

Effects of Prey Size, Abundance, and Population Structure on Piscivory by Yellow Perch

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Abstract.—To examine how predator and prey body sizes, prey abundance, and prey population structure affect piscivore–prey interactions, feeding experiments were conducted on large (>190 mm total length, TL) and small (150–189 mm) yellow perch *Perca flavescens* given small (43–55 mm TL), medium (60–66 mm), and large (71–80 mm) fathead minnows *Pimephales promelas* as prey. Handling costs suggested that large yellow perch should not discriminate among prey sizes, but small yellow perch should select small fathead minnows over large. Results of feeding trials with only one size of prey were consistent with the cost indications. Large yellow perch consumed similar numbers and biomasses of the three size-classes of fathead minnows in trials with only one size of prey available. Small yellow perch ate more small fathead minnows than medium and more medium than large. Thus, small yellow perch gained less weight with large fathead minnows than with small ones as their prey. When all three prey sizes were available, both large and small yellow perch consistently captured more small fathead minnows than large, even when total prey abundance or the size structure of prey populations varied. Overall consumption by large yellow perch was not affected by prey abundance, but small yellow perch increased consumption at higher abundances by eating more small and medium prey. Increasing the proportion of medium fathead minnows, while decreasing the proportion of large prey, did not affect total consumption by either large or small yellow perch. However, small yellow perch responded to this shift by eating more medium and fewer large fathead minnows. Selection by yellow perch for prey fish smaller than expected based on gape limitations and handling times, and the responses of yellow perch to changes in their prey base under experimental conditions, help explain patterns of predation and coexistence between this piscivore and its prey in nature.

Size selection of prey by fish that are large relative to their food organisms (e.g., zooplanktivores) has been studied intensively (e.g., Werner and Hall 1974; Stein et al. 1984; Ryer 1988). Piscivores are less well studied, especially experimentally. Factors presumed to affect prey size selection by piscivores are often extrapolated from data on other foragers rather than documented from direct observation. Even among piscivorous fish, relatively large, specialized predators (e.g., *Micropterus* and *Esox* spp.) have received most of the attention (e.g., Hoyle and Keast 1988; Wahl and Stein 1988). It is not clear how well the assumptions and predictions made by studies of large predators apply to smaller, less-specialized piscivores.

Perca spp. range widely throughout North America and Eurasia and are often the most commonly encountered species in lakes within a region (Harvey 1981; Appelberg et al. 1989; Tonn et al. 1990). Although usually viewed as generalists (Keast 1979), yellow perch *Perca flavescens* or Eurasian perch *P. fluviatilis* can be the most abundant, or only, piscivore in small lakes. Thus, the importance of predation by *Perca* spp. in the dynamics of fish communities should not be under-

estimated (Tonn and Paszkowski 1986; Persson et al. 1992).

Predation patterns of *Perca* are known to be affected by prey size (Popova 1967; Tonn and Paszkowski 1986; Post and Evans 1989; Tonn et al. 1991). This predation can, in turn, have significant, long-lasting impacts on prey populations by reducing densities, limiting recruitment, and skewing size distributions toward large, less-vulnerable body sizes (Tonn and Paszkowski 1986; Tonn et al. 1989, 1992). Risk of predation by *Perca* spp. can also selectively alter habitat use and diel activity patterns of prey fish of different sizes (Tonn and Paszkowski 1987; Holopainen et al. 1991), and thus their availability to piscivores may be indirectly affected.

To further understand factors shaping size-biased piscivory and its potential impacts on prey populations, we addressed the following questions:

- (1) How do postcapture handling times and return rates (biomass of prey ingested per unit handling time) vary with prey size?
- (2) Are these relationships reflected in the number and biomass of different sizes of prey consumed by piscivores?

- (3) Do predation patterns change when total prey abundance is varied but the size distribution of prey is held constant?
- (4) Do predation patterns change when the total abundance of prey is held constant but size distributions are varied?
- (5) Do small and large piscivores respond differently to the above manipulations of prey, and if so, how?

Our study used two sizes of yellow perch and three sizes of fathead minnow *Pimephales promelas*. "Small" yellow perch (150–189 mm total length, TL) represented individuals at the lower end of the size range that regularly feeds on fish and are especially sensitive to prey size (Tonn and Paszkowski 1986). "Large" yellow perch (190–229 mm) were expected to be able to capture and handle all sizes of fathead minnows. Fathead minnows, like other small-bodied, soft-rayed fishes, are particularly vulnerable to piscivores (Harvey 1981; Robinson 1989; Robinson and Tonn 1989; Savino and Stein 1989). However, yellow perch and fathead minnows commonly co-occur in small lakes, where yellow perch is often the only piscivore (Tonn and Magnuson 1982; Tonn et al. 1990). Because of the fathead minnow's sexual dimorphism and semelparous reproductive pattern (Scott and Crossman 1973; Unger 1983), its populations are characterized by seasonally distinct size distributions (Price et al. 1991). Size-selective or size-limited piscivory, interacting with size-structured prey populations, could therefore strongly affect both the foraging success of yellow perch and the impact of this predation on fathead minnow populations.

Methods

Handling Times

To determine if patterns of prey consumption could be related to a measure of prey profitability, we calculated return rate, the mass of prey ingested per unit time spent handling the prey. Handling time, from capture of prey through ingestion, has been used widely in evaluating foraging behavior (e.g., Werner and Hall 1974; Stein et al. 1984). Prey handling after capture is dictated largely by the morphologies of predator and prey (Werner 1974), influenced little by spatial constraints, and thus can be observed realistically in captivity.

