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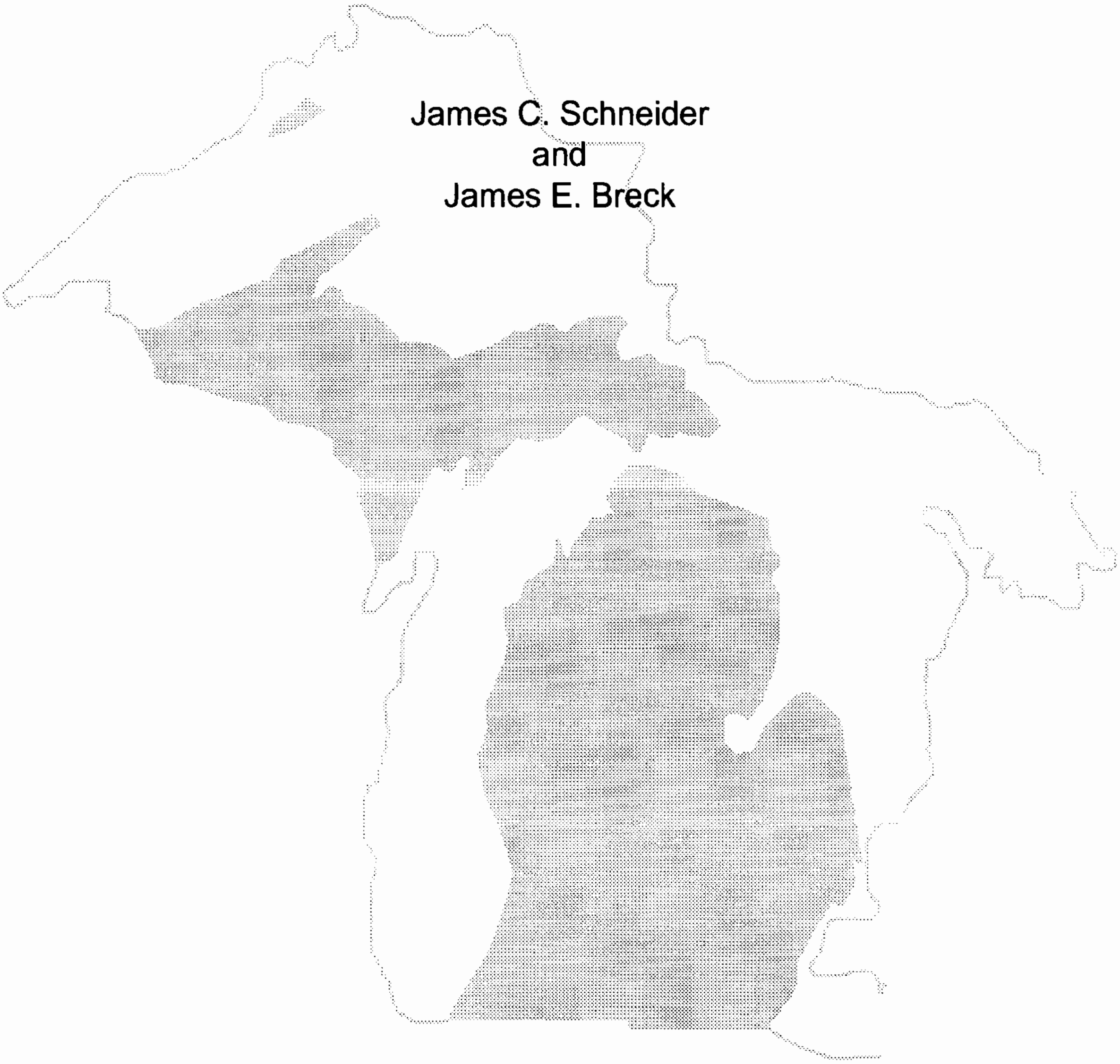

FISHERIES DIVISION
RESEARCH REPORT

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# OVERWINTER CONSUMPTION OF BLUEGILLS BY WALLEYE AND YELLOW PERCH

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# Overwinter Consumption of Bluegill by Walleye and Yellow Perch

