than for perch (0·45) (*t*-test, ln transformed data, one-tailed test, $n = 4$, $P = 0{\cdot}01$).

VARIATION IN POPULATION SIZE STRUCTURE

The population L_T structures of pike in different sampling years in each stream did not differ from an average L_T frequency distribution even with an α level of 0·05 (Fig. 1). The analysis of all possible among-date pair-wise comparisons within a given stream revealed that 10 out of 21 comparisons were significantly different in stream 1, two out 21 comparisons in stream 2 and three out of 21 comparisons in stream 3.

In contrast to pike, the population L_T structures of perch in different sampling years differed significantly from an average L_T frequency distribution. Furthermore, all the possible (43) pair-wise comparisons among dates were significantly different at an α level $\leq 0{\cdot}004$. The differences in perch population L_T structure over time were a result of changes in the number of medium-sized adult perch, the number of 1 year-old perch and the number of large gigantic perch (Persson *et al.*, 2000, 2003).

INDIVIDUAL GROWTH

Growth trajectories of pike were obtained from L_T measured on individuals of known age. The L_T data were averaged by half-year and by cohort for each stream. Growth trajectories differed between sexes and among populations (Fig. 2). In all populations, females grew faster than males, but these differences were relatively small in stream 1 where both sexes showed $L_\infty < 400$ mm. In stream 3, growth patterns were markedly distinct between sexes, and on average pike grew better than in the other two streams, with L_∞ of 1004 and 1600 mm for males and females, respectively. A similar growth curve as for both sexes in stream 1 was observed for males in stream 2, whereas females in this stream showed $L_\infty > 1000$ mm. The maximum size of pike as estimated by the von Bertalanffy growth equation showed a clear decrease with increasing pike density. Because of the small sample size (three streams), it was not possible to test the significance of this correlation.

The growth trajectories of different pike cohorts showed only small among year variation (Fig. 3). A general trend toward a reduction in growth from 1985 to 1989 was observed, but the overall shape of the growth trajectories