Handling times were measured for yellow perch eating fathead minnows in the laboratory (Meanook Biological Research Station and Department

of Zoology aquatic facility, University of Alberta). Yellow perch were captured in Baptiste and Amisk lakes near Athabasca, Alberta, from May through September with Windermere perch traps or a beach seine. Fathead minnows were captured with minnow traps or a seine from several small lakes near Athabasca. Upon capture, fish were treated with Furan-2 (Aquarium Pharmaceuticals) for 12–24 h to prevent bacterial and fungal infections. Yellow perch were held individually at 15–19°C and a photoperiod of 12 h light : 12 h darkness in aerated tanks, 122 × 51 × 61 cm, with one glass side. Before data were recorded, yellow perch were acclimated to the observation tank for 1–2 weeks and were presented one fathead minnow daily. Data collection began when a yellow perch routinely ate fathead minnows in the presence of an observer within 30 min of prey introduction.

Handling times were determined during daylight hours for 7 large yellow perch (198–210 mm TL) and 15 small yellow perch (156–189 mm TL) eating fathead minnows that were 43–80 mm TL. Experimental yellow perch received one fathead minnow per day based on a feeding schedule that randomized the order in which the prey size-classes (see below) were presented. Prior to a trial, prey were weighed and measured for total length.

At the beginning of a trial, a fathead minnow was transferred into the observation tank, held for 1 min in a hand net, and then released. Timing began when the yellow perch captured and immediately ingested the fathead minnow. If the predator repeatedly struck and released the prey (which occurred in <5% of all ingestions observed), only the final capture was used to measure handling time. Yellow perch typically captured fathead minnows headfirst (87% of all ingestions observed), sunk toward the bottom of the tank, and became immobile while handling prey. Eye movement decreased and opercular movements were slow and exaggerated. Handling was deemed complete when typical eye movement, respiratory movement, and swimming resumed (Paszkowski et al. 1989). If a yellow perch did not capture the prey within 30 min, the fathead minnow was removed and the trial was repeated later the same day. If a yellow perch failed to feed on a given day, a fathead minnow of the same size was presented the next day.

Predation Experiments

General protocol.—Predation experiments were conducted in four circular fiberglass tanks, 1.5 m in diameter, that were filled with water to a depth

of 0.75 m and aerated. Trials were conducted during May–September in a room illuminated by natural daylight and isolated from other activity. Water temperatures in tanks varied between 14 and 20°C. To compensate for seasonal changes in the condition of the environment and the fish, different treatments within an experiment (see below) were assigned in a stratified random design among the four tanks and run simultaneously.

Experimental fish came from the same lakes as those used for handling time measurements. Yellow perch and fathead minnows were held separately in outdoor tanks 1.8 m in diameter. Every 1–2 d, yellow perch were fed fathead minnows and similarly sized northern redbelly dace *Phoxinus eos*. Fathead minnows received flaked fish food daily.

The day before a trial, six yellow perch, all from either the small or large size-class, were measured for total length and wet mass, and each was marked differently by severing one dorsal spine (second through seventh). To standardize size distributions, each group of six fish comprised three sets of pairs based on fish size (size ranges of pairs were 190–201, 202–219, and 220–229 mm for large yellow perch and 150–162, 163–175, and 176–189 mm for small yellow perch). Large yellow perch averaged 120.5 g (± 23.6 g, SD) and small yellow perch averaged 55.9 g (± 13.9 g). Yellow perch were introduced into the experimental tanks and held overnight without fathead minnows to standardize hunger levels and allow acclimation.

We used three size-classes of prey that represented natural groupings found in local fathead minnow populations, based on age and sex (Price et al. 1991). Small fathead minnows (TL range, 43–55 mm; mean weight \pm SD, 1.1 \pm 0.3 g) corresponded to sexually immature age-1 fish. Medium fathead minnows (60–66 mm, 2.5 \pm 0.4 g) corresponded primarily to mature females but could have been the largest juveniles and smallest sexually mature males. Large fathead minnows (71–80 mm, 4.3 \pm 0.5 g) corresponded to large sexually mature males and females. To allow for easy recognition of size-classes, a small nick was cut from the upper lobe of the caudal fin of medium fathead minnows. On the first day of a trial, all prey were introduced simultaneously to the tank containing yellow perch. We never observed yellow perch attacking newly introduced fathead minnows and there was no indication of unusual vulnerability to predation at this time. During trials, fathead minnows were fed daily with flaked fish food.

Every 2 d, fathead minnows were captured with large hand nets and counted by size-class. The number eaten per size-class was recorded and new fathead minnows were added to restore populations to their original abundances and size distributions. Trials lasted 8 d. At the end of a trial all fish were removed, fathead minnows were counted by size-class, and yellow perch were weighed individually. The total number of fathead minnows eaten in 8 d from each size-class was recorded and numbers were converted to biomass by using mean weights for each size-class. Fish were returned to holding tanks and, after a minimum of 8 d, were considered available for use in subsequent trials. Fish were drawn randomly from these large stocks (50–150 yellow perch; 500–1,000 fathead minnows) when new groups of predators and prey were assembled. Thus, we ensured that group composition changed across trials and each group was a unique entity.