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*Abstract*.–The potential for predation by walleye or yellow perch to improve stunted bluegill populations was evaluated by lake observations combined with pond and laboratory experiments. There was substantial predation on age-0 bluegill by adult yellow perch during winter and fall in Michigan lakes. The highest calculated consumption rate, as percent of predator weight per day (%BW/d), was 0.43 for Cedar Lake. For two lakes, Blueberry Pond and Cassidy Lake, total December-March consumption of bluegill was estimated at 3,500/hectare and 8,600/hectare, respectively. Walleye also ate appreciable numbers of bluegill during fall in some lakes. Overwinter studies in experimental ponds measured the predatory effect of adult yellow perch and juvenile walleye on bluegill. Survival of age-0 bluegill in ponds without predators (controls) averaged 90±6% ($N$ = 7, ±SD) over four winters; survival was reduced to 61±16% ($N$ = 9) in ponds with predators. In a fifth winter experiment, bluegill survival averaged 19±6% ($N$ = 3) in control ponds and 3.1±2.4% ($N$ = 4) in walleye ponds. Predation on age-0 bluegill in the ponds was estimated to be 0.38±0.10 %BW/d for walleye and 0.27±0.08 %BW/d for yellow perch. In parallel laboratory experiments at 4.4°C, consumption rates were 0.11 %BW/d for adult yellow perch and 0.34 %BW/d for small walleye, and maintenance rations were 0.075 %BW/d and 0.32 %BW/d, respectively. Complete gastric evacuation of a 1% bluegill meal was estimated to take 41 h for yellow perch and 77 h for walleye. Most, but not all, predators lost weight in ponds or tanks at approximately 4°C. Laboratory experiments at higher temperatures, typical of fall and spring, indicated higher consumption and metabolic rates. Measurements of predator gape and bluegill body depth and length were also taken to determine predatory capabilities of walleye and yellow perch.

In Michigan lakes, young-of-the-year bluegill, which are usually less than 50 mm TL during fall and winter, may be ingested by walleye of any size likely to be present and by yellow perch larger than 158 mm TL. We conclude that fingerling walleye and adult yellow perch consume many age-0 bluegill during winter when they co-occur. When appropriate-sized predators are present at a sufficient biomass, their predation can help control bluegill stunting.

Populations of small-sized, slow-growing (stunted) bluegill *Lepomis macrochirus* that provide little or no sportfishing occur in many southern Michigan lakes, and throughout the midwest, and are a major concern to fisheries managers. Studies on the population biology of bluegill have demonstrated that the species has high reproductive potential, density-dependent growth, and density-independent mortality after about age 2 (Schneider 1971; Beyerle 1977; Latta and Merna 1977). Consequently, bluegill often produce a large year class, and unless drastically reduced by mortality before age 2, the large year class will persist for up to 6 years in a stunted condition. Furthermore, individuals are relatively invulnerable to even large piscivores such as northern pike *Esox lucius* and largemouth bass *Micropterus salmoides* after reaching a length of 100-125 mm total length (TL), and are usually not a preferred prey even at smaller sizes (Beyerle and Williams 1968; Wahl and Stein 1988). Consequently, unless these piscivores have uncommonly high densities, they cannot consume enough bluegill to significantly reduce competition among bluegill and induce satisfactory growth rates in stunted bluegill populations (Hooper et al. 1964; Beyerle 1971).

There may be potential for both small and large percids to affect bluegill control in some lakes. During winter, lethargic young bluegill school in deep water and, in at least one lake, are heavily preyed upon by yellow perch *Perca flavescens* (Moffett and Hunt 1943). Walleye *Stizostedion vitreum*, like yellow perch, feed even at cold temperatures and could conceivably eat many age-0 and age-1 bluegill - perhaps enough to control bluegill recruitment and improve bluegill growth. Bluegill could also be an important energy source for percids.

This idea has been partially tested in simple communities in which only bluegill and walleye were present (Schneider 1975; Forsythe 1977; Beyerle 1978; Forsythe and Wrenn 1979; Beard 1982; Beyerle 1983). In these experiments, walleye did eat bluegill and were able to survive and grow satisfactorily. However, walleye generally survive and grow better in communities in which minnows, yellow perch, or large invertebrates are available (Schneider 1975; Beyerle 1978; Schneider 1983). Thus in naturally diverse waters, walleye may select other food types over bluegill and not consume enough bluegill to control recruitment. Indications from the simple community experiments (in which bluegill were expected to be severely stunted) were that walleye predation would not be intensive enough to significantly control bluegill recruitment and improve growth. However, walleye may be more effective agents in situations where less control is required.

Theoretically, walleye and yellow perch have the potential to eat significant numbers of small bluegill. Given certain assumptions about the likely rate of walleye growth and survival, we calculated from a bioenergetics model that large walleye fingerlings stocked at 37 per hectare might consume 15,430 age-0 bluegill per hectare per year (if walleye ate only bluegill). Adult yellow perch, which are abundant in some lakes, could also eat substantial numbers of small bluegill. Based on our knowledge of bluegill density and dynamics, this might be enough predation (cumulatively over a period of several years) to improve the growth of bluegill populations in some stunted lakes.

