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Predation by Pellet-Reared Tiger Muskellunge on Minnows and Bluegills in Experimental Systems

ALAN L. GILLEN

Ohio Cooperative Fishery Research Unit[1]

ROY A. STEIN

Department of Zoology, The Ohio State University

ROBERT F. CARLINE

Ohio Cooperative Fishery Research Unit, The Ohio State University
1735 Neil Avenue, Columbus, Ohio 43210

Abstract

Studies in Wisconsin lakes have shown that stocked tiger muskellunge (F_1 hybrids of female muskellunge, *Esox masquinongy* × male northern pike, *E. lucius*) reared on live food survive better than those reared entirely on dry pellet food. We evaluated the ability of pellet-reared hybrids to convert to a minnow (*Notropis* spp. and *Pimephales promelas*) or bluegill (*Lepomis macrochirus*) diet in laboratory aquaria and hatchery ponds. In aquaria, 86–310-mm (total length) tiger muskellunge selected cyprinids that were about 40% of their own length and bluegills that were about 30% of their length, sizes closely predicted by an optimal foraging construct (time from prey capture to complete prey ingestion ÷ prey dry weight). Using these prey sizes, we tested hybrids (130, 150, and 170 mm long) in conversion experiments in aquaria and ponds. During experiments, prey were maintained at a constant density and predators were sampled periodically to determine the proportion eating fish. Tiger muskellunge converted more slowly to bluegills than to minnows in both aquaria and ponds. In aquaria, 85% of the hybrids converted from pellets to minnows by day 3, whereas only 68% converted to bluegills. By day 5, conversions to minnows and bluegills were 95% and 82%, respectively. In ponds, 73% of the hybrids converted to minnows by day 5 and 89% by day 14. No hybrids had eaten bluegills by day 3 and only 53% converted by day 14. The apparently limited ability of pellet-reared tiger muskellunge to switch to a bluegill diet may influence survival and growth of these predators in reservoirs dominated by a centrachid forage base.

The tiger muskellunge (F_1 hybrid of female muskellunge, *Esox masquinongy* × male northern pike, *E. lucius*) is stocked in lakes for sportfishing and control of undesirable fishes (Graff 1978). It can be economically cultured on artificial diets and may reach large sizes after stocking. However, field studies in Wisconsin lakes have shown that survival of hybrids reared on fish in hatcheries was much higher than that of hybrids reared on pellets (Johnson 1978). Poor survival could result if hybrids do not develop their ability to stalk and catch live prey by the time they reach stocking size, or if the time for

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this behavioral change is so long that starvation reduces their viability. We conducted experiments in the laboratory and small ponds to determine how quickly hybrids reared on pellets converted to a diet of minnows (*Notropis* spp. and *Pimephales promelas*) or bluegills (*Lepomis macrochirus*).

Methods

Hybrids, reared entirely on dry pellet food, were obtained from Wolf Lake Hatchery, Michigan and Kincaid Fish Farm, Ohio. We held these fish in 500-liter tanks at 15–17 C and fed them pellets. For laboratory trials, individuals were acclimated over 24 hours to experimental temperatures. During the acclimation period, fish were fed pellets or minnows or bluegills. Hereafter, we refer to fish that were always fed pellets as naive, whereas those that were fed live prey for at least 1 day were termed experienced. Once a hybrid captured its first prey, its predatory efficiency did not increase during subsequent captures (see Results).

Prey-Size Selection

In preliminary trials, we determined the appropriate size of minnows and bluegills to use in subsequent experiments based on optimal foraging theory (Schoener 1971; Werner 1974, 1977; Werner and Hall 1974). Optimal prey size is operationally defined as the size with a minimal ratio of handling time (time from prey capture to complete prey ingestion, H_t, in seconds) per unit of dry weight of prey (Wt, in milligrams); that is, with a minimal cost/benefit ratio, $C/B = H_t/Wt$ (Werner 1974). This approach has been used successfully to predict prey sizes chosen by predators in the laboratory and field (Werner 1974; Kisalalioglu and Gibson 1976; Stein 1977).

Size-selection and optimal foraging experiments were conducted in 100-liter aquaria at water temperatures of 19–23 C. Hybrids were separated into six total-length classes (millimeters): 86–90, 126–130, 146–150, 166–170, 246–250, and 306–310. Prey types also were divided into six length classes (millimeters): 26–30, 36–40, 46–50, 56–60, 66–70, and 76–80. Throughout the paper, we identify these length classes of predator and prey by the highest value in each range. Experienced hybrids were acclimated individually in aquaria and starved for at least 24 hours. We placed one prey from each length class in aquaria, and recorded the size class of the first prey that was eaten (usually within 5 minutes after prey introduction). Twenty such trials for each hybrid length class were conducted. During size-selection experiments, we measured handling times (N = 12) for each predator and each prey length class. We dried 10 each of bluegills and minnows from each length class (N = 60 per prey type) for 48 hours at 80 C, and weighed them (nearest 1.0 mg). We compared handling time per prey dry weight (C/B) with the prey sizes most frequently chosen in size-selection experiments.

We measured total length (to the nearest 1.0 mm) and greatest body depth (nearest 0.1 mm) of 60 minnows and 60 bluegills (10 per length class) and established equations relating these variables. We used these relationships to establish if hybrids based their prey selection on length or body depth.

Hybrid Behavior

We compared predatory efficiencies of naive and experienced hybrids. Naive individuals were starved for 24 hours in 100-liter aquaria before minnows were introduced. Minnows that were not eaten within 30 minutes were removed. This procedure was repeated daily until the hybrid ate its first minnow. On the day the first minnow was consumed, we recorded the time from prey introduction to capture. Times to capture for these naive fish were compared to times to capture for experienced hybrids (1–14 days on a fish diet). We also compared the number of strikes per capture for 25 naive and 25 experienced hybrids (170 mm) that were given 60-mm minnows.