Types of experiments.—We ran three sets of experiments for each of the two sizes of yellow perch. Replicates of a given treatment varied between 5 and 7 for large yellow perch and between 7 and 10 for small yellow perch. In experiment 1, where we examined the effects of prey size, prey populations consisted of 90 small, medium, or large fathead minnows. In experiment 2, where we examined the effects of prey abundance, fathead minnow populations were composed of equal proportions of the three size-classes and comprised 60, 120, or 180 fish. In experiment 3, where we examined the effects of prey population structure, prey abundance was held constant at 90 fathead minnows; 30 of these were small, and the remainder of the population was medium and large fish in different proportions: (1) 30 medium and 30 large, (2) 40 medium and 20 large, (3) 50 medium and 10 large, or (4) 55 medium and 5 large. This proportion series mimicked seasonal changes in natural populations of fathead minnow, in which large, age-2 individuals die after reproducing in late spring and age-1 fish grow through the summer months (Price et al. 1991).

Statistical Analyses

We used one-way analysis of variance coupled with Tukey–Kramer multiple-comparison tests to analyze handling times and return rates, changes in weight for yellow perch, and the results of experiment 1. We examined effects of prey size, population-level treatments, and the interactions of these factors in experiments 2 and 3 by two-way analysis of variance. Data were \log_{10} -transformed

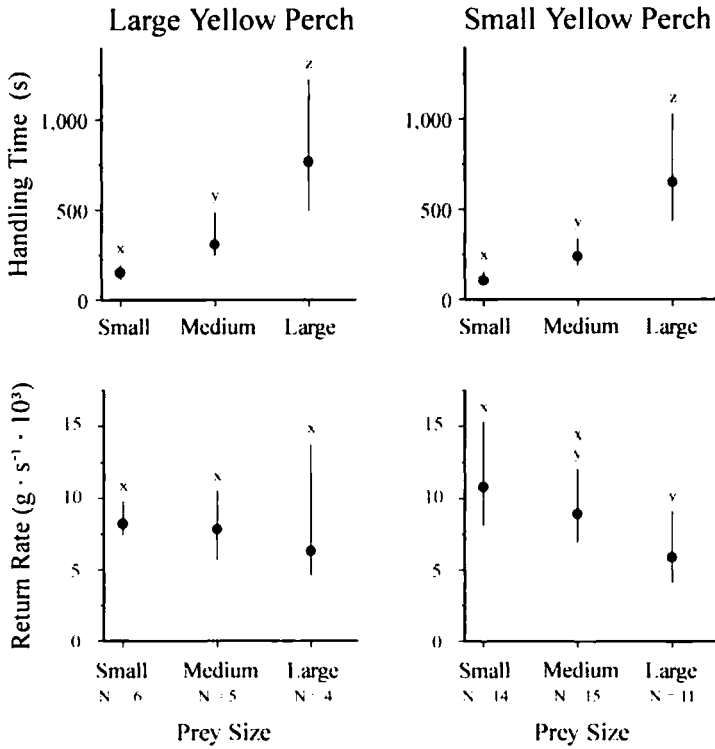


FIGURE 1.—Mean handling times and return rates (biomass of prey consumed per unit handling time) for large (198–210 mm total length, TL) and small (156–189 mm) yellow perch consuming small (43–55 mm TL), medium (60–66 mm), and large (71–80 mm) fathead minnows. Error bars = 95% confidence intervals (calculated from \log_{10} -transformed data). Sample sizes (N) represent the number of individual yellow perch observed; for each yellow perch, we used the median value from multiple trials (the mean number of trials \pm SD for an individual yellow perch handling a given size of prey was 4.1 ± 3.5). Means labeled with the same letter did not differ significantly from each other (Tukey–Kramer tests, $P \geq 0.05$).

to homogenize variance. In all cases, $P < 0.05$ was considered statistically significant.

Results

Handling Times and Return Rates

We observed the 7 large yellow perch capture and ingest 39 fathead minnows (14 small, 12 medium, and 13 large) and the 15 small yellow perch capture and ingest 184 fathead minnows (80 small, 73 medium, and 31 large). For individual yellow perch, we calculated median handling times and return rates for each prey size and we used these median values for analysis. For both large and small yellow perch, handling time differed significantly with size-class, increasing with prey size (Figure 1).

In terms of return rate, however, the performances of large yellow perch did not vary significantly with prey size (Figure 1). Return rate differed with prey size for small yellow perch: small

fathead minnows offered significantly higher returns than large ones (Figure 1).

Experiment 1: Effects of Prey Size

The total number of and biomass of prey captured and consumed by large yellow perch did not differ with prey size in experiment 1 (Figure 2). Correspondingly, mean weight change (\pm SD) of individuals within groups of large yellow perch did not differ across treatments (small prey offered, -1.6 ± 2.0 g; medium, -0.9 ± 2.3 g; large, 0.8 ± 3.6 g).