One area of uncertainty in the calculation was how much predation would occur during Michigan's long overwinter period, when young bluegill might be most vulnerable. Little work has been done on consumption by young-of- the-year walleye or adult yellow perch at very cold temperatures (Sullivan 1986). Some insights can be gained by examining existing information on: (a) winter food consumption by yellow perch; (b) overwinter walleye growth; (c) walleye maintenance ration; and (d) winter gastric evacuation rate:

a) In the lab, at 10°C, fingerling yellow perch given minnows in excess consumed an average of 2.5% of their body weight per day (%BW/d) (Schneider 1973a). By linear extrapolation from data at 10 to 23°C, it is likely that perch (and walleye) would eat about 0.4 %BW/d at 4°C.

b) Fingerling walleye or adult yellow perch consuming more than a maintenance ration overwinter should grow. Indications are that winter growth in length or wet weight is negligible (Kelso and Ward 1972; Schneider 1975). However, the possibility of winter growth in terms of dry weight, fat, or calories, with corresponding changes in water content, has not been examined. Negative growth is also possible.

c) Kelso (1972) estimated the maintenance ration for walleye at 4°C to be 0.4 %BW/d. The maintenance ration for adult yellow perch is probably similar to that of walleye.

d) The gastric evacuation rate of walleye at 4°C was studied by Hofman (1969). He reported it took about 6 days for a force-fed adult walleye to clear a meal weighing 1-2 %BW. This averages to about 0.3 %BW/d. Consumption rates of walleye and yellow perch would be limited to the same level, but this is only an approximation, because evacuation rate would probably be more rapid with larger meals (Persson 1986).

The implications from this analysis are that overwinter consumption by walleye and yellow perch would most likely be close to maintenance levels, about 0.4 %BW/d. For a 30-g predator, this would be about 72 bluegill (average 0.2 g) per winter (120 d). The implication from (a) is that consumption could be as high as 150 bluegill per fingerling walleye per winter. Thus the most likely range of consumption is 72-150 bluegill per walleye per winter. Actual rates depend on sizes of walleye, yellow perch, and bluegill; on physiological limitations; on the predator's ability and desire to capture bluegill; and on the abundance of alternate food.

We designed a series of field, pond, and laboratory experiments to quantify consumption of bluegill and constraints on overwinter predation. First, we quantified percid predation on bluegill in Michigan lakes, particularly during the winter period. Second, we measured percid predation in experimental ponds where densities of bluegill and percids could be controlled precisely, both predatory and nonpredatory mortality of bluegill could be estimated, and winter growth of predators could be measured. Third, we directly measured prey consumption and percid growth in laboratory tanks. In addition to these measures of consumption rate, we measured constraints on winter predation due to gastric evacuation rate, maintenance ration, and body morphology. The effect of low temperature on evacuation rate sets a limit on the rate at which food can be processed, and therefore, on the daily number of given-sized bluegill that can be consumed. The maintenance ration specifies the consumption rate required to keep from losing energy. Percid mouth gape and bluegill body depth set limits on the sizes of predators required to ingest bluegill.

In summary, we had two major objectives in this study. The first objective was to estimate overwinter consumption rates of bluegill by walleye and adult yellow perch in lakes, experimental ponds, and laboratory tanks. The second objective was to quantify constraints on overwinter consumption rates by walleye and yellow perch, including gastric evacuation rates, maintenance rations, and the morphological limits imposed by predator mouth gape compared to bluegill body depth. The term "overwinter", as used here, includes late fall and early spring because these seasons also comprise a major portion of the long overwinter period in Michigan when percid growth is minimal but percid predation could be important.

## Consumption Rates in Lakes

### *Methods*

Lakes were sampled in winter, and to a lesser extent fall, with the objectives of (1) quantifying the frequency of percid predation on bluegill and (2) determining size selectivity.

Information on winter and fall diet of yellow perch has been obtained at eight Michigan lakes since 1941, but most of the data were collected since 1985. Winter samples (December-March) were taken through the ice by angling; fall samples (September-October) were collected with trapnets, gillnets, electrofishing, and angling. Stomach contents were either removed by dissection or by flushing (Foster 1977). Food items were identified to the lowest practical taxon, counted, and their total length (TL; all length measures in this paper refer to TL) was estimated when possible. Fish remains were identified to species if possible (bluegill, pumpkinseed *Lepomis gibbosus*, yellow perch, etc.), or to shape (sunfish or slender). For this report the most important statistic is the total of bluegill and pumpkinseed; this will be referred to as sunfish. No green sunfish *Lepomis cyanellus* or other species of sunfish were found in percid stomachs. Length estimates of bluegill prey were multiplied by a factor of 1.1 to compensate for shrinkage during digestion and our tendency to underestimate the original length of incomplete remains. This factor was derived from laboratory digestion experiments on 16 bluegill of known length. Thus, the data presented in this report for bluegill are for estimated live length. Weight of food present in stomachs by taxon was either estimated directly by weighing remains (Gilead and Marble lakes), or computed from mean counts, median lengths, and length-weight regressions (Schneider 1993). The computed estimates were stratified by 25-mm size groups of yellow perch. Average diets by weight (%BW), by lake and season, were obtained by dividing each strata by the corresponding mean weight of yellow perch, then averaging across all size groups. Daily consumption rates (ration, %BW/d) were derived by multiplying %BW by 0.58 for winter samples (40.8 h are required for complete gastric evacuation of a typical meal, see below) and by 1.0 for fall samples (Schneider 1973b).

