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Analysis of sibling cannibalism among pike, *Esox lucius*, juveniles reared under semi-natural conditions

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Synopsis

Sibling cannibalism in pike, *Esox lucius*, larvae and juveniles living in outdoor rearing ponds was studied using stomach contents analysis. For the two initial densities tested (6 and 18 larvae m^{-2}, equivalent to 12 and 36 larvae m^{-3}), cannibalism was non-existent during the larval period (13 to 35 mm total length) and was observed only during the juvenile stages. Initial density of larvae influenced both the date of first detection of cannibalistic individuals and the rate of development of cannibalism in the population. At initial stocking densities of 18 larvae m^{-2} (36 larvae m^{-3}), cannibalism was observed from 21 days after the start of exogenous feeding (mean total length: 60 mm) onwards. At a mean total length of 100 mm and for initial stocking densities of 6 and 18 larvae m^{-2} (12 and 36 larvae m^{-3}), the average proportions of cannibals in the populations of juveniles were 7.8% and 41.3% and the cannibals accounted for 15.5% and 65.9% of the total pike biomass, respectively. In stomachs of cannibals, young pike were the dominant prey in terms of weight. Dry weights of invertebrate-prey were lower in cannibals than in non-cannibals of similar size. Cannibalism among pike juveniles was characterized by the prey being swallowed whole and head first in the vast majority of cases. There was a strong positive correlation between predator and prey size and the mouth size of a cannibal was found to be an important constraint determining maximum victim size. The overall mean ratio of pike prey length to pike cannibal length was 66.2% and the average ratio of prey head depth to predator mouth width amounted to 87.6%. Prey size selection could be demonstrated for several length-groups of cannibals. These results are compared with the characteristics of early cannibalism in other fish species.

Introduction

Cannibalism is a relatively common phenomenon, which may influence life history styles in many species (Polis 1981). In fish, intraspecific predation has been reported mostly among larval and/or juvenile stages, especially in situations characterized by a high density of young fish, a certain degree of size dispersal, and a limited availability of alternative food (e.g. DeAngelis et al. 1980, Brownell 1985, Hecht & Appelbaum 1988). Cannibalism is of frequent occurrence during the early life stages of predatory fish species such as walleye, *Stizostedion vitreum* (Cuff 1980, Loadman et al. 1986), perch, *Perca fluviatilis* (Chodorowski 1975), largemouth bass, *Micropterus salmoides* (DeAngelis et al. 1980), striped bass, *Morone saxatilis* (Braid & Shell 1981), sea bass, *Dicentrarchus labrax* (Katavic et al. 1989) and yellowtail, *Seriola quinqueradiata* (Fujiya 1976). Precocious intraspecific aggression has also been observed in omnivores such as common carp, *Cyprinus carpio* (van Damme et al. 1989) and sharptooth catfish, *Clarias gariepinus* (Hecht & Appelbaum 1988).

There are over thirty scientific reports mentioning or studying the phenomenon of cannibalism in pike, *Esox lucius*, a typical predatory fish (Crossman & Casselman 1987, Raat 1988), both among early stages of the same cohort (e.g. Hunt & Carbine 1951, Giles et al. 1986) and among individuals of different year classes (Grimm 1981, Craig & Kipling 1983). Cannibalism among pike larvae may start at a total length of 21–23 mm in the vicinity of spawning grounds (Hunt & Carbine 1951), as well as under intensive culture conditions (Rahn 1972, Ivanova & Lopatko 1983). In the small, shallow ponds devoted to the extensive culture of pike larvae and juveniles, care must be taken to recover the juveniles at stages when cannibalism is nonexistent or moderate: a delayed draining may lead to a sharp fall in numerical density and an excessive size heterogeneity (Huet 1976). Although the occurrence of early cannibalism in pike is frequently mentioned, no quantitative study has been published regarding the development of cannibalism within a population of young pike, in a natural or seminatural environment. The present paper therefore considers cannibalism among pike siblings in a battery of small vegetated ponds, i.e. in an environment which is comparable in many respects to a natural situation. Specifically, the present study was designed to determine: (1) the time-course of cannibalism, (2) the effect of initial density of larvae on cannibalism intensity, and (3) the prey size selectivity by cannibalistic individuals.