As suggested by return rates, small yellow perch proved more sensitive to prey size. Both the total number of prey captured and the total biomass consumed differed significantly across treatments in experiment 1 (Figure 2). Most notably, small yellow perch ate significantly less biomass when only large prey were available than under the other treatments. Mean weight change of individuals

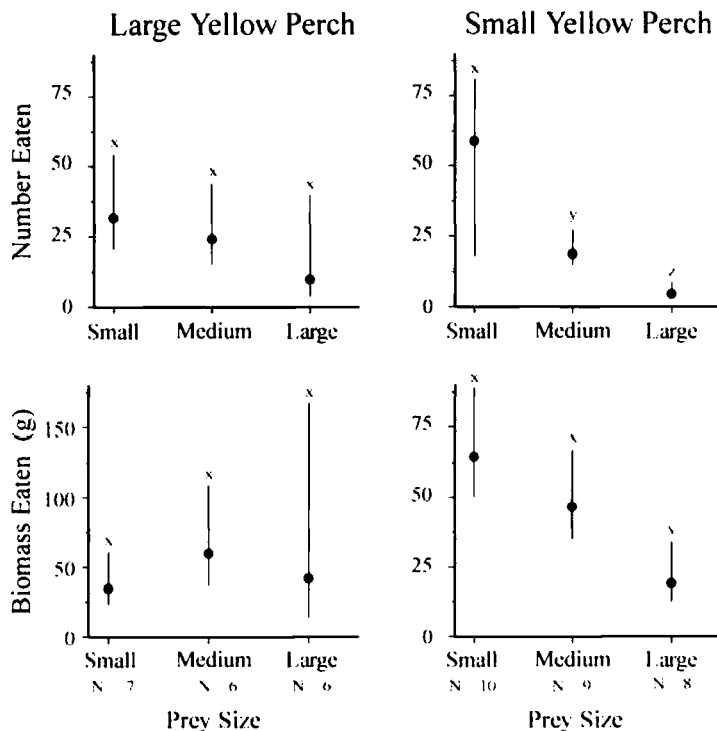


FIGURE 2.—Mean values for the total number and total biomass of fathead minnows eaten by groups of six large yellow perch (190–229 mm TL) or six small yellow perch (150–189 mm) in 8 d when presented 90 fathead minnows, either all small, all medium, or all large (experiment 1). Sample sizes (N) represent the number of groups of yellow perch tested. Error bars = 95% confidence intervals (calculated from \log_{10} -transformed data). Means labeled with the same letter did not differ significantly from each other (Tukey–Kramer tests, $P \geq 0.05$).

within groups of small yellow perch differed significantly with prey size, and weight gain (mean \pm SD) was greater when small fathead minnows were available than when large ones were offered (small-prey treatment, 0.7 ± 1.4 g; medium, 0.3 ± 1.2 g; large, -1.5 ± 1.7 g).

Experiment 2: Effects of Prey Abundance

Total prey abundance did not affect the number of fathead minnows eaten by large yellow perch in experiment 2. Prey size, however, did affect numbers eaten. Large yellow perch ingested significantly more small fathead minnows than medium or large fathead minnows, even though the size-classes were equally available (Figure 3). The interaction between size and abundance was not significant. Biomass of prey eaten by large yellow perch in this experiment was not significantly affected by prey size, abundance, or their interaction. Large yellow perch did not display significant differences in weight change across the three levels of prey abundance.

As was observed for large yellow perch in this experiment, prey size affected significantly the number of fathead minnows eaten by small yellow perch (Figure 3). Consumption differed significantly between each prey size not only in terms of numbers, but also in terms of biomass. In contrast to the results for large yellow perch, prey abundance significantly affected predation patterns of small yellow perch in terms of prey number, and in terms of biomass, the effect was almost significant ($P = 0.08$). Total biomass (mean \pm SD) consumed by small yellow perch was 20.7 ± 7.4 g with 60 prey present and increased to 66.3 ± 19.4 g with 120 prey and 66.1 ± 24.4 g with 180 prey present. Prey abundance interacted significantly with prey size. Small yellow perch captured more small and medium fathead minnows, but not more large prey, at the two higher levels of prey abundance (Figure 3). Small yellow perch did not, however, display significant differences in weight change across the three levels of prey abundance.

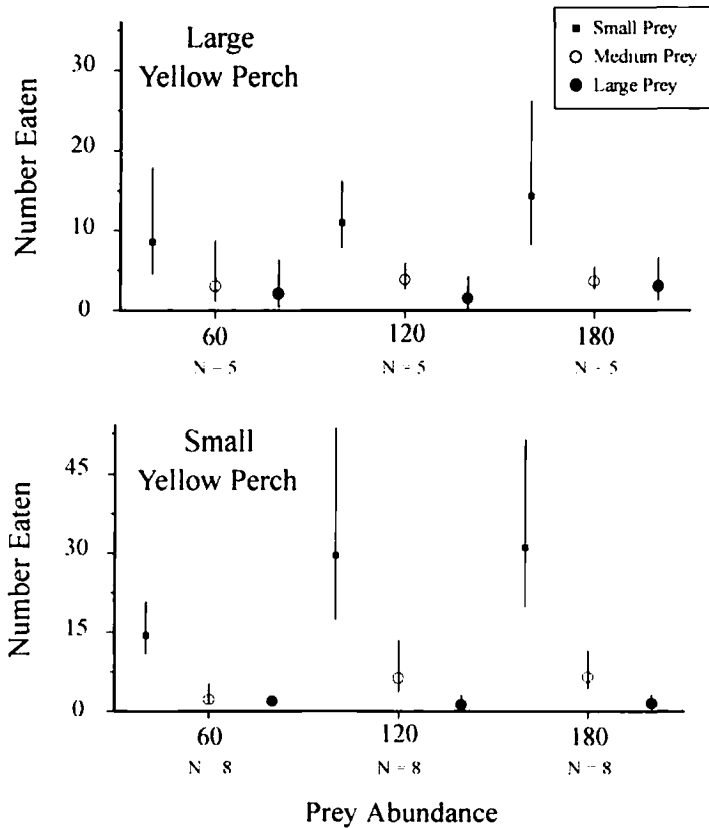


FIGURE 3.—Mean numbers of small, medium, and large fathead minnows eaten in experiment 2 by groups of six large yellow perch or six small yellow perch in 8 d under three prey abundances (60, 120, or 180 fish, divided equally among the size-classes). Sample sizes (N) represent the number of groups of yellow perch tested. Error bars = 95% confidence intervals (calculated from \log_{10} -transformed data).