Information on the fall diet of walleye in lakes where bluegill were common to abundant was obtained at 10 lakes in 1987-93. One of the lakes, Jewett, was sampled intensively. The other 9 lakes, sampled infrequently, were divided into two regional groups: northern (Upper Peninsula) and southern (southern Lower Peninsula). No data were obtained during winter. Walleye were collected by electrofishing or trapnetting in September and October. Stomach contents of Jewett Lake walleye were flushed out; stomach contents of walleye obtained elsewhere were removed by dissection. Analytical procedures were the same as used for yellow perch. The factor used to compute fall %BW/d was 0.75 (18 h for complete gastric evacuation, Swenson and Smith 1973).

## *Results*

Sunfish were an important food item of yellow perch in four out of five lakes sampled extensively in winter (Table 1). In those four lakes, sunfish constituted 59-88% of the food weight and occurred in 13-84% of the yellow perch stomachs. Bluegill far outnumbered pumpkinseeds (390:10) among those specimens fresh enough to be identified to species. Unexpectedly, sunfish were not an important food item for yellow perch from Sugarloaf Lake even though this lake is limnologically and biologically similar to the others. The presence of sunfish in yellow perch stomachs has been observed at six additional lakes where smaller samples were taken. We conclude that yellow perch predation on sunfish is widespread. Although sunfish were an important fraction of the diet, the rate of total food intake during winter was low (Table 1). The average total stomach content was 0.55 %BW, and the average daily ration was 0.32 %BW/d. For sunfish prey only, the corresponding averages were 0.33 %BW and 0.19 %BW/d.

Sunfish were much less important in the fall diet of yellow perch (Table 1). They comprised 0-58% of the food biomass and occurred in 0-11% of the yellow perch stomachs. However, fall samples were not taken from the two lakes with the highest winter feeding rates (Cedar and Cassidy). Sunfish also have been found in small samples taken from two additional lakes not shown in Table 1. The two measures of average rate of food intake, total %BW and total %BW/d, were both 0.55, equal because food turnover (evacuation ) rates are about 24 h at fall temperatures.

A perch as small 78 mm had eaten a sunfish (27 mm), but sunfish were uncommon in perch less than 152 mm. Generally, the number of sunfish eaten increased with yellow perch size. At Cassidy Lake, large yellow perch (254-276 mm) contained an average of 3 bluegill apiece.

Male and female yellow perch over 152 mm long consumed sunfish at similar rates during winter. The average number of sunfish per stomach was 0.674 for males (*N*=434) and 0.714 for females (*N*=498), and the frequency of occurrence was 35.5% and 33.0%, respectively.

Yellow perch selected small bluegill (Figure 1). Of 239 bluegill measured, 92% were less than 50 mm long and must have been less than 12 months old. Size range was 16-85 mm, with 34% between 27 and 33 mm. Bluegill over 50 mm long were rarely found in perch less than 225 mm long.

Sunfish were important in the fall diet of walleye in Jewett Lake and the three southern lakes (Table 1). In these lakes, 36-37% of the diet by weight was sunfish, which occurred in 20-35% of the stomachs. Few sunfish were found in walleye stomachs from northern lakes, perhaps because yellow perch and minnows were more available or preferred alternatives. All sunfish which could be identified to species were bluegill, but walleye are known to eat pumpkinseed (Schneider 1975).

Size of bluegill eaten generally increased with walleye size (Figure 2). Even so, the largest walleye ate some small bluegill. Most (62%) of the bluegill eaten were less than 50 mm; the largest was 137 mm.

## Consumption Rates in Ponds

### *Methods*

We measured overwinter consumption of age-0 bluegill by juvenile walleye and adult yellow perch in replicated pond experiments under conditions which should maximize consumption. The ponds had little vegetation which could afford the bluegill a structural refuge from predators. There were no alternate forage fish for the predators and the ponds contained little alternative food other than naturally occurring zooplankton. Because of recent drawdowns, benthos was limited to sparse numbers of midges and to crayfish that were too large for the predators to eat. Each experiment involved one to three control ponds, which contained only bluegill, and two to four treatment ponds, which contained both bluegill and predators.

Pond experiments were conducted during the five winters of 1988-93 at the Saline Fisheries Research Station, Saline, Michigan. The ponds are each about 0.2 ha in area, have mean depths of about 1 m and the volumes shown in Tables 2 and 3. Each pond can be individually drained and censused.

A target stocking density of small bluegill (0.40 g/m$^3$ in most experiments) was chosen to induce maximum consumption by walleye (Swenson 1977). The number of age-0 bluegill required to produce a density of 0.40 g/m$^3$ was calculated from the average weight of age-0 bluegill and pond volume. Required number of juvenile bluegill were reared in ponds, collected by draining, counted, and stocked into the experimental ponds in November-December of each year. In most years, average total length of age-0 bluegill at stocking was 28 mm and average weight was 0.24 g (Tables 2 and 3). They were small enough to be readily swallowed by the predators (Figures 1 and 2; Knight et al. 1984). Stocking rates were equivalent to 10,740-21,000 bluegill/ha and 47-111 predators/ha. Relative to densities found in lakes, we slightly overstocked the predators to avoid working with small numbers of fish per pond. For lakes, a walleye stocking rate of 30 large fingerlings/ha has been recommended for general use (Laarman and Schneider 1986).