Diet Conversion in Aquaria

During 5-day experiments in a 700-liter aquarium (19–21 C), 40 minnows or bluegills that spanned the optimal size were introduced to 40 naive hybrids (150 or 170 mm) that had been starved 24 hours. The smaller hybrids were given 51–60-mm minnows or 31–40-mm bluegills; the larger hybrids were given 61–70-mm minnows or 41–50-mm bluegills. Every 12 hours, enough prey were added to maintain a density of 40 prey per tank (57/m^3). Twenty hybrids were removed daily and the proportion that had eaten fish was determined by pumping (days 2 and 4) or dissecting (days 1, 3, 5) the stomachs. Fish whose stomachs were pumped were returned to the aquarium; dissected fish were replaced from stock tanks in the same proportion (naive:experienced) revealed by stomach analyses. This insured no change in group learning conditions. For 150-mm hybrids, there were three experiments with minnows and two with bluegills; for 170-mm predators, there were two experiments with minnows and three with bluegills. In the first bluegill experiment conversion by hybrids was low; therefore, sampling was extended to 9 days in subsequent experiments.

Diet Conversion in Ponds

Two diet conversion experiments were conducted in 0.05-hectare ponds at London Fish Farm, Ohio. Ponds were 1.5 m deep and contained a moderate (about 18%) bottom cover of macrophytes (average density, about 40 stems/m^2). Reed canary grass (*Phalaris arundacea*) and terrestrial grasses grew out of the water within 1 m of pond margins; *Chara* spp. was widely distributed throughout the ponds. Secchi disc readings always exceeded 1.5 m (N = 10) and oxygen was always above 12 mg/liter. A maximum-minimum thermometer, submerged to a depth of 1 m, was read every other day. Mean water temperatures were 23 C during the first experiment (termed the August experiment) and 17 C for the second experiment (termed the October experiment).

We stocked each of five ponds with 125 tiger muskellunge between 120 and 130 mm at the beginning of the August experiment and with 124 between 160 and 175 mm at the beginning of the October experiment. Two ponds contained bluegills; three ponds contained fathead minnows (*P. promelas*). For each prey type, two ponds were stocked with 250 prey per pond every other day; density increased from 0.25 to 1.9 prey/m^3 during the course of the experiment. These densities were somewhat higher than inshore prey densities in Ohio reservoirs (R. F. Carline and R. A. Stein, unpublished data). Length ranges of minnows and bluegills spanned the optimal sizes for hybrids. For the August and October experiments, respectively, mean lengths of minnows were 53 mm (range 36–60 mm) and 59 mm (31–90 mm), and mean lengths of bluegills were 32 mm (21–45 mm) and 37 mm (21–55 mm). The fifth pond contained at least 10,000 minnows (range 16–80 mm), or about 10 prey/m^3, for the duration of

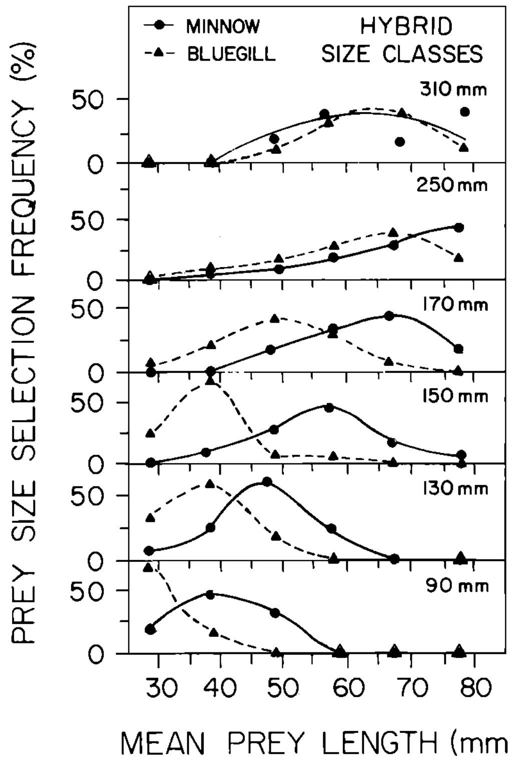

FIGURE 1.—*Proportion of times experienced tiger muskellunge chose different sizes of minnows or bluegills during 20 trials run in 100-liter aquaria. For each predator size class, hybrids were given a choice of six prey-length classes of minnows or bluegills.*

both experiments. This pond was used to determine the ability of tiger muskellunge to convert from pellets to minnows in the presence of particularly abundant prey. At least 100 prey from each pond were measured at the beginning and end of each 14-day experiment.

Naive hybrids, obtained from Kincaid Fish Farm, were stocked in the ponds; prey were added the next day. The percentage of hybrids converting to fish was determined from a sample of 15 per pond, obtained by seining on days 1, 3, 5, 7, 11, and 14. Sample fish were weighed, measured, and dissected. Gut contents were identified; minnows and bluegills were measured.

Results

Prey-Size Selection

Size of prey selected by experienced hybrids increased with predator size (Fig. 1). Lengths of prey offered were not large enough to ade-