Materials and methods

General

The experimental system consisted of 16 drainable ponds measuring approx. 300 m^2 each and containing vegetation (for details, see Bry & Souchon 1982, Bry et al. 1991). In these shallow ponds, the feeding regime of young pike between 13 mm (approx. total length at onset of exogenous feeding) and 145 mm (mean final size in the present study) typically consists of a sequence of invertebrate-prey (Manelphe 1989): copepod nauplii and adults, small cladocerans (larval period); chironomid larvae and pupae (larval and juvenile periods); large-sized benthic invertebrates (macrocrustaceans, misc. insect larvae, oligochaetes and other macroinvertebrates: juvenile period).

In April 1988, the ponds were simultaneously filled with river water and stocked 2 weeks later with pike free embryos originating from a single female (Bry & Gillet 1980) and obtained as previously described (Bry et al. 1991). In order to determine the effect of initial density on cannibalism intensity, 8 ponds were stocked at the rate of 6 free embryos m^{-2} (i.e. 12 free embryos m^{-3}: a commonly used low density, LD) and the other 8 ponds at the rate of 18 free embryos m^{-2} (36 free embryos m^{-3}: high density, HD). The free embryos were nearing the end of yolksac absorption and the start of larval exogenous feeding was observed in all ponds on day 2 after stocking. Growth of pike larvae, then of juveniles, was estimated twice a week by capturing 10 to 20 young in each pond and individually measuring total length (TL). When TL approximately reached 30 mm (wet weight close to 0.2 g), two ponds from each density group were drained. The surviving larvae were counted and gathered in a flow-through tank (one tank per pond). About 300 fish were then sampled at random and classified into two groups according to their size: individuals from the upper one-third were measured (TL) to the nearest 0.5 mm, weighed to the nearest 0.01 g and preserved in 10% formaldehyde for stomach contents inspection; fish from the lower two-thirds were measured and weighed, and half of them preserved. The same procedure (draining of four ponds) was repeated when juveniles reached approximately 60, 75 and 100 mm TL (i.e. wet weights close to 1.5, 2.5 and 5 g). For each stock, pike survival, biomass and coefficient of weight variation at the time of draining were calculated. In order to widen the scope of the study of the cannibal-prey size relationship, we also examined the cannibals and pike-prey from two ponds stocked with 6 free embryos m^{-2} in 1986 and drained at later stages (mean TL close to 125 mm and 145 mm, mean weight close to 10 and 15 g).

Quantification of cannibalism and of cannibal-prey size relationship

All preserved specimens were measured (TL), then dissected. Cannibalistic individuals were characterized from the presence of ingested pike remains. The total number of cannibals in a pike stock was calculated as the sum of the number of cannibals identified from the analyzed samples (extrapolated to the whole stock) and of the number of pike juveniles regurgitated by cannibals during pond draining and tank stocking. Partial or complete regurgitation may be important in pike following gill netting (Treasurer 1988). In our experimental situation, regurgitation of partially digested pike-prey involved 0 to 9.3% of the cannibals in a stock.

We did not attempt to evaluate the growth of cannibals, since the possible recruitment of new cannibalistic juveniles between two successive draining dates rendered the composition of the cannibals' stock variable with time.