At pond draining in early spring all surviving bluegill were counted and their bulk weight determined. The average final bluegill weight for each pond was computed by dividing total weight of surviving bluegill by number of survivors. Individual TL (to the nearest mm) was measured on a random subsample. In some years individual measurements of length, wet weight, and dry weight were made on a subsample stratified by length (three fish per 1-mm size group). Dry weight was measured after drying to constant weight at 55°C. Length and weight data were used to develop weight-length regressions (Appendix 2) and compute relative weight (Murphy et al. 1991).

In order to estimate the number of bluegill consumed by predators in the ponds, one must account for both predatory and nonpredatory deaths. We used an analysis similar to the Baranov catch equation (which partitions total mortality between fishing and natural mortality, Ricker 1975) to partition total mortality between predatory and nonpredatory sources (Appendix 1). To summarize our method, nonpredatory mortality rates were estimated for control ponds and total mortality rates were estimated for ponds with predators. We subtracted instantaneous *nonpredatory* mortality rate from instantaneous *total* mortality rate to estimate instantaneous *predatory* mortality rate. Number of bluegill lost to predators ($N_{p,t'}$) was estimated as total number of bluegill lost multiplied by the ratio of instantaneous rates of predatory and total mortality.

A second method of estimating predatory mortality assumed that predators were consuming a constant number of bluegill per day rather than a constant daily proportion of survivors (Appendix 1). Differences between the two methods of estimating predatory mortality tend to increase as mortality increases.

Consumption of bluegill was expressed as the daily number lost per predator and per gram of predator. Average number of bluegill consumed per predator per day ($N_c$) was calculated:

$$N_c = N_{p,t'}/(Pt')\,, \qquad (1)$$

where $P$ is the geometric mean of the initial and final numbers of predators in the pond during the experiment, and $t'$ is the number of days after stocking predators. The average number of bluegill consumed per gram of predator per day ($N_{cg}$) was computed as:

$$N_{cg} = N_{p,t'}/(Bt')\,, \qquad (2)$$

where $B$ (g) is the geometric mean of the initial and final total biomass of predators in the pond during the experiment. Bluegill consumption was also expressed as the daily ration of bluegill ($C_g$), expressed as a percentage of predator weight [$100\cdot$(g bluegill)$\cdot$(g predator) $^{-1}\cdot d^{-1}$, or %BW/d]:

$$C_g = 100\, N_{cg} W_{bg}\,, \qquad (3)$$

where $W_{bg}$ (g) is the geometric mean of the initial and final mean weight per bluegill.

The predators, either juvenile walleye or adult yellow perch, were individually measured for weight and TL at the beginning and end of each experiment. The number recovered at draining was used to compute percent survival. In 1988 individual walleye were not marked, but in subsequent years individual predators were given a unique mark by clipping various fin rays in the second dorsal fin. At the beginning of certain experiments additional predators were sacrificed to determine wet weights of gonads, liver, and viscera, as well as dry weights of these organs and the carcass. These same measurements were made on a subsample of predators surviving to the end of the experiment. Growth was measured for each individual predator by computing the change in wet weight and also the instantaneous specific growth rate, expressed as a percent ($G$, $100\cdot g\cdot g^{-1}\cdot d^{-1}$, or %BW/d):

$$G = 100\,(1/t')\log_e(W_{fp}/W_{ip})\,, \qquad (4)$$

where $W_{fp}$ is the final weight (g), $W_{ip}$ is the initial weight (g) of a predator, and $t'$ is the number of days after stocking predators. Average values for each pond were computed for change in weight and for $G$.

Water temperature in a representative pond (No. 7) was measured at hourly intervals with a Ryan TempMentor recording digital thermometer at a depth of 1.5 m. Daily average water temperature was computed from hourly measurements. Daily averages were used to compute average water temperatures for each month and for the December-February winter period.

For the 1988-89 experiment, age-0 walleye were obtained from state-operated rearing ponds. These, and all other walleye used, were typical products of fish culture operations, originating from eggs of adults captured from the Muskegon River, Michigan. Four ponds were stocked at densities of 0.33-0.36 g/m$^3$ with either small or large fingerling walleye (Table 2). Small fingerlings were the typical size available from rearing ponds in the fall; large fingerlings were the most aggressive cannibals.

For the 1989-90 experiment, adult yellow perch were obtained by hook and line through the ice in Cassidy Lake and stocked at a density of 0.41 g/m$^3$ in three ponds (Table 3). For the 1990-91 experiment, we used age-0 yellow perch that had been raised in Pond 13 at Saline and stocked them in two ponds at a density of 0.44 g/m$^3$ (Table 3).