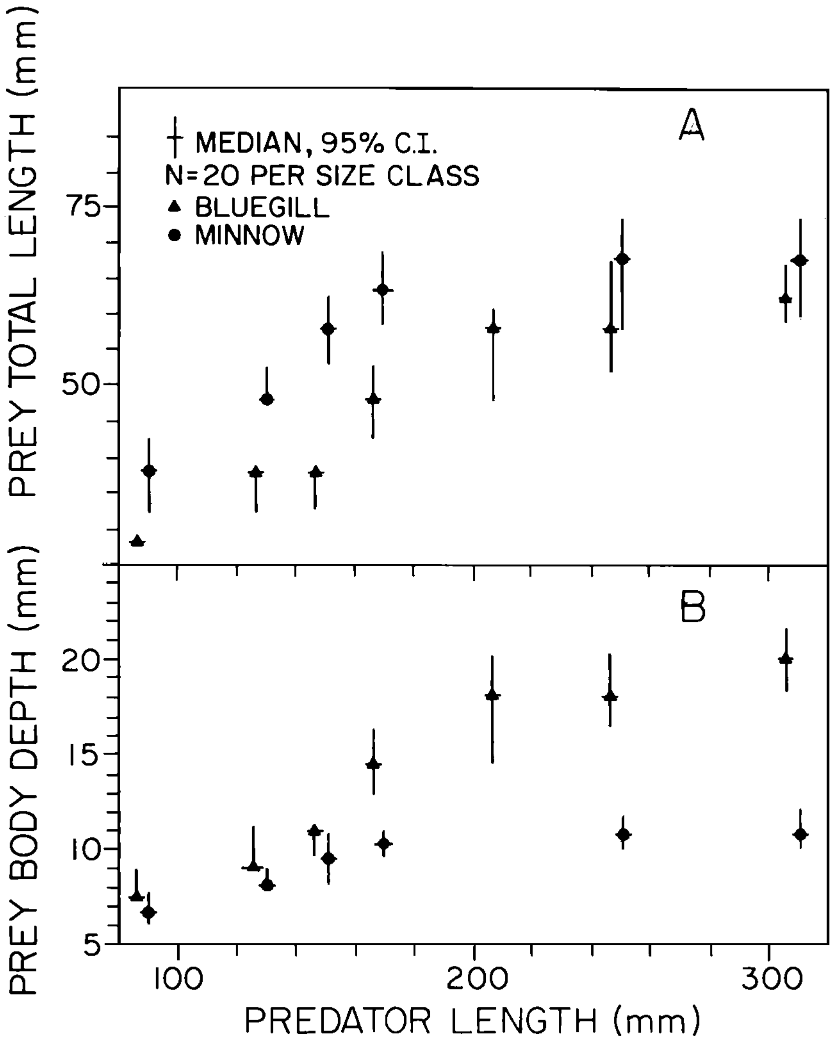

FIGURE 2.—*Median lengths and body depths of minnows and bluegills chosen by different sizes of experienced tiger muskellunge in size-selection experiments. To convert body lengths* (BL) *to body depths* (BD) *we used the equation: minnows, BD = 1.13 + 0.14*BL, N = *60,* r = *0.91; bluegills,* BD = *3.38 + 0.36*BL, N = *60,* r = *0.98. Confidence intervals for medians were calculated by means of Walsh averages (Hollander and Wolfe 1973).*

quately determine preferred sizes of 250- and 310-mm hybrids. Predators, 90 to 170 mm, most frequently selected minnows 37–43% of their mean length and bluegills 25–30% of their length. However, when prey size selected was measured in terms of body depth rather than length, hybrids selected larger bluegills than minnows (Fig. 2). While prey length provides a convenient variable for measuring prey size selection, body depth may be equally important in influencing predator choice.

Cost/benefit analysis (H_t/Wt) was useful in explaining size-selection results. Cost of handling prey increased with prey length; prey of a given size were handled in less time by large predators than by small ones (Fig. 3). Handling times were longer for bluegills than for minnows of the same length. When these handling times are incorporated into cost/benefit calculations ($H_t Wt$), it is apparent that the range of "profitable" prey sizes (low handling costs per food return) broadens as these predators grow (Fig. 4). The lowest point on each curve, which represents the theoretical optimal prey size in

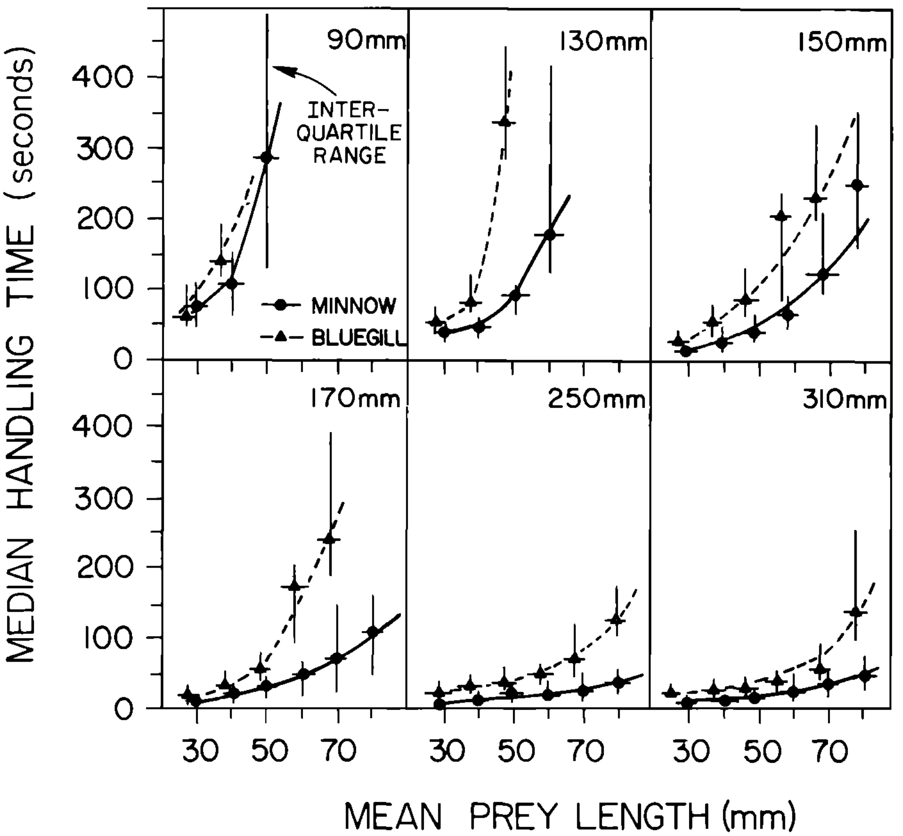

FIGURE 3.—*Handling time as a function of the total length of bluegills and minnows for six length classes of experienced tiger muskellunge (indicated in the upper right-hand corner of each panel).*

terms of energetics, was about 40% of total length of tiger muskellunge for minnows and about 30% of predator total length for bluegills. The shape of a *C/B* curve provides a relative measure of diet breadth (Werner 1974). Tightly folded curves suggest a narrow range of profitable prey sizes or narrow diet breadth, whereas broad *C/B* curves indicate a wide diet breadth. Clearly, for small (90, 130 mm) predators, the curve was tightly folded, and a relatively small increase in prey length beyond the minimum H_t/Wt resulted in a large increase in handling costs per food return. In hybrids longer than 170 mm, *C/B* ratios remained low over a wide range of prey lengths. Thus, diet breadth increased gradually as predator size increased.