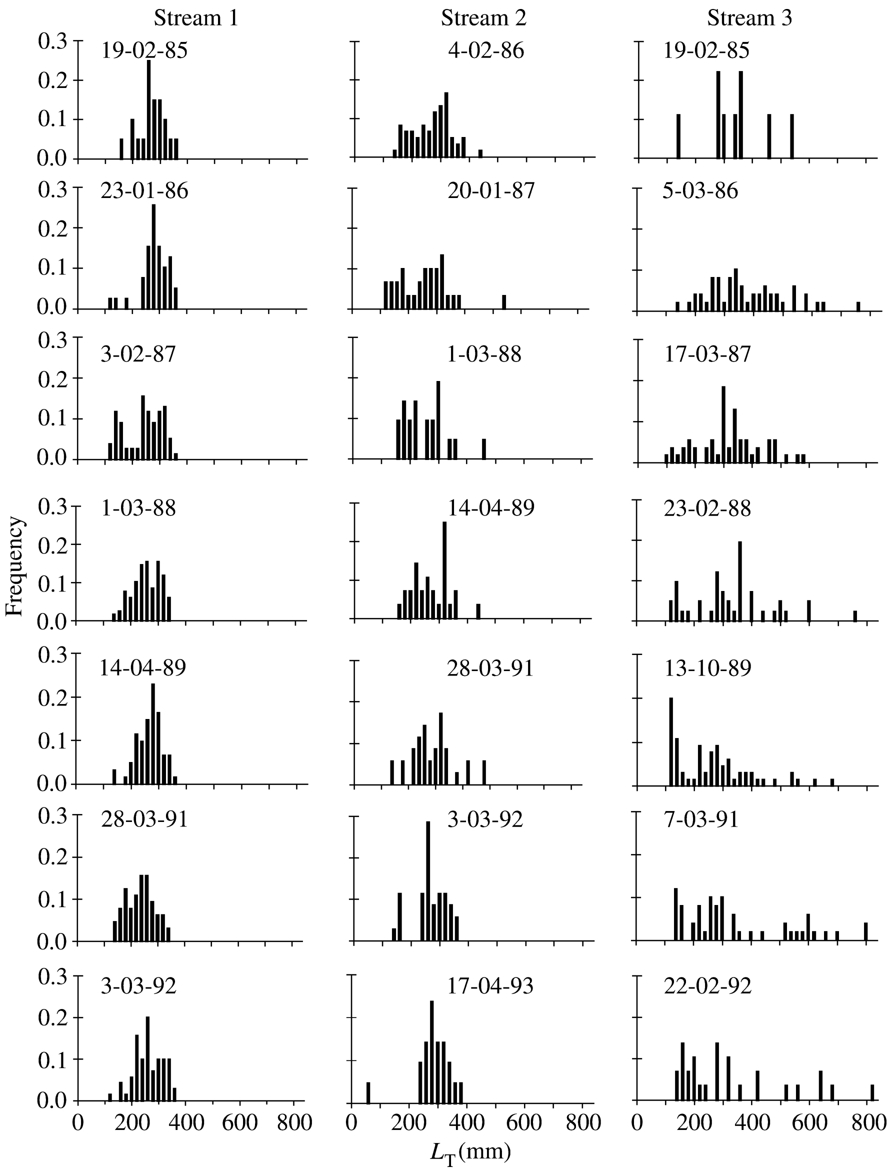

FIG. 1. Total length frequency distributions of pike from 1985 to 1993 in the three study streams.

did not change among cohorts within a given stream. Fewer data were available for streams 2 and 3, but the pike populations in these streams showed a trend with small between year variation similar to that of stream 1 for which more data were available.

In contrast to growth of different pike cohorts, growth of different cohorts of perch varied substantially over time. In years with high cannibalistic rate, cannibals were shown to have gained very little energy from cannibalizing (Persson *et al.*, 2003) and their L_T did not exceed 180 mm (1986 cohort, Fig. 4).

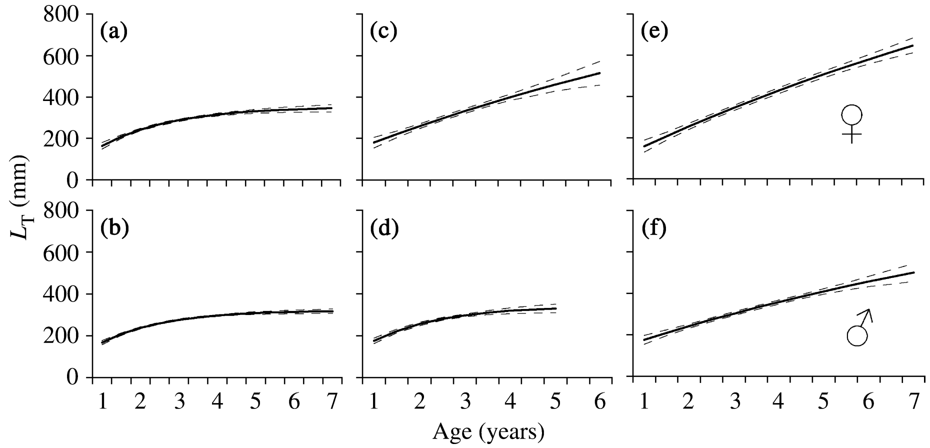

FIG. 2. von Bertalanffy growth curves with 95% CI (---) for (a), (c) and (e) female and (b), (d) and (f) male pike in streams (a), (b) 1, (c), (d), 2 and (e) (f) 3. The coefficients for the von Bertalanffy growth curves were: (a) $L_\infty = 353{\cdot}1$, $k = 0{\cdot}5320$ and $t_0 = -0{\cdot}1798$, (b) $L_\infty = 320{\cdot}8$, $k = 0{\cdot}6140$ and $t_0 = -0{\cdot}1967$, (c) $L_\infty = 1146{\cdot}4$, $k = 0{\cdot}0850$ and $t_0 = -1{\cdot}0086$, (d) $L_\infty = 341{\cdot}6$, $k = 0{\cdot}6646$ and $t_0 = -0{\cdot}0800$, (e) $L_\infty = 1602{\cdot}8$, $k = 0{\cdot}0688$ and $t_0 = -0{\cdot}5146$ and (f) $L_\infty = 1004{\cdot}3$, $k = 0{\cdot}0828$ and $t_0 = -1{\cdot}3246$.

In years with low cannibalistic rate, and consequently higher survival of young-of-the-year (YOY) perch, cannibals grew fast and approached a size of 380 mm (1990 cohort, Fig. 4).