Experiment 3: Effects of Prey Population Structure

The number (Figure 4) and biomass of fathead minnows eaten by large yellow perch did not differ in response to changes in the overall structure of the prey population in experiment 3, but were affected significantly by prey size. The number of fathead minnows eaten differed significantly between each prey size, and greater biomass of small and medium fathead minnows than of large prey was consumed. The interaction between prey size and population structure was not significant. Large yellow perch did not display significant differences in weight change in response to changes in prey population structure.

As in the case of large yellow perch, prey population structure did not affect the total number and biomass of fathead minnows eaten by small yellow perch in experiment 3, but prey size had significant effects (Figure 4). Consumption by

numbers differed significantly between each prey size, and greater biomasses of small and medium fathead minnows were eaten than large. Unlike the pattern for large yellow perch, predation by small yellow perch displayed a significant interaction between prey size and population structure for both numbers and biomass of prey consumed. As medium fathead minnows became more common within a prey population and large fathead minnows became rarer, consumption of medium fathead minnows increased while the consumption of large prey decreased (Figure 4). Thus, total biomass consumed by small yellow perch for all sizes combined remained relatively stable, averaging 58.6 g (± 31.6 g, SD) with 30 medium fathead minnows available, 41.8 g (± 12.3 g) with 40, 52.3 g (± 37.1 g) with 50, and 61.6 g (± 23.7 g) with 55 medium prey. Small yellow perch did not display significant differences in weight change across the series of treatments.

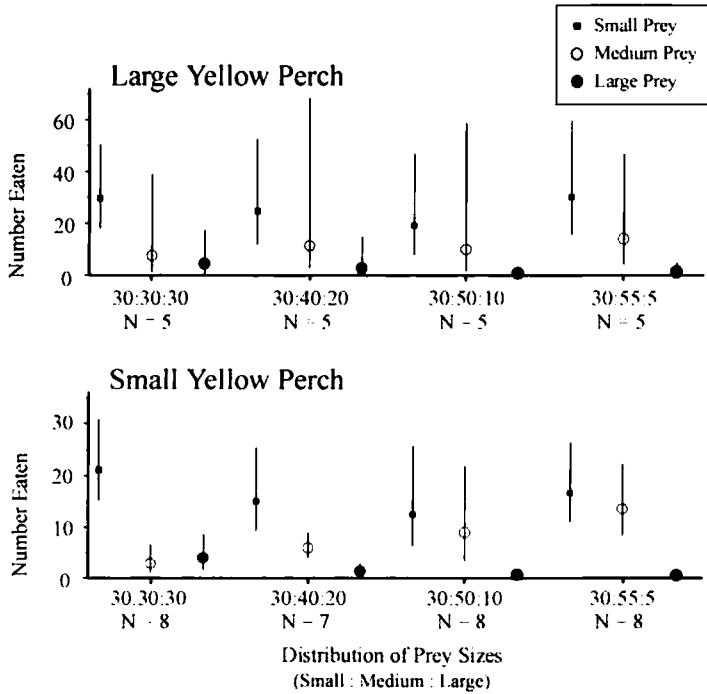


FIGURE 4.—Mean numbers of small, medium, and large fathead minnows eaten in experiment 3 by groups of six small yellow perch or six large yellow perch in 8 d. Prey populations consisted of 90 fish and had one of four size distributions (small : medium : large). Sample sizes (N) represent the number of groups of yellow perch tested. Error bars = 95% confidence intervals (calculated from \log_{10} -transformed data).

Discussion

Return rates based on handling times indicated that large yellow perch feeding on fathead minnows should be insensitive to prey size, whereas small yellow perch should discriminate, specifically between small and large prey. Return rates proved to have some utility in predicting feeding patterns of yellow perch in experiments 1–3, but also showed appreciable shortcomings.

The clearest agreement between predictions and results occurred in experiment 1, where only one prey size was available. Larger yellow perch adjusted the number of small, medium, or large fathead minnows eaten in order to maintain a constant intake of biomass and constant weight change. However, when only large fathead minnows were available, small yellow perch were unable to attain this “balance” and had significantly less growth. These differences between large and small yellow perch are consistent with the simple explanation that the larger the body and gape sizes of the predators, the greater their handling efficiency of large prey.