Hybrid Behavior

Diet history influenced predatory behavior of tiger muskellunge in aquaria. Experienced hybrids captured minnows more quickly than did their naive counterparts (Mann-Whitney *U*-test, $P < 0.025$, $N = 90$). Median time to capture by experienced hybrids was 75 seconds (range 5–600 seconds, $N = 77$) compared with 540 seconds (range 10–740 seconds, $N = 13$) for naive predators. Thus, some learning may have occurred as these predators converted to live food. Experienced hybrids had fewer strikes per capture than naive ones, although this difference was not quite significant (mean, 1.3 and 2.0 strikes/capture, respectively, *t*-test, $P = 0.15$). Once hybrids had eaten their first fish, strikes per capture in subsequent predation acts did not change (Mann-Whitney *U*-test, $P > 0.05$). Overall, experienced predators captured prey more efficiently than naive ones.

Diet Conversion

In laboratory experiments a large portion of naive hybrids converted to minnows or bluegills

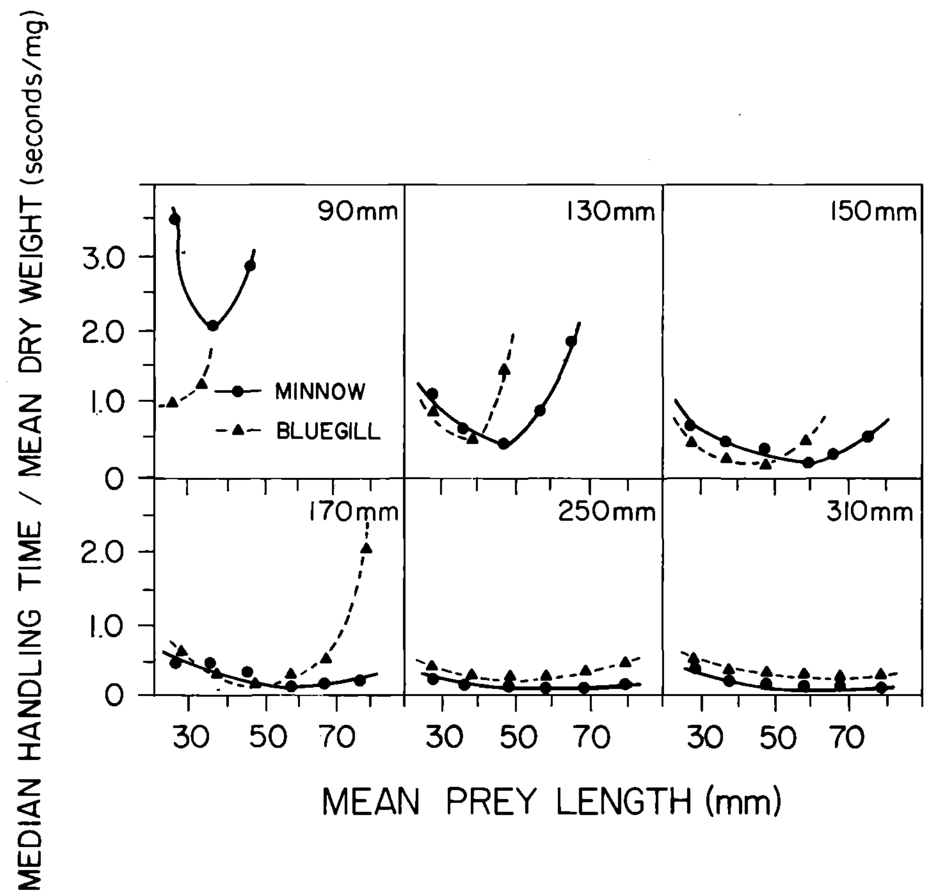

FIGURE 4.—*Cost/benefit curves (handling time/dry weight), as a function of minnow or bluegill length, for six length classes of experienced tiger muskellunge (indicated in the upper right-hand corner of each panel).*

after 5 to 9 days, but conversion to minnows was more rapid than to bluegills (arcsin transformation, t-test, $P < 0.05$; Fig. 5). By day 5, 90–95% of both hybrid sizes had converted to minnows, whereas only 70–85% had converted to bluegills (Fig. 5). By day 7, 80% of the 150-mm hybrids had converted to bluegills and by day 9, nearly 100% of 170-mm predators had converted. The conversion by 170-mm hybrids was generally faster than that of 150-mm fish.

In both the August and October pond experiments, naive hybrids converted rapidly to minnows. Because conversion rates did not differ among the three minnow ponds (Friedman's test, $P > 0.05$; Fig. 6), data were combined for each experiment. More than 70% of the hybrids had converted to minnows by day 5 and more than 90% by day 14. In two of the ponds, minnow densities ranged from 0.25 to 1.9 prey/m^3; in the third pond, densities were 10 prey/m^3. Thus, prey densities within this range did not influence conversion rate of naive hybrids to minnows. In both experiments, naive tiger muskellunge converted slowly to bluegills and no differences existed between ponds within either experiment (Friedman's test, $P > 0.05$; Fig. 6). No predator ate a bluegill before day 3. Less than 10% had converted by day 5 and only 28–53% by day 14.

In both experiments, conversion to bluegills was highest on day 14, after ponds had been partly drained overnight. This reduction in pond volume prevented access by bluegills to inshore cover, possibly increasing their vulnerability to predation. Percentages of hybrids converting to bluegills were much lower than