The identification of cannibals was carried out in samples from all ponds. Dimensions of prey body parts and of cannibal stretched mouth width however were recorded in samples from one pond replicate out of two. Whenever possible, the direction of ingestion of the pike-prey (head-first or tail-first) was noted. In most cases, pike-prey were only partially digested and their original total length was calculated from one of the following morphometric variables: POL (preorbital length, from anteriormost point of head to middle of orbit) and DCL (distance from anterior insertion of dorsal fin to end of caudal peduncle), both measurements being parallel to the main body axis. We used linear regression equations developed from preserved intact pike juveniles within the same size range (30 to 130 mm TL) as the observed pike-prey:

$$TL = -4.63 + 7.47\ POL,\ r^2 = 0.98,\ n = 111,$$

and

$$TL = 0.82 + 4.37\ DCL,\ r^2 = 0.99,\ n = 111.$$

Proportionally large prey fish are caught by pike crosswise to the body and held transversely between the jaws, then orientated head first down the throat and swallowed (e.g. Hoogland et al. 1957, Christiansen 1976). Consequently, in order to compare the potential maximum size of pike-prey for a cannibal of given size and the actually observed prey sizes, another morphometric relationship was established, between head depth (HED) and TL ($30 < TL < 130$ mm):

$$HED = 0.08 + 0.12\ TL,\ r^2 = 0.98,\ n = 111.$$

All the above-mentioned lengths were measured to the nearest 0.1 mm.

The size of a cannibal before pike-prey ingestion was back-calculated as follows: the length increment resulting from the partial digestion of a young pike was computed from the prey TL and the weight of ingested pike remains, then deducted from the measured TL of the cannibal. To achieve this computation: fresh weights were evaluated from the weights of preserved pike or pike remains using a correction factor specific to each group of fish; fresh weights were converted to TL (and conversely) by means of appropriate length-weight relationships; and a standard gross conversion efficiency of 3.3 was applied to the initial weights of the digested parts (Johnson 1966, Bialokoz & Krzywosz 1978, Ivanova et al. 1982).

The prey size preferences of cannibalistic juveniles were evaluated in four situations using the prey-selection index C proposed by Pearre (1982). This index may range from -1 to $+1$, is zero-valued for no selection, and is statistically testable. To compute this index, care was taken to consider as potential prey in the environment only young pike that were small enough for the studied cannibals to ingest.

In order to make a gross comparison of feeding habits between cannibals and non-cannibals, the stomach contents of six cannibals and six non-cannibals of similar size and from the same pond were dried in an oven at 80° C until constant weight and the dry weights of invertebrate-prey (main alternative prey: macrocrustaceans, chironomid larvae, oligochaetes and other macroinvertebrates) and of pike-prey were determined. Such a comparison

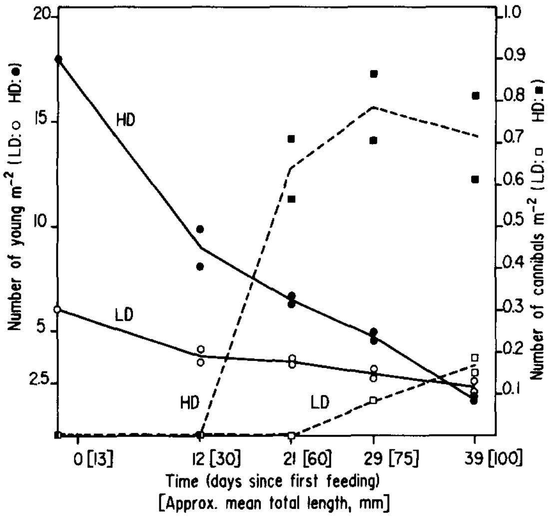

Fig. 1. The effect of initial density upon temporal patterns of numerical densities (overall stock and cannibalistic individuals) of *Esox lucius* sibling larvae and juveniles in small ponds. LD and HD are respectively low and high initial densities (6 and 18 young pike m^{-2}). Time 0 is the first day of exogenous feeding. For each initial density and each of four time points, the harvest from two replicate ponds was analyzed with respect to cannibalism.