Walleye were stocked into several Saline holding ponds as fry on 23 April 1991 and as small fingerlings on 11 June 1991. These walleye were used as age-0 fish for the 1991-92 experiment, and as age-1 fish for the 1992-93 experiment (Table 2). In the 1992-93 experiment we compared walleye predation on two sizes of prey, age-0 and age-1 bluegill. The number of age-0 bluegill stocked into each pond was 10 times the number of age-1 bluegill, but the total biomass of age-0 fish was 60% that of age-1 fish (Table 2). We used one control pond and two with walleye at densities of 0.91-0.94

$g/m^3$. The estimation of nonpredatory and predatory mortality was done separately for each age group of bluegill in each pond.

*Results*

Pond temperatures hovered around 4°C during the experiments and the ponds were ice-covered most of the time. Average daily water temperatures (±SD) during December-February for the five winters were 4.0±0.7 ($N$ = 90), 4.2±0.6 ($N$ = 90), 3.7±0.8 ($N$ = 81), 3.2±1.3 ($N$ = 90), and 3.7±0.7°C ($N$ = 77), respectively. The highest average daily temperature during each of the five December-February periods was 5.0, 5.5, 5.8, 6.2, and 4.7°C, and the lowest was 1.9, 2.0, 2.0, 0.3, and 1.1°C, respectively. Water temperatures typically increased by late March.

Overwinter survival of juvenile bluegill was generally quite high in control ponds (Tables 2 and 3). For the four winters of 1989-90 to 1992-93 ($N$ = 7 ponds), average survival of age-0 bluegill was 90±6%. The same value (90%) was obtained by computing 110-d survival from the average instantaneous nonpredatory mortality rate ($0.00094 \cdot d^{-1}$) in these seven ponds, a calculation which adjusts for slight differences in length of the experiments. Age-1 bluegill in the 1992-93 experiment had a survival of 89% in the single control pond, very close to the 92% survival of the age-0 bluegill stocked in the same pond (Table 2).

In the same four winters, 1989-90 to 1992-93, overwinter survival of age-0 bluegill in the ponds with predators was 61±16% compared to 90±6% in the control ponds (Tables 2 and 3). Age-1 bluegill in 1992-93 had 73% and 78% survival in the two ponds with walleye, compared to 89% survival in the control pond (Table 2).

In winter 1988-89, average bluegill survival in the control ponds (19.5±6.1%, Table 2) was much lower than in the other years (90%). Survival in the four ponds with predators was even lower (3.1±2.4%). These fish were in poorer condition than usual when stocked due to rearing at high density (Breck 1993); they had a relative weight of only 65±14% ($N$ =20) and probably were more prone to starvation and disease. Though the longest experiment occurred in 1988-89 (the bluegill were in Pond 7 for 168 d), longer duration alone is not enough to explain the lower survival; the average $M_{np}$ for the other years equates to a 168-d survival estimate of 85%.

In the 1988-89 experiment, there was no effect of walleye size on bluegill survival. Bluegill survival was 5.8% and 0.2% in the two ponds with small walleye (19 g), and 3.9% and 2.5% in the two ponds with large walleye (129 g) (Table 2).

In general, bluegill length changed only slightly overwinter (Tables 2 and 3) and the final mean lengths were within 1 SD of the initial mean lengths. This indicates insignificant occurrence of either bluegill growth or predator size selectivity within the size ranges studied. One exception was Pond 3 in 1988-89, where final mean length (44.8 mm) was much larger than initial mean length (27.8±6.5 mm); this almost certainly was the result of size-selective survival of larger bluegill because only 8 survived of the 3,400 stocked. Gains in bluegill average weight were noted by the end of some experiments, but this was probably due to feeding on early spring pulses of large *Daphnia* just before ponds were drained.

Overwinter survival of both walleye and yellow perch was high. The average was 85% for walleye ponds ($N$ = 8), including four ponds with 100% survival (Table 2). The average survival was 75% for yellow perch ponds ($N$ = 5), with a range of 50-91% (Table 3).

The unique clips of the soft dorsal fin-rays were very useful for unintrusively monitoring the growth of predators. Individual walleye and yellow perch could easily be identified at pond draining 16 weeks later. The membrane between fin rays usually grew back, but there was little growth of the rays.

Most, but not all, predators lost weight overwinter. Instantaneous growth rates ($G$) of walleye were negative in five out of six ponds where changes in individual weight could be estimated (Table 2). In winter 1991-92, walleye in Pond 13 grew at an average rate of 0.0555% BW/d, whereas those in Pond 7 lost a similar amount. Yellow perch growth was negative in three out of five ponds (Table 3). The better growth occurred among females, and especially during the 1990-91 experiment. The latter perch had been raised in ponds and, perhaps, were better acclimated to the pond environment than wild perch obtained from a lake for the 1989-90 experiment.

Estimates of predatory and non-predatory mortality of bluegill based on the second method (Appendix 1) are shown in Table 4. The two calculation methods produced nearly identical results, except for the 1988-89 experiment when total bluegill mortality was unusually high. For Pond 3, where bluegill total mortality was 99.8%, the first method gave 1,103 nonpredatory and 2,289 predatory deaths, whereas the second method gave 2,076 nonpredatory and 1,316 predatory deaths. The first method appeared to overestimate the predatory mortality when mortality was high, especially during the first part of the experiment, and we favor results based on the second method. To obtain close estimates of consumption during 1988-89 by the first method, multiply corresponding figures in Table 4 by 1.5.

We calculated that predators were responsible for 58% of the bluegill mortality in ponds containing predators (Table 4). This percentage was similar for walleye (55%, $N = 8$, range: 25-89%) and yellow perch (63%, $N = 5$, range: 0-93%). For age-1 bluegill in 1992-93, for which only one control pond was used, the predators were estimated to be responsible for 55% ($N = 2$) of the total mortality.

In the 13 ponds containing either walleye or yellow perch, the predators consumed age-0 bluegill at an average rate ($N_c$) of about 1 per day: 0.81±0.18 (mean±SE) bluegill$\cdot$predator$^{-1}\cdot$d$^{-1}$ (Table 4). The mean weight-specific daily consumption ($N_{cg}$) was 0.0105±0.0019 bluegill$\cdot$g$^{-1}\cdot$ d$^{-1}$. The mean weight-specific daily ration ($C_g$) was 0.34±0.07 %BW/d. For the 8 ponds containing walleye, the corresponding values were 0.79±0.26 bluegill $\cdot$ walleye$^{-1}$ $\cdot$d$^{-1}$, 0.0108 ±0.0027 bluegill$\cdot$g$^{-1}\cdot$d$^{-1}$, and 0.38±0.10 %BW/d. For the 5 ponds with yellow perch, the corresponding values were 0.83±0.22 bluegill$\cdot$perch$^{-1}\cdot$d$^{-1}$, 0.0100±0.0028 bluegill$\cdot$g$^{-1}\cdot$d$^{-1}$, and 0.27±0.08 %BW/d.

Larger walleye captured more bluegill per day than smaller walleye (Table 4). In 1988-89, average daily capture rate for 129-g walleye was 1.85 bluegill$\cdot$predator$^{-1}\cdot$d$^{-1}$, whereas the rate for 19-g walleye was 0.26 bluegill$\cdot$predator$^{-1}\cdot$d$^{-1}$. However, the daily capture rate was virtually identical for large and small walleye when expressed per g of walleye (0.015 bluegill$\cdot$g$^{-1}\cdot$d$^{-1}$ for 129-g walleye and 0.013 bluegill$\cdot$g$^{-1}\cdot$d$^{-1}$ for 19-g walleye). Walleye used in 1991-92 were intermediate in size (51 and 38 g) and had capture rates of 0.005 and 0.021 bluegill$\cdot$g$^{-1}$ $\cdot$d$^{-1}$, respectively.

In the 1992-93 experiment, age-1 bluegill were exposed to predation by large (age-1) walleye, but the rate of predation was very low (Table 4). We estimate that in 100 days each walleye consumed only 1 or 2 age-1 bluegill compared to 45-60 age-0 bluegill.

## Consumption Rates in the Laboratory

### *Methods*

Laboratory experiments paralleled studies in ponds and provided additional information on consumption rates under conditions of high bluegill availability. The experiments also measured the metabolic limitations on feeding and growth imposed by cold temperatures. Specific objectives were to (1) directly measure maximum bluegill consumption rates by walleye and yellow perch under ad-libitum feeding conditions, and (2) determine weight-specific growth rate and maintenance ration. Experiments were conducted in winter, and also in early spring to provide consumption data representative of spring and fall temperatures.

Experiments were conducted in 320- or 760-L indoor tanks at the Saline Fisheries Research Station from fall 1988 to spring 1993. Water temperatures comparable to those in lakes and ponds were obtained by diverting small amounts of outdoor reservoir water through the tanks and keeping the room cold. Temperature, monitored continuously, was relatively stable (2.2-7.8°C) during winter. Average temperatures during experiments were calculated from daily medians. Samples of water strained through a plankton net demonstrated that insignificant numbers of potential food items entered the tanks. Laboratory windows provided natural photoperiod. Tanks were partially covered and disturbances were kept to a minimum, with regular observations no more than once a week. Juvenile walleye of two size groups (about 30 g or 150-220 g) were tested; they were from the same sources used in pond experiments. Adult wild yellow perch (about 70 g) were obtained from Cassidy Lake or Mill Lake by angling through the ice. All perch used in winter 1990-91 were mature females.Prey were young-of-the-year bluegill (about 0.8 g) reared in Saline ponds.

Six sets of experiments were conducted in tanks (Table 5). The main winter experiments lasted 98-112 days and the main spring experiments lasted 40-59 days. The basic design was to supply a tank of 10 predators (usually with a replicate) with excess bluegill and deny food to predators in another tank. Starvation was necessary to assure that one group would be below maintenance ration. No predators, neither starved nor fed, died during experiments and all appeared to be healthy and active at all times. About 150 bluegill (375 $g/m^3$) were maintained in feeding tanks, a density believed to be high enough to stimulate maximum feeding rate. Tanks were monitored weekly to determine condition of predator and prey and number of bluegill eaten. Predators were weighed at the start and end of experiments and at monthly intervals. In some experiments, samples of predators and prey were sacrificed and dried at 55°C to obtain estimates of water content.

Rates of consumption and growth of predators were calculated on a daily basis for each tank. Growth of individual predators could be monitored since each fish had unique binary fin-ray clips, however consumption by individual fish was not known. Therefore, average consumption rates were calculated by dividing total number or weight of prey eaten by number of predators per tank and number of days. Specific growth ($G$, %BW/d) was calculated from Equation 4. Specific ration ($R$, %BW/d) was calculated from the equation:

$$R = 100\,(\Sigma\text{food})/(W_{pg}t')\,, \qquad (5)$$

where $\Sigma$food is total food eaten (g), $W_{pg}$ is the geometric mean weight of all predators (g), and $t'$ is the number of experimental days.

Specific growth was regressed against specific ration. Maintenance ration was defined as the point on the regression at which growth = 0.

### *Results*

Bluegill consumption rates were low even in this laboratory environment where there was high bluegill density, no alternative food, and no opportunity for spatial segregation (Table 5). For predator and prey sizes typical of lakes, at mid-winter temperatures (4-5°C), average consumption rates were 0.11%BW/d (0.347 bluegill$\cdot$ predator$^{-1}\cdot$d$^{-1}$) for adult yellow perch and 0.34%BW/d (0.495 bluegill$\cdot$predator$^{-1}\cdot$d$^{-1}$) for small juvenile walleye. At 11-15°C, average consumption rates increased to 0.78 %BW/d (2.399 bluegill$\cdot$predator$^{-1}\cdot$d$^{-1}$) for adult perch and 2.02 %BW/d (1.838 bluegill$\cdot$predator$^{-1}\cdot$d$^{-1}$) for small walleye. Large juvenile walleye generally ate less than expected at both temperatures, 0.095-0.75 %BW/d (0.16-1.45 bluegill$\cdot$predator$^{-1}\cdot$d$^{-1}$). This is attributed to reduced weight-specific metabolism because of larger body size and, probably, difficulty in acclimating to the laboratory environment enough to feed at a maximum rate.

Maintenance rations were also low because of cold temperatures. In winter (4.4-5.3°C), adult yellow perch required a maintenance ration of just 0.075 %BW/d. Small walleye had maintenance rations that were four-times higher, 0.316 %BW/d (0.306 % BW/d on a dry weight basis). At 15°C, small walleye maintenance ration increased to 1.049 %BW/d (1.092 %BW/d on a dry weight basis).

## Stomach Evacuation Rates

### *Methods*

Stomach evacuation rates of walleye and yellow perch were studied under laboratory conditions during mid-winter. Objectives were to (1) determine length of time food items could be identified, as an aid in the interpretation of stomach samples collected at lakes, and (2) define the physiological limit on consumption rate at low temperatures.

Adult yellow perch (61-101 g) were force-fed 1-3 bluegill totaling 1% of the perch's weight (range 0.5-1.4 %BW). They were returned to 30-L aquaria and held 24, 36, or 48 h at average temperatures of 2.2-5.0°C. Stomachs were flushed and food remains were weighed and identified as bluegill, sunfish, or fish. Some perch were tested repeatedly, with no mortality or disease problems and consistent results. These perch had acclimated to the aquaria and were allowed to rest and feed normally for 1 or more weeks between tests. Data were obtained from 36 tests. Evacuation rate was estimated from a linear regression, forced through the origin, of percent evacuated versus hours. Excluded were five outliers (>2 SD), all low.

Juvenile walleye (30-78 g) were force-fed 1 (occasionally 2 or 3) small bluegill totaling either 1% or 2% of the walleye's weight (ranges, 0.9-1.3 or 1.8-2.1 %BW). They were returned to 30-L aquaria for 24, 48, 60, or 72 h where median temperatures were 2.8-5.0°C. Stomach contents were flushed out, identified, and weighed in the usual manner. Data were obtained from 42 tests. Excluded from a regression analysis were three outliers, all lower than 2 SD.

### *Results*

All 11 perch examined at 48 h had already completely evacuated the bluegill. Therefore, to obtain a more accurate estimate of percent gastric evacuation rate by perch ($GE_p$), a regression line was fit through the 24- and 36-h percent evacuated data and forced through the origin (Figure 3). The equation is:

$$GE_p = 2.448(\pm 0.082)\,H, \qquad (6)$$

where $H$ is time (hours) since ingestion, $N = 20$, ±1 SE in parentheses. Complete evacuation was calculated to occur in 40.8 h, and 50% evacuation in 20.4 h. Average evacuation rate was 0.0061 $g \cdot g\ perch^{-1} \cdot d^{-1}$ for a 1% meal. A bluegill could be identified as a sunfish until about