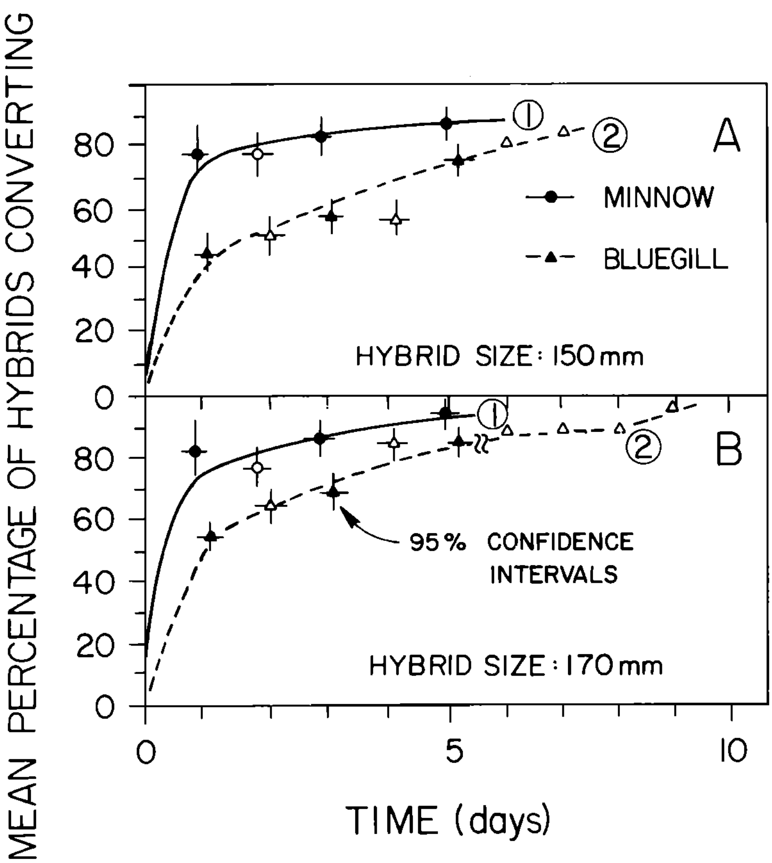

FIGURE 5.—*Percentage of naive tiger muskellunge converting to minnows and bluegills through time in a 700-liter aquarium. The partition in the bluegill curve (panel B) separates data taken during regular sampling (left of partition) and data taken from extended sampling (right of partition). For curves A_2 and B_1, each value plotted represents two experiments (N = 20/sample day); for curves A_1 and B_2 (left of partition), each value plotted represents three experiments (N = 20/sample day). For B_2 to the right of the partition N_{Total} = 38 hybrids. Open symbols (○, △) represent conversion determination by inspection or stomach pumping; closed symbols (●, ▲) represent determination by dissection.*

percentages of those converting to minnows during both pond experiments (Friedman's test, $P < 0.001$). Even though a large proportion of hybrids in bluegill ponds were not eating fish, they did consume benthic invertebrates, including mayfly nymphs (*Baetis*), dragonfly naiads, snails, leeches, algae, cladocerans, and detritus. Growth of hybrids was greater in ponds stocked with minnows compared to those stocked with bluegills in both experiments (nonparametric multiple range test, $P < 0.05$, Zar 1974; Fig. 7). No differences in these variables were found among the three minnow or between the two bluegill ponds, within either experiment (Friedman's test, $P > 0.05$); growth differences appeared to be related to the ability of these predators to convert to bluegills or minnows.

We stocked ponds with bluegills and minnows whose length range spanned sizes most frequently selected by hybrids in laboratory experiments, so that conversion rates by hybrids would not be biased by prey length. In both experiments, hybrids consumed bluegills that were smaller than the most abundant size groups (Fig. 8). In contrast, hybrids ate minnows that were generally similar in size to the most abundant size groups. These distributions do not provide the best test of prey size selection by predators, because predator lengths increased during experiments.

To determine if hybrids of a given size were

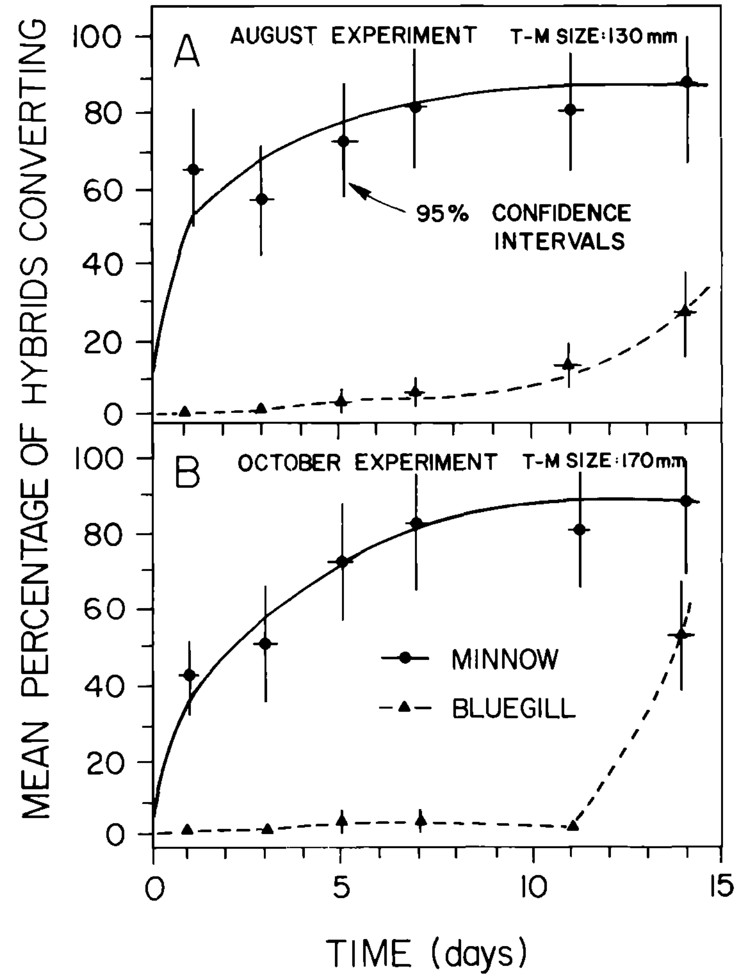

FIGURE 6.—*Percentages of two sizes (130, 170 mm) of naive tiger muskellunge (T-M) converting to minnows and bluegills in 0.05-hectare ponds. For the minnow ponds, each point represents 45 predators (15 per pond); for the bluegill ponds, each point represents 30 predators (15 per pond). Lines were fitted by inspection.*

selecting a given size group of prey, we plotted hybrid length against the ratio of length of prey consumed to mean length of prey stocked. If hybrids selected prey at random, this ratio should remain at unity irrespective of predator length. We used only data from ponds with high densities of minnows (about $10/m^3$) because these wide length ranges of prey provided the best opportunity for size-selective predation by hybrids. Length ratios (prey consumed to prey available) increased with predator length when data from both experiments were combined, suggesting that as hybrids increased in length they chose larger prey (Fig. 9). We then recomputed ratios using length of prey most frequently selected in laboratory experiments divided by mean size of stocked prey and plotted these on the same graph. If hybrids chose similar sizes of minnows in the laboratory and ponds, data points should be clustered about those lines (Fig. 9, lines A and B). Lengths of minnows eaten by the smaller hybrids (149–152 mm) in the August experiment approximated predicted ratios; however, larger deviations might have resulted if a wider size range of minnows were available. Larger hybrids (161–197 mm) consumed prey that were smaller than predicted from the laboratory data; 39 of 41 length ratios were less than would be expected based on size-selection experiments.