In experiments 2 and 3, where yellow perch for-

aged under a more complex, realistic prey regime and choices among prey sizes were possible, return rates were less effective in predicting feeding patterns. In these experiments, large as well as small yellow perch displayed a dichotomy: high consumption of small fathead minnows, in terms of numbers and biomass, and low consumption of large fathead minnows. Although neither size of yellow perch was expected to discriminate intermediate-sized fathead minnows from small or large, they often did in ways that varied with treatment and size of predator (Figures 3, 4). Concentration on smaller-than-expected prey, often the smallest available, is a consistent attribute of *Percas* feeding on fishes (Tonn and Paszkowski 1986; Tonn et al. 1991, 1992) and of other predatory fishes feeding on vertebrates (e.g., Mauck and Coble 1971; Gillen et al. 1981; Hamilton and Powles 1983; Hoyle and Keast 1987; Schlosser 1988; Hart and Hamrin 1990; East and Magnan 1991; Hambricht 1991). This is especially true when the predicted size of prey is based solely or partially on postcapture handling time. Similar trends have been observed for some predatory invertebrates (e.g., decapod crustaceans eating molluscs; Juanes

1992). Numerous explanations have been proposed, but none are completely satisfactory. Hoyle and Keast (1987), for example, related differences between observed and expected prey size for large-mouth bass *Micropterus salmoides* to the relatively greater availability of small prey because of population structure and seasonal patterns in nature. However, this cannot adequately account for our results in experiments 2 and 3, which suggest a more active role for piscivores in shaping their diets (see below).

Escape behavior of prey fish also deserves consideration. The assumption that stages of the predatory process other than handling (e.g., pursuing or subduing prey) represent negligible investments in time or energy (Werner 1974) may be applicable to planktivores but not to piscivores. Fast-start performance (Webb 1978), maneuverability (Moody et al. 1983), and schooling skills and position (Pitcher and Parrish 1993) improve with increased age and size and thus may contribute to better escape capabilities and lower capture probabilities for larger prey fish. Nonrandom capture success could explain many patterns observed in our experiments, even if yellow perch attacked prey of different sizes at random. We did not quantify attack rates, but selective attack on prey of sizes that are likely to be captured and handled efficiently has been reported for other piscivores (East and Magnan 1991), and represents a possible tactic of yellow perch as well.

Large yellow perch were apparently effective enough as piscivores to be insensitive to our manipulations of their food base in experiments 2 and 3. In contrast, feeding patterns of small yellow perch were clearly affected by changes in prey abundance and size distribution. In experiment 3, shifts in the relative abundance of different sizes of prey affected the diet of small yellow perch, not in terms of total number or biomass of prey, but by altering dietary composition. Medium prey were substituted for large prey as the medium ones became increasingly more common and as the large ones became more rare. In 10 of 16 trials where large fathead minnows composed 11% or less of the population, they disappeared completely from the diet of small yellow perch. Hart and Hamrin (1988) reported similar responses by northern pike *Esox lucius* capturing rudd *Scardinius erythrophthalmus* from schools with different size structures.

In experiment 2, small yellow perch foraged more successfully when total prey numbers were doubled or tripled. However, equivalent increases

in consumption of all three prey sizes, implying nonselective predation driven primarily by increased rates of prey encounter and detection (Magnhagen 1985), were not observed. Only the number of small and medium fathead minnows eaten increased, supporting the proposal that yellow perch selectively pursue prey of different sizes. Yet even in the presence of elevated concentrations of smaller prey, which offered higher returns, small yellow perch ate large fathead minnows in 13 of 16 trials conducted at the two higher prey abundances. Foraging experiments have demonstrated repeatedly that, although fish may concentrate on particularly profitable food types, they rarely restrict their diet to the "best" prey, even if it is abundant enough to meet energetic demands (e.g., Werner and Hall 1974). This pattern could be due to imperfect discrimination among prey types by foraging fish, "deliberate" sampling by foragers, or prey selection based on criteria not measured by the investigator (Stephens and Krebs 1986).

Our study offers several insights into the nature of piscivory by *Perca* spp. and its potential impact on fathead minnows and other prey fishes. First, even when prey are continually available, piscivory by perch is a relatively uncommon event; in all 135 trials, individual yellow perch captured an average of only one fathead minnow every 35 h. The infrequency of successful piscivory might explain the scarcity of fish remains in the guts of yellow perch of even larger size-classes collected in dietary studies (e.g., Keast 1977; Jansen and MacKay 1992). Small yellow perch, being particularly sensitive to the size of prey and the size structure of prey populations, may do poorly as piscivores in communities dominated by larger prey fishes, even if they are ultimately capable of capturing and handling these prey. In such environments, small yellow perch might concentrate their foraging efforts on benthic invertebrates or seasonally available age-0 fish (Tonn et al. 1992).

Small yellow perch also appear to be less-effective piscivores at lower overall prey abundances, which may help explain why the ontogenetic shift to a piscivorous diet is more difficult for perch species in less-productive lakes (Alm 1946; Deedler 1951). Our results from experiment 2 suggest that, in addition to a scarcity of benthic and pelagic invertebrates in such lakes (e.g., Rask 1983; Persson 1987), low densities of fish prey may contribute to stunting of *Perca*.

Unlike changes in prey abundance, changes in prey population structure that simulated seasonal

shifts in natural populations of fathead minnows (shifts caused by the death of large individuals after reproduction; Price et al. 1991) did not affect total consumption by yellow perch. Both large and small predators were able to track the progressive increase of medium prey and decrease of large prey. In these manipulations the abundance (absolute and relative) of small fathead minnows remained constant. However, in another experiment on piscivory by yellow perch, in which the population structure of the prey (central mudminnow *Umbra limi*) shifted from predominantly small (vulnerable) to predominantly large (invulnerable) individuals, the results were different; total predation, especially by small yellow perch, declined (Tonn and Paszkowski 1986). Predation levels by *Perca* spp., and the impact of that predation on prey populations, should be even more sensitive to population structures of large-bodied prey, such as many species of European cyprinids that can achieve absolute refuges from piscivory by perch through growth (Holopainen et al. 1991).