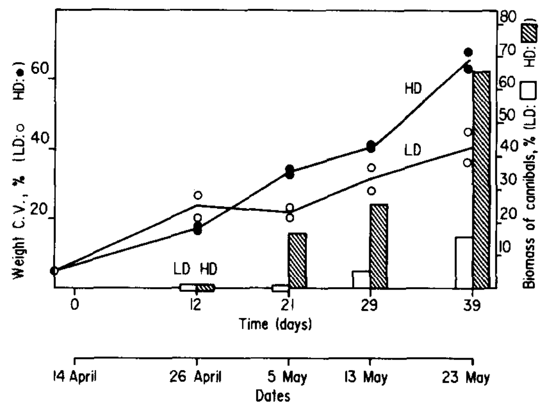

Fig. 2. The temporal patterns of weight coefficient of variation (C.V.) among pike siblings and of biomass of cannibals (expressed as a percentage of total pike biomass), as influenced by initial sibling density. See Fig. 1 for definitions. For each initial density and each of four time points, the coefficients of weight variation relative to the stocks of two ponds are indicated. The biomass figures (LD: clear columns; HD: hatched columns) are averaged data from two replicate ponds.

was carried out at three time points (one pond per time point).

Data analysis

A nonparametric analysis of variance (Kruskal-Wallis test) was used: to assess the effects of initial density of larvae upon numerical densities and biomass of cannibals, and to compare mean prey dry weights. The association between biomass of cannibals and weight coefficient of variation was analyzed via the Spearman nonparametric rank correlation procedure. Linear regressions were computed using standard regression statistics (Sokal & Rohlf 1981). Departure of prey-selection indices from randomness was evaluated with the chi-square statistics proposed by Pearre (1982).

Results

Temporal patterns of cannibalism

By day 12 since first exogenous feeding, average mortalities of pike larvae were 4.1 times as high in HD lots as in LD lots (mean numerical densities on day 12: 8.9 and 3.8 young m^{-2}, respectively). There was, however, no evidence of cannibalism, even in HD lots (Fig. 1). Numerical densities of young pike were significantly influenced by initial stocking rate up to day 29 ($p < 0.01$), but were no longer significantly different on day 39 ($p > 0.05$; LD: 2.3 young m^{-2}; HD: 1.7 young m^{-2}), as the overall number of young declined more sharply in HD ponds than in LD ponds. Mean survival rates at 100 mm TL were 37.5% (LD) and 9.6% (HD). Cannibalism was observed only during the juvenile period: minimum cannibal size (pre-predation TL) was 60.9 mm. Initial density of larvae significantly influenced the numerical density of cannibals ($p < 0.05$): in LD ponds, cannibalistic individuals were first detected on day 29 and their mean density rose to 0.17 indiv. m^{-2} on day 39; in HD ponds, cannibalism started between day 12 and day 21 and the mean density of cannibals reached maximum levels

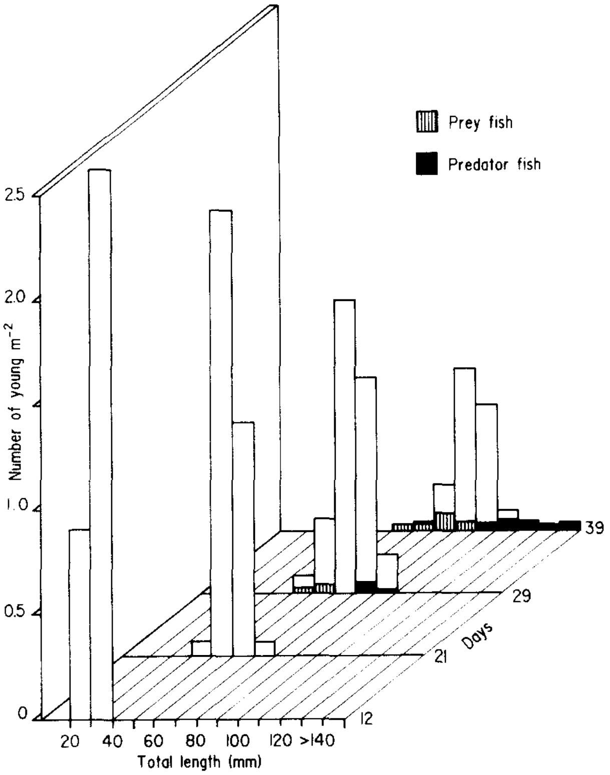

Fig. 3. Length frequency distribution of extensively cultured pike larvae and juveniles, including victims of cannibalism, at 12, 21, 29 and 39 days since first exogenous feeding (initial density: 6 larvae m^{-2}). For each initial density and each of four time points, the distribution relative to the stock from one pond (out of two replicate ponds) is shown. Vertical shading of bars shows prey pike occurring in the stomachs of larger cannibals (black shading). Non-cannibalized fish were measured directly. Total length of victims was calculated from morphometric variables. The size indicated for cannibals is the size before prey ingestion (see Materials and methods). Total number of fish measured was approx. 300 per lot.