These results were not unexpected because

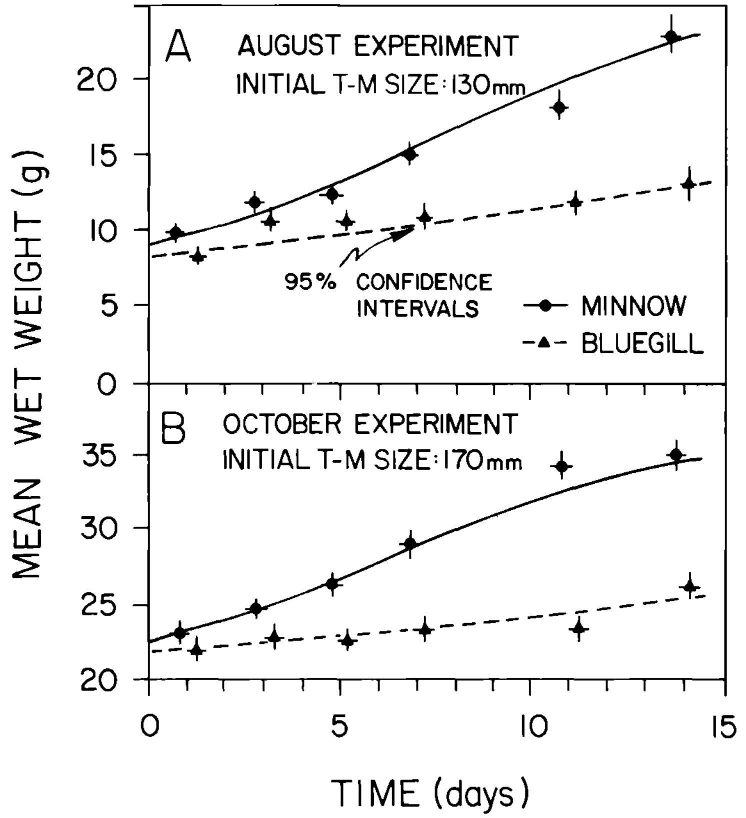

FIGURE 7.—*Growth of tiger muskellunge (T-M) in 0.05-hectare ponds with minnows and bluegills as prey. For the minnow ponds, each point represents 45 predators (15 per pond); for the bluegill ponds, each point represents 30 predators (15 per pond). Lines were fitted by inspection.*

cost/benefit curves for hybrids less than 150 mm were tightly folded (Fig. 3), suggesting that only a restricted size range of prey is profitable. Cost/benefit curves for hybrids over 170 mm were rather flat, indicating that these larger predators would derive approximately equal benefit from a relatively wide range of prey sizes. While these results indicate good correspondence between predictions from optimal foraging theory and field results, theory could have been more rigorously tested in our experiments if a wide range of prey size groups had been stocked in similar proportions.

Discussion

Prey Selection

Pond experiments broadly confirm laboratory findings concerning optimal foraging by tiger muskellunge. The congruence is particularly marked for naive hybrids presented with minnow prey. Similar confirmation of foraging theory has occurred in a variety of other studies (Kisalalioglu and Gibson 1976; Stein 1977; Werner 1977). Thus, laboratory-derived cost/benefit ratios may be useful in predicting optimal prey size and type.

However, not all of our laboratory results were borne out in the field. Bluegill H_t/Wt curves did not predict the small sizes that were chosen by tiger muskellunge in ponds. Because hybrids converted so slowly to bluegills, their hunger levels were probably much higher than those in the minnow ponds. As hunger increases, predators generally become less selective in their choice of prey (Emlen 1968; Ware 1972); this could explain the lack of size selection for bluegills. In addition, if pursuit and search contributed substantially to the cost term for tiger muskellunge preying on bluegills, H_t/Wt may not accurately predict optimal size. In similar experiments in small ponds, Schneider (1975) found that walleyes (*Stizostedion vitreum*) reared on artificial diets also chose the smallest

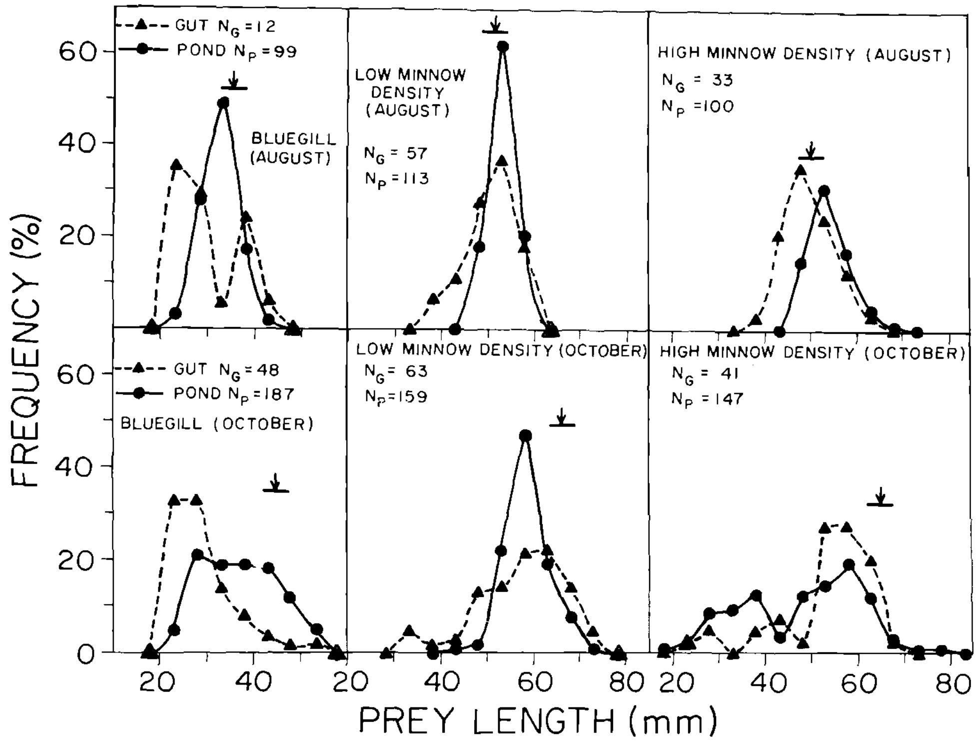

FIGURE 8.—*Length-frequency distributions of bluegills and minnows at the start of the August and October pond experiments and of fish removed from hybrid guts. Sample sizes for available prey and those in guts are represented by* N_P *and* N_G, *respectively. Arrows indicate the length of prey most frequently selected in laboratory experiments, 25% of mean hybrid length for bluegills and 37% for minnows. Horizontal adjacent bars under the arrows represent ±SD of mean hybrid length times the appropriate proportion, 25 or 37%.*