Perca spp. are less specialized and have relatively smaller mouths than many piscivores (Keast 1985). Therefore, as with other prey species (e.g., central mudminnow, Tonn and Paszkowski 1986; yellow perch, Post and Evans 1989), the impact of yellow perch piscivory was strongest on small fathead minnows corresponding in size to sexually immature fish. In nature, predation by *Perca* may actually be concentrated on fish even smaller than those used in this study and thus may have its largest effect through limiting recruitment (Tonn et al. 1992).

Other piscivores, such as largemouth bass and northern pike, reach large body sizes, have relatively larger gapes, display their highest return when handling large prey fish, and will feed preferentially on larger fathead minnows (Hambright 1991). Fathead minnows from populations sympatric with large piscivores display well-developed predator recognition and antipredator responses (Mathis et al. 1993), but surveys have repeatedly shown that fathead minnows are typically absent from lakes where large predators are present (Harvey 1981; Tonn and Magnuson 1982; Robinson and Tonn 1989). Strong predation pressure on large, sexually mature individuals by *Esox* or *Micropterus* spp. might interfere with the complex reproductive behavior of the fathead minnow, particularly obligate parental care (McMillan and Smith 1974), and ultimately drive populations to extinction. Predation by yellow perch, concentrated on smaller individuals, would

be less likely to suppress reproduction and recruitment totally. Thus, the yellow perch and the fathead minnow may have morphological and behavioral characters, undoubtedly evolved independently under different selective regimes, that permit them to live together in appropriate habitats. In light of the varied and unique distributions and histories of temperate freshwater fish species during and following the Pleistocene, this type of "permissive coexistence" is probably a common process shaping fish assemblages.

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References

- Alm, G. 1946. Reasons for the occurrence of stunted fish populations with special reference to perch. Institute of Freshwater Research Drottningholm Report 25:1-146.
- Appelberg, M., E. Degerman, and P. Nyberg. 1989. Species composition and relative abundance of the fish fauna in acidified and limed lakes in Sweden. Pages 143-160 in J. W. S. Longhurst, editor. Acid deposition: sources, effects and controls. British Library, Technical Communication, London.
- Deedler, C. L. 1951. A contribution to the knowledge of the stunted growth of perch (*Perca fluviatilis* L.) in Holland. *Hydrobiologia* 3:357-378.
- East, P., and P. Magnan. 1991. Some factors regulating piscivory of brook trout, *Salvelinus fontinalis*, in the lakes of the Laurentian Shield. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1735-1743.
- Gillen, A. L., R. A. Stein, and R. F. Carline. 1981. Predation by pellet-reared tiger muskellunge on minnows and bluegills in experimental systems. *Transactions of the American Fisheries Society* 110: 197-209.
- Hambright, K. D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society* 120:501-508.
- Hamilton, J. G., and P. M. Powles. 1983. Fish predation and other distinctive features in the diet of Nogies Creek, Ontario, largemouth bass, *Micropterus salmoides*. *Canadian Field-Naturalist* 97:47-56.
- Hart, P. J. B., and S. F. Hamrin. 1988. Pike as a selective predator. Effects of prey size, availability, cover and pike jaw dimensions. *Oikos* 51:220-226.
- Hart, P. J. B., and S. F. Hamrin. 1990. The role of