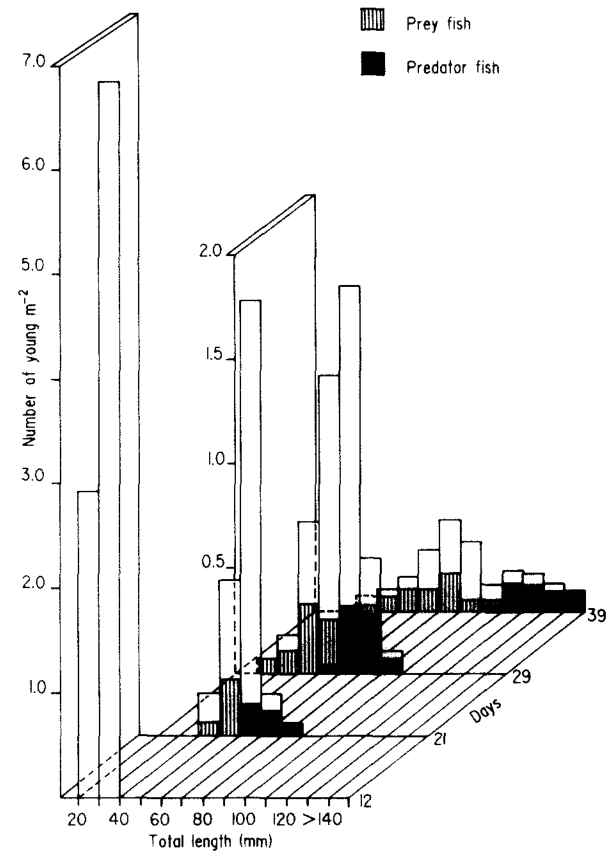

Fig. 4. Length frequency distribution of young pike at 12, 21, 29 and 39 days since first exogenous feeding (initial density: 18 larvae m^{-2}). Because of the considerable reduction in pike numbers with time in HD lots, two different scales were used to express the number of young m^{-2}: one at 12 and 21 days, the other at 29 and 39 days. Other specifications are as in Fig. 3.

(0.64 to 0.78 indiv. m^{-2}) between day 21 and day 39. On day 29, the mean numerical density of cannibals was 9.4 times higher in HD ponds than in LD ponds (0.78 vs 0.08 indiv. m^{-2}, Fig. 1). The mean final proportions of cannibalistic individuals in the populations of juveniles were 7.8% (LD) and 41.3% (HD).

Between day 21 and day 39, the relative biomass of cannibals was significantly higher in HD lots ($p < 0.05$). After onset of cannibalism, the contribution of cannibals to the pike biomass steadily increased with time and reached the mean levels of 15.5% (LD) and 65.9% (HD) on day 39 (Fig. 2).

The coefficient of variation (c.v.) relative to individual weights within a population increased from 4.9% at the end of yolksac absorption to 17.2–26.7% on day 12. In LD ponds, the weight c.v. remained stable between day 12 and day 21, then increased between day 21 and day 39, as cannibalism developed (mean final level: 40.6%). In HD ponds, the weight c.v. showed a continuous increase, up to a mean level of 69.2%. From day 12 onwards, the weight c.v. and the relative biomass of cannibals were positively correlated (Spearman coefficient = 0.94).