PIKE DIETS IN THE THREE STREAMS

The stomach analysis of pike showed that invertebrate prey consisted mainly of isopods and amphipods while the most common prey fish were small benthic gobids and cottids. Invertebrate prey constituted a substantial proportion of the pike diet in all three populations (Table II). This fraction varied among populations being most important for the pike population in stream 1. For this population, 84% of the stomachs of pike <15 cm contained exclusively invertebrates, a proportion that declined to 50% for pike >35 cm. The proportion of stomachs with pike and other prey fishes increased with pike size from 7 to 25%. The proportion of empty stomachs also followed a size-dependent pattern increasing from 9% for pike <15 cm to 25% for pike in the size range between 35 and 45 cm (Table II). Empty stomachs were more frequent (≥30% of the individuals) in pike from streams 2 and 3 where sample sizes were also smaller and particularly so for stream 2. For stream 3, the proportion of individuals with fish prey in their stomach varied between 23 and 53%. Invertebrates were only found in the stomachs of individuals in the size range between 15 and 30 cm in this stream, whereas cannibalism was restricted to larger individuals (Table II). Pike in stream 2 showed a similar pattern in diets as pike in stream 3 with the exception that no cannibalism was documented for pike in stream 2.

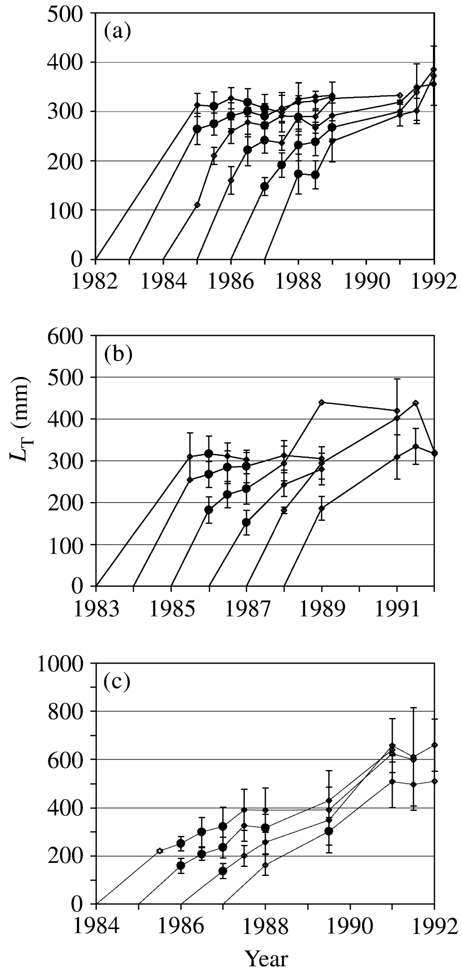

FIG. 3. Mean ± S.D. growth in total length of different age cohorts of pike from 1982 to 1992 in study streams (a) 1, (b) 2 and (c) 3. Growth trajectories were based on samples of different sizes: $n \leq 5$, ○; $5 < n \leq 10$, •; $n > 10$, ●.

DISCUSSION

The analyses of the population structures of the pike populations showed that all three populations exhibited smaller variation over time in population L_T structure and growth trajectories of different year classes of pike than the perch population studied by Persson *et al.* (2003). This observed difference in population dynamics of pike and perch can be related to differences in their life-history characteristics with respect to minimum victim:cannibal size ratios (Claessen *et al.*, 2002; Persson *et al.*, 2004). Pike had a lower minimum victim: cannibal L_T ratio and pike populations are therefore also expected to exhibit sustained low amplitude cannibal-driven dynamics where the recruitment of YOY pike to 1 year-old pike is controlled by cannibalism. In contrast, perch had a higher minimum victim:cannibal size ratio than pike and are expected

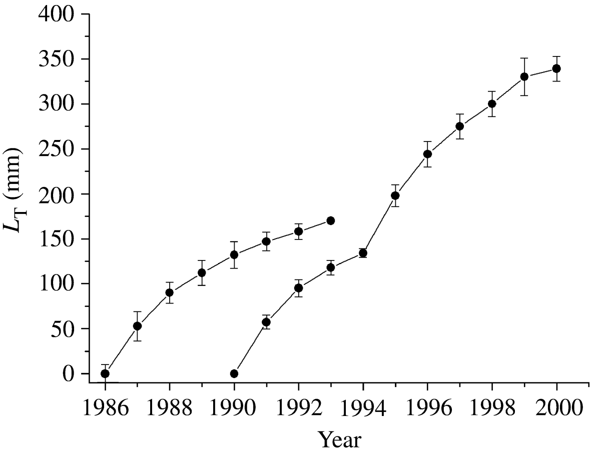

FIG. 4. Mean ± S.D. growth in total length of two different cohorts of perch born in 1986 and 1990, respectively. Data from Persson *et al.* (2003).