- behaviour and morphology in the selection of prey by pike. Pages 235–254 in R. N. Hughes, editor. *Behavioural mechanisms of food selection*. Springer-Verlag, Berlin.
- Harvey, H. H. 1981. Fish communities of the Bruce Peninsula. *Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen* 21:1222–1230.
- Holopainen, I. J., W. M. Tonn, and C. A. Paszkowski. 1991. Ecological responses of crucian carp populations to predation by perch in a manipulated pond. *Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen* 24:2412–2417.
- Hoyle, J. A., and A. Keast. 1987. The effects of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). *Canadian Journal of Zoology* 65:1972–1977.
- Hoyle, J. A., and A. Keast. 1988. Prey handling time in two piscivores, (*Esox americanus vermiculatus*) and (*Micropterus salmoides*), with contrasting mouth morphologies. *Canadian Journal of Zoology* 66:540–542.
- Jansen, W. A., and W. C. MacKay. 1992. Foraging in yellow perch, *Perca flavescens*: biological and physical factors affecting diel periodicity in feeding, consumption, and movement. *Environmental Biology of Fishes* 34:287–303.
- Juanes, F. 1992. Why do decapod crustaceans prefer small-sized molluscan prey? *Marine Ecology Progress Series* 87:239–249.
- Keast, A. 1977. Diet overlap and feeding relationships between the year classes in the yellow perch (*Perca flavescens*). *Environmental Biology of Fishes* 2:53–70.
- Keast, A. 1979. Patterns of predation in generalist feeders. Pages 243–255 in H. Clepper, editor. *Predator-prey systems in fisheries management*. Sport Fishing Institute, Washington D.C.
- Keast, A. 1985. The piscivore feeding guild of the fishes in small freshwater ecosystems. *Environmental Biology of Fishes* 12:119–129.
- Magnhagen, C. 1985. Random prey capture or active choice? An experimental study on prey size selection in three marine fish species. *Oikos* 45:206–216.
- Mathis, A., D. P. Chivers, and R. J. F. Smith. 1993. Population differences in responses of fathead minnows (*Pimephales promelas*) to visual and chemical stimuli from minnow predators. *Ethology* 93:31–40.
- Mauck, W. L., and D. W. Coble. 1971. Vulnerability of some fishes to northern pike (*Esox lucius*) predation. *Journal of the Fisheries Research Board of Canada* 28:957–969.
- McMillan, V., and R. J. F. Smith. 1974. Agonistic and reproductive behaviors of the fathead minnow (*Pimephales promelas* Rafinesque). *Zeitschrift für Tierpsychologie* 34:25–58.
- Moody, R. C., J. M. Helland, and R. A. Stein. 1983. Escape tactics used by bluegills and fathead minnows to avoid predation by tiger muskellunge. *Environmental Biology of Fishes* 8:61–65.
- Paszkowski, C. A., W. M. Tonn, and I. J. Holopainen. 1989. An experimental study of body size and food size relations of crucian carp, *Carassius carassius*. *Environmental Biology of Fishes* 24:275–286.
- Persson, L. 1987. The effect of resource availability and distribution on size class interactions in perch, *Perca fluviatilis*. *Oecologia* (Berlin) 73:170–177.
- Persson, L., S. Diehl, L. Johansson, G. Andersson, and S. F. Hamrin. 1992. Trophic interactions in temperate lake ecosystems: a test of food chain theory. *American Naturalist* 140:59–84.
- Pitcher, T. J., and J. K. Parrish. 1993. Functions of shoaling behaviour in teleosts. Pages 363–440 in T. J. Pitcher, editor. *Behaviour of teleost fishes*. Chapman and Hall, London.
- Popova, O. A. 1967. The predator-prey relationship among fish. Pages 359–376 in S. D. Gerking, editor. *The biological basis of freshwater fish production*. Blackwell, Oxford, UK.
- Post, J. R., and D. O. Evans. 1989. Experimental evidence of size-dependent predation mortality in juvenile yellow perch. *Canadian Journal of Zoology* 67:521–523.
- Price, C. J., W. M. Tonn, and C. A. Paszkowski. 1991. Intraspecific patterns of resource use by fathead minnows in a small boreal lake. *Canadian Journal of Zoology* 69:2109–2115.
- Rask, M. 1983. Differences in growth of perch (*Perca fluviatilis* L.) in two small forest lakes. *Hydrobiologia* 101:139–144.
- Robinson, C. L. K. 1989. Laboratory survival of four prey in the presence of northern pike. *Canadian Journal of Zoology* 67:418–420.
- Robinson, C. L. K., and W. M. Tonn. 1989. The influence of environmental factors and piscivory in structuring fish assemblages of small Alberta lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 46:81–89.
- Ryer, C. H. 1988. Pipefish foraging: effects of fish size, prey size and altered habitat complexity. *Marine Ecology Progress Series* 48:37–45.
- Savino, J. F., and R. A. Stein. 1989. Behavioural interactions between fish predators and their prey: effects of plant density. *Animal Behaviour* 37:311–321.
- Schlosser, I. J. 1988. Predation risk and habitat selection by two size classes of a stream cyprinid: experimental test of a hypothesis. *Oikos* 52:36–40.
- Scott, W. B., and E. J. Crossman. 1973. *Freshwater fishes of Canada*. Fisheries Research Board of Canada Bulletin 184.
- Stein, R. A., C. G. Goodman, and E. A. Marschall. 1984. Using time and energetic measures of cost in estimating prey value for fish predators. *Ecology* 65:702–715.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey.
- Tonn, W. M., and J. J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* 63:1149–1166.

- Tonn, W. M., J. J. Magnuson, M. Rask, and J. Toivonen. 1990. Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes. *American Naturalist* 136:345-375.
- Tonn, W. M., and C. A. Paszkowski. 1986. Size-limited predation, winterkill, and the organization of *Umbra-Perca* fish assemblages. *Canadian Journal of Fisheries and Aquatic Sciences* 43:194-202.
- Tonn, W. M., and C. A. Paszkowski. 1987. Habitat use of the central mudminnow (*Umbra limi*) and yellow perch (*Perca flavescens*) in *Umbra-Perca* assemblages: the roles of competition, predation, and the abiotic environment. *Canadian Journal of Zoology* 65:862-870.
- Tonn, W. M., C. A. Paszkowski, and I. J. Holopainen. 1989. Responses of crucian carp populations to differential predation pressure in a manipulated pond. *Canadian Journal of Zoology* 67:2841-2849.
- Tonn, W. M., C. A. Paszkowski, and I. J. Holopainen. 1991. Selective piscivory by perch: effects of predator size, prey size, and prey species. *Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen* 24:2406-2411.
- Tonn, W. M., C. A. Paszkowski, and I. J. Holopainen. 1992. Piscivory and recruitment: mechanisms structuring prey populations in small lakes. *Ecology* 73:951-958.
- Unger, L. M. 1983. Nest defense by deceit in the fathead minnow, *Pimephales promelas*. *Behavioral Ecology and Sociobiology* 13:125-130.
- Wahl, D. H., and R. A. Stein. 1988. Selective predation by three esocids: the role of prey behavior and morphology. *Transactions of the American Fisheries Society* 117:142-151.
- Webb, P. W. 1978. Fast-start performance and body form in seven species of teleost fish. *Journal of Experimental Biology* 74:211-226.
- Werner, E. E. 1974. The fish size, prey size, handling relation in several sunfishes and some implications. *Journal of the Fisheries Research Board of Canada* 31:1531-1536.
- Werner, E. E., and D. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1216-1232.

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