Figures 3 and 4 show the length frequency distributions of pike larvae and juveniles between day 12 and day 39 since first exogenous feeding, according to initial density of larvae (LD or HD). At initia-

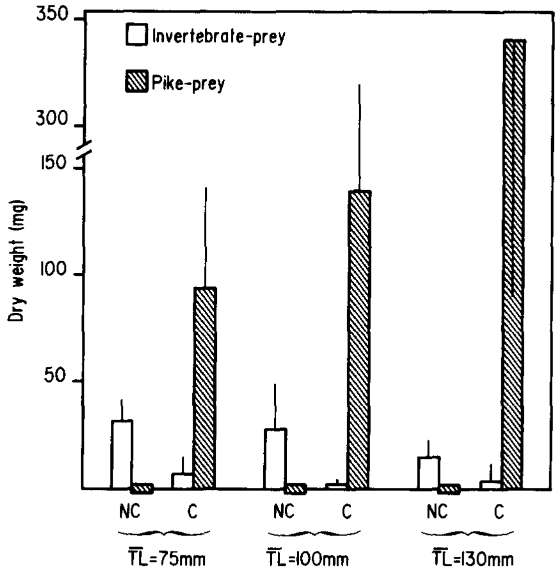

Fig. 5. Comparison of stomach contents among cannibalistic (C) and non-cannibalistic (NC) pike juveniles. At three time points, dry weights of invertebrate-prey and pike-prey were measured in cannibals and non-cannibals of similar size (T̄L: mean total length), harvested from a given pond. Mean dry weights with one SD are shown (n = 6 fish per lot).

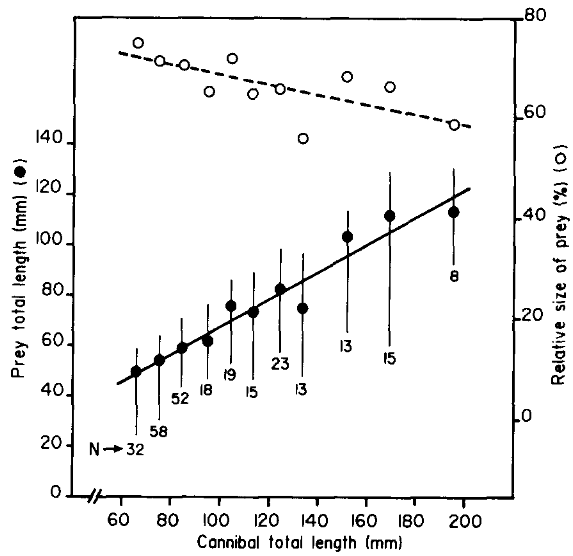

Fig. 6. Relationship between cannibal size and victim size: mean and range of total lengths (TL) for pike larvae and juveniles eaten by juvenile pike of various sizes in outdoor rearing ponds (full line). The dotted line is the regression line of mean relative size of prey (prey TL/predator TL, in %) vs. cannibal TL. Cannibal size is the size before pike-prey ingestion (see Materials and methods). N is the number of prey per cannibal length-interval.

tion of cannibalism (LD population on day 29), cannibals and prey belong to clearly separated size classes, at opposite ends of the size range. When the relative biomass of cannibals reached 10–20% (LD population on day 39: Fig. 3; HD population on day 21: Fig. 4), individuals from all size classes could be involved in cannibalism, as predators or as prey, but the smallest cannibals and largest victims still belong to different, although adjacent, size classes. When the relative biomass of cannibals exceeded 25% (HD population on days 29 and 39), the size distributions of cannibals and pike-prey overlapped at the level of an intermediate size class.

In stomach contents of cannibals, pike-prey accounted for 93.3–98.8% of undigested prey, in terms of dry weight (Fig. 5). Dry weights of invertebrate-prey were significantly lower in cannibals than in non-cannibals ($p < 0.001$).

Cannibal-prey relationship

In all cannibals examined, the last ingested end of the victim was intact, indicating that the prey was swallowed completely. Pike-prey were ingested either head-first (96.5% of all victims; n = 284) or tail-first (3.5%). Double cannibalism (two pike victims within a single cannibal) was observed in a few cases (5.5% of all cannibals).