and observed to exhibit a dynamics fluctuating between cannibal-driven dynamics and inter-cohort competition including the temporary appearance of very large fast-growing individuals (Claessen *et al.*, 2002; Persson *et al.*, 2003). The comparison is based on populations geographically far apart (perch population in Sweden and pike populations in Italy), and it can be argued that the differences observed in dynamics might have been due to a stronger seasonality and between year variation in environmental conditions in Sweden. This hypothesis, however, is not supported by data from the studied perch lake showing no effects of environmental conditions (temperature, nitrogen or phosphorous) on the perch population dynamics (Persson *et al.*, 2003). The situation that low temporal variation was observed in both pike population L_T

TABLE II. Per cent frequency of occurrence of empty stomachs and different prey types in the diet of three total length classes of pike in streams 1–3

L_F class (cm)	Empty	Other fishes	Pike	Invertebrates	*n*
Stream 1					
<15	9	7	0	84	43
15–30	15	17	10	58	40
30–45	25	12	13	50	8
Stream 2					
<15	50	17	0	33	6
15–30	33	11	0	56	9
30–45	67	33	0	0	3
Stream 3					
<15	47	53	0	0	17
15–30	41	23	0	36	22
30–45	43	43	14	0	14

distributions and growth of different pike cohorts for all three pike populations despite differences in stream openness lend support for the robustness of the low variability dynamics of pike populations.

Cannibalism has frequently been observed in both perch and pike and has been suggested to be an important regulating mechanism (Persson *et al.*, 2000; Soupir *et al.*, 2000; Skov & Koed, 2004). Cannibalism was also documented in pike in two of the three streams studied. The lack of evidence for cannibalism in stream 2 might have been due to the lower sample size in this stream. It should also be noted that in systems where cannibals impose a high mortality on their prey, their prey only make up a minor fraction of the cannibal's diet as the former are eaten at a very early stage (Claessen *et al.*, 2000, Persson *et al.*, 2003).

The maximum L_T of pike was considerably larger in streams 2 and 3 (females in stream 2, both females and males in stream 3) than in stream 1. A possible explanation for this difference in maximum L_T is that pike in the two larger streams could move out of the local stream and obtain access to prey fishes in downstream locations. Irrespective of this explanation, the difference in L_∞ between streams did, however, not transfer into a difference in year-to-year variation in pike population L_T structure. Furthermore, the fact that all three pike populations showed a similar low temporal variability in L_T structure and individual growth trajectories over time, despite differences in stream openness, points to the fact that intrinsic density-dependent factors (in this case cannibalism) may be strong in shaping the observed population variation. Correspondingly, field studies of cycling consumer-resource systems show that single cohort cycles are commonly present in multispecies systems, and hence that the intrinsic dynamics of cohort dynamics may generally be robust to environmental conditions (Hamrin & Persson, 1986; McCauley & Murdoch, 1987; Townsend *et al.*, 1990; Shiomoto *et al.*, 1997; Murdoch *et al.*, 2002).

Studies of the population dynamics of different cannibalistic fish species including pike suggest that their dynamics may be predicted based on the width of the cannibalism window and the lower size limit for cannibalism (Persson *et al.*, 2004). For example, North American yellow perch, which has a higher minimum victim:cannibal size ratio than perch exhibits a dynamics driven by cohort competition without periods of cannibal control (Persson *et al.*, 2004). Another example comes from time series of the population dynamics of largemouth bass *Micropterus salmoides* (Lacepéde) which show that cannibalistic cohorts in this species may exhibit periods of acceleration in growth similar to what is found in perch (Post *et al.*, 1997, 1998). In contrast to perch, however, 1 year-old largemouth bass do not seem to suffer from inter-cohort competition by YOY largemouth bass but instead profit from cannibalism on them (Post *et al.*, 1997, 1998; Persson *et al.*, 2000, 2003). The difference between largemouth bass and perch in the major interaction between 1 year-old and YOY cohorts (cannibalism in largemouth bass and cohort competition in perch), in turn, meant that the extended time period with fast-growing perch was absent in largemouth bass. Instead, the largemouth bass population rapidly returned to the cannibal-controlled phase after the strong recruitment events. Also, this difference between largemouth bass and perch population dynamics can be related to individual level piscivory traits with largemouth bass having a higher piscivory capacity in terms of the gape size-body size relationship than perch (Mittelbach & Persson, 1998).

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