bluegills available (14–26% of their total length). Thus, high hunger levels of predators in the pond environments, coupled with no consideration of the costs of pursuit or search, may explain disagreements between our laboratory-generated optimal size predictions and pond results.

Tiger muskellunge captured and handled minnows more efficiently than they did bluegills. This was due, in part, to the difference in morphology between the two prey types. Minnows are cylindrical and soft-rayed; bluegills are deep-bodied and spiny-rayed. Body length and body depth appeared to be important factors in selecting and handling prey. In related work, Johnson (1969) concluded that body depth of bluegills influenced selection by northern pike. In preliminary experiments, we found that hybrids handled spineless bluegills nearly as efficiently as minnows, suggesting that spines contribute to the costs of predation. Northern pike (110–335 mm) prefer soft-rayed fish over spiny-rayed fish in laboratory aquaria (Beyerle and Williams 1968), swimming pools (Mauck and Coble 1971), and hatchery ponds (Mauck and Coble 1971; Weithman and Anderson 1977). Long handling times may explain why esocid food studies show that spiny-rayed fish are less desirable than soft-rayed ones. Spiny-rayed fish are more costly prey, in terms of both energy required for ingestion and risk of mortality; spines can puncture throat or stomach linings (of 290 hybrids feeding on bluegills, 14 died).

Conversion by Tiger Muskellunge

Experiments in laboratory aquaria and hatchery ponds both demonstrated that naive tiger muskellunge converted more rapidly to minnows than to bluegills. Most hybrids were able to convert within the first 7 days in the laboratory. Confinement of prey in aquaria

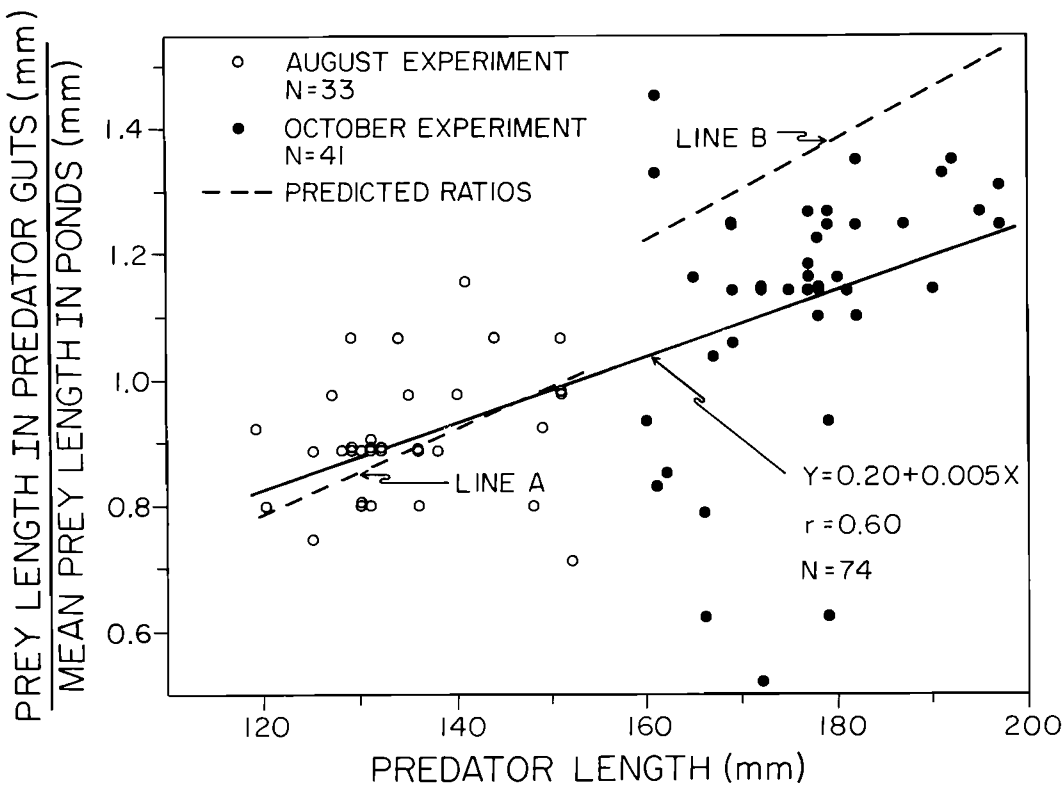

FIGURE 9.—*Relationship between predator length* (X) *and the ratio* (Y) *of prey length in predator guts to mean prey length in ponds for the August and October pond experiments. Only data from high-density minnow ponds are given. Lines A and B were calculated from data derived from prey size-selection experiments when ratios equalled 0.37 times predator length divided by mean prey length in ponds. Lines A and B are offset because mean prey length in ponds differed between experiments (see Fig. 8).*

may have facilitated capture by hybrids; predators often trapped prey in aquarium corners. Hybrids converted to minnows at similar rates in both laboratory aquaria and ponds; however, conversion to bluegills was far slower in the ponds than in the laboratory. From preliminary observations, bluegills appear more difficult to capture in the pond situation; in the laboratory, hybrids required fewer strikes/capture (mean = 2.0, range 1–13, $N = 30$) than in the pond (mean = 4.3, range, 1–5, $N = 12$). In turn, differences for minnows between laboratory (mean = 1.3, range 1–3, $N = 30$) and pond (mean = 1.5, range 1–2, $N = 5$) were not as great. Apparently, confinement in small aquaria modified the escape tactics of bluegills more dramatically than those of minnows. In ponds, bluegills may well have avoided predators owing to their superior maneuverability compared to the more fusiform minnows (Alexander 1967). In addition to superior maneuverability, bluegills reduce their vulnerability by swimming in schools deep in the water column, near vegetated areas (Hall and Werner 1977), whereas minnows in our experiments remained in open water, seeking little refuge. Because of these habitat differences, bluegills may have been less available to predators than minnows. Consistent with this description of behavior and habitat use by bluegills was the marked increase in predation rate on day 14 of the pond experiments. On day 13, ponds were partly drained, dense macrophytes along the pond margin no longer provided refuge for bluegills, and the percentage of tiger muskellunge converting on the last day increased from 13 to 28 in the August experiment and 0 to 53 in the October experiment.