Pike-prey total length was linearly related to cannibal total length (Fig. 6) according to the following relationship:

$$\text{Prey TL} = 12.90 + 0.54\ \text{Cannibal TL},\ r^2 = 0.95,\ p < 0.001.$$

For example, cannibals 70 mm long selected pike victims 51 mm long, whereas 150 mm TL cannibals consumed 94 mm TL prey. For 60–200 mm TL cannibals, the average size of the prey was 66.2% (overall range 35.0–85.4%) of the predator's length. Prey relative size decreased moderately with increasing cannibal size:

$$\text{Prey TL/Cannibal TL} = 0.78\text{–}9.5\ 10^{-4}\ \text{Cannibal TL},\ r^2 = 0.47,\ p < 0.05.$$

The relationships between prey head depth (HED) or maximum prey head depth and cannibal mouth width (MW) were linear and defined by the equations:

Prey HED = $-0.54 + 0.93$ Cannibal MW, $r^2 = 0.95$, $p < 0.001$;
Maximum Prey HED = $0.40 + 0.99$ Cannibal MW, $r^2 = 0.98$, $p < 0.001$.

The latter regression does not differ significantly ($p > 0.05$) from the regression between Maximum Prey HED and Cannibal MW. The head depth relationship to maximum victim size was always very close to that for cannibal mouth width. The average ratio of prey head depth to predator mouth width was 87.6%.

In each of the four situations analyzed with respect to size-selectivity by pike cannibals, a positive selection for one length-group of potential prey juveniles was demonstrated (Table 1). However, the relatively low values of the prey-selection index (+0.14 to +0.17) suggest that these preferences for prey of a given size were moderate.

Discussion

Our work represents the first quantitative study of early cannibalism in pike in a semi-natural or natural environment. It should be emphasized however, that our data probably underestimate the numbers of cannibalistic individuals, since some of the largest individuals found with no pike in their gut might be cannibals that had fully digested their pike-prey. On the other hand, a more complete understanding of cannibalism as a regulatory mechanism in populations of young pike will require to: (1) estimate total losses due to cannibalism and (2) determine the relative importance of cannibalism and other mortality factors during the early juvenile period.

The convergence of the HD and LD density curves by day 39 may have interesting management implications: under our experimental conditions, the recovery of high densities of young during early stages would be favored by the use of a relatively high stocking density. In the case of a late harvest however (mean juvenile TL > 100 mm) a lower stocking density would probably be more desirable to optimize numerical density and reduce size heterogeneity. On the other hand, as the variations of the weight c.v. reflected the time-course of the relative biomass of cannibals, this parameter might be used to estimate the amount of cannibalism without having to perform stomach analysis.

In our study, survival was found to be density-dependent even in the absence of cannibalism (days 0–12). This contrasts with the density-independent survival of young pike (mean TL: 22 mm) reported by Wright & Giles (1987) in sectored ponds before the initiation of cannibalism. The

Table 1. Values of prey-selection index C (Pearre 1982) for various length-groups of cannibals and pike-prey collected from extensive culture ponds. Only young pike that were small enough for cannibals to ingest were considered.

Cannibal TL	N[a]	Experimental lot	Prey-selection index			
			Pike-prey TL (mm)			
			30–40	40–50	50–60	60–70[b]
60–70 mm	21	HD, day 21	−0.02	+0.14*	−0.18*	–
70–80 mm	18	HD, day 21	–	+0.03	+0.14*	−0.17*
70–80 mm	24	HD, day 29	+0.07	+0.17*	+0.01	−0.18*
80–90 mm	19	HD, day 29	–	–	+0.16*	−0.09

* Significantly different from zero ($p < 0.05$).
[a] N = number of stomachs with measurable pike-prey.
[b] TL range restricted to 60–65 mm for 70–80 mm TL cannibals.

most plausible explanation for such a discrepancy is that the latter study may have been conducted under conditions such that availability of food of the appropriate type and size was not a limiting factor of young pike survival.

In our experiment, sibling cannibalism was positively density-dependent: a 3-fold initial difference in density led to a 9.4 times difference in terms of cannibals' numerical density, on day 29. A similar conclusion was reached by Giles et al. (1986) in young pike raised in tanks and by Hecht & Appelbaum (1988) in young sharptooth catfish.

In this study, the mean proportion of cannibals attained 41.3% in the HD stocks sampled on day 39. In natural nursery areas, under conditions of mixed broods and varying ages of conspecifics, high proportions of cannibals and an earlier onset of cannibalism may occur. Thus, Hunt & Carbine (1951) observed 25% of cannibals in a 21–25 mm size group and 32% in a 26–30 mm size group, within the same pike stock in a drainage ditch.

Under our experimental conditions, there was no evidence of cannibalism during the larval period. The first cannibalistic individuals to be detected (HD lots, day 21) measured 60 to 70 mm (TL), and cannibalism was well developed in HD lots at mean sizes of approx. 60 and 75 mm TL (up to 17.6% of cannibals in a population). These figures are higher than the 21, 23, 30, 38 and 49 mm minimum cannibal sizes observed respectively by Hunt & Carbine (1951), Rahn (1972), Giles et al. (1986), Fago (1977) and Wright & Giles (1987). Our results however are close to the size of 75 mm TL in relation to a 20% proportion of cannibals reported by Chodorowska & Chodorowski (1975) in larger ponds. The late onset of cannibalism under our experimental situations, even at the highest initial density of 18 larvae m^{-2}, suggests that the ratio of alternative prey density to young pike density might have been particularly favorable. Hunt & Carbine (1951) found that cannibalism in *E. lucius* was initiated once the size differences within a population reached 20–30%. Our own results show that this is not a general rule since there was no cannibalism in LD lots on day 21, despite a 40% difference between extreme size classes, and although 22% of the individuals were potential prey for the 10% of largest fish.

The low representation of invertebrate-prey in cannibals' stomachs suggests that invertebrates had become minor components in the diet of cannibals. Similarly, McIntyre et al. (1987) found that invertebrate-prey contributed less than 0.2% to the dry weight of stomach contents in cannibalistic walleyes. The numerical values of the proportions of invertebrate-prey and pike-prey in cannibals' stomachs however should be viewed with some caution, due to possible differences in digestion rates.

In contrast with studies on early cannibalism in Koi carp, *Cyprinus carpio* L. (van Damme et al. 1989), sharptooth catfish, *Clarias gariepinus* (Hecht & Appelbaum 1988), and walleye, *Stizostedion vitreum* (Cuff 1977, 1980, Krise & Meade 1986), we did not observe in young pike any case of 'Type I cannibalism', characterized by tail-first capture and subsequent head rejection. In our study, most cannibals had swallowed their prey head first and whole ('Type II cannibalism'). However, we cannot completely rule out in pike the possibility of 'Type I cannibalism', often associated with the larval period, since there was no cannibalism among pike larvae under our experimental conditions.

The relative size of pike-prey (66.2% of the predator's length, this study) seems particularly high, when compared to the figures observed in older pike preying on forage-fish (25 to 33%: Nursall 1973, Hart & Connellan 1984) and during 'Type II cannibalism' in *Clarias gariepinus* (44%, Hecht & Appelbaum 1988) and *Dicentrarchus labrax* (approx. 50%, Katavic et al. 1989). Clearly, young pike cannibals of various sizes tended to ingest large pike-prey on the average. This result is probably related to: (1) the relatively large jaw width and moderate head depth of this species at different stages of development, and (2) the fact that the size of many pike-prey was close to the maximum possible size cannibals could take.

The analysis of cannibal-prey size relationship indicated both a certain degree of size-selectivity by young pike cannibals and some variability in the size of prey ingested by cannibals from a given length-group. It should be kept in mind however that these conclusions, drawn from the measurement of ingested prey and not of attacked prey, only take into account the results of successful attacks and do not therefore reflect exhaustively the preferences of cannibals.

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