Because these predators converted more rapidly to minnows than to bluegills, they grew faster in minnow ponds than in bluegill ponds. Predators with food in their stomachs had either fish or invertebrates, seldom both; those not eating fish had small organisms in their stomachs, such as cladocerans and benthic insects, and stomachs were less full than those of piscivores. Beyerle (1978) found that age-II northern pike in bluegill lakes fed largely on insect larvae, crayfish, and tadpoles despite an abundance of edible-sized bluegills. Our results suggest that when centrarchids dominate the forage base in reservoirs, tiger muskellunge will be unsuccessful predators during the first 2 weeks after stocking. Under stressful conditions these fish may have lower survival than those stocked into lakes with a cyprinid or clupeid forage base.

In experiments similar to ours, when pellet-reared walleyes were combined with bluegills or minnows in 0.3-hectare ponds, 70–90% of the mortality occurred within 6 months after stocking and appeared to be associated with handling and adaptation to a new environment (Schneider 1975). Annual survival in bluegill and minnow ponds was 53 and 79%, respectively. After adjustment of growth rates for density, walleyes were 41% heavier in the minnow pond than in the bluegill pond 1 year after stocking (Schneider 1975). Thus, our experiments support Schneider's findings in suggesting that pellet-reared (naive) fishes may have difficulty preying on bluegills.

In addition to prey type, conversion of naive predators to live forage will be influenced by prey size. Cost/benefit calculations suggest that larger hybrids would consume a wider size range of prey than smaller ones once stocked in the wild. Food habit studies of young-of-year walleyes (60–390 mm) in Lake Erie support this contention. Large walleyes consume a wider range of prey sizes than smaller ones (Parsons 1971). With more prey available to them, larger hybrid muskellunge should enjoy better growth and survival than their smaller counterparts. In support of this suggestion, stocking success of 50-mm northern pike appeared directly related to availability of small forage fish, whereas these correlations were not evident with 377-mm northern pike (Flickinger and Clark 1978).

Results from our study and others suggest that prey type and size may influence stocking success of predators. Naive tiger muskellunge stocked in centrarchid-dominated reservoirs may exhibit poor survival due to their failure to convert to live forage. We believe that naive hybrids stocked in systems with a cyprinid or clupeid forage base would quickly convert to live forage and survival would be governed by other factors. Stocking programs using small predators must be precisely coordinated with size and abundance of prey owing to the narrow size range of vulnerable prey. Agencies can afford to be less precise in their choice of stocking sites for large esocids; wide diet breadths coupled with reduced susceptibility to predators improves the likelihood of high rates of growth and survival.

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References

Alexander, R. McN. 1967. Functional design in fishes. Hutchinson, London, England.

Beyerle, G. B. 1978. Survival, growth, and vulnerability to angling of northern pike and walleyes stocked as fingerlings in small lakes with bluegills or minnows. American Fisheries Society Special Publication 11:135–139.

Beyerle, G. B., and J. E. Williams. 1968. Some observations of food selectivity by northern pike in aquaria. Transactions of the American Fisheries Society 97:28–31.

Emlen, J. M. 1966. The role of time and energy in food preference. The American Naturalist 100:611–617.

Flickinger, S. A., and J. H. Clark. 1978. Management evaluation of stocked northern pike in Colorado's small irrigation reservoirs. American Fisheries Society Special Publication 11:284–291.

Graff, D. R. 1978. Intensive culture of esocids: the current state of the art. American Fisheries Society Special Publication 11:195–201.

Hall, D. J., and E. E. Werner. 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. Transactions of the American Fisheries Society 106:545–555.

HOLLANDER, M., AND D. A. WOLFE. 1973. Nonparametric statistical methods. John Wiley and Sons, New York, New York, USA.

JOHNSON, L. D. 1969. Food of angler-caught northern pike in Murphy Flowage. Wisconsin Department of Natural Resources Technical Bulletin 42.

JOHNSON, L. D. 1978. Evaluation of esocid stocking program in Wisconsin. American Fisheries Society Special Publication 11:298–301.

KISALALIOGLU, M., AND R. N. GIBSON. 1976. Prey 'handling time' and its importance in food selection by the 15-spined stickleback, *Spinachia spinachia*. Journal of Experimental Marine Biology and Ecology 25:151–158.

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.

PARSONS, J. W. 1971. Selective food preferences of walleyes of the 1959 year class in Lake Erie. Transactions of the American Fisheries Society 100:474–485.

SCHNEIDER, J. C. 1975. Survival, growth, and food of 4-inch walleyes in ponds with invertebrates, sunfishes, or minnows. Fisheries Research Report 1833. Michigan Department of Natural Resources, Ann Arbor, Michigan, USA.

SCHOENER, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369–404.

STEIN, R. A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. Ecology 58:1237–1253.

WARE, D. M. 1972. Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density, and prey size. Journal of the Fisheries Research Board of Canada 29:1193–1201.

WEITHMAN, A. S., AND R. O. ANDERSON. 1977. Survival, growth, and prey of Esocidae in experimental systems. Transactions of the American Fisheries Society 106:424–430.

WERNER, E. E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. Journal of the Fisheries Research Board of Canada 31:1531–1536.

WERNER, E. E. 1977. Species packing and niche complementarity in three sunfishes. The American Naturalist 111:553–578.

WERNER, E. E., AND D. J. HALL. 1974. Optimal foraging and the size selection of the bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042–1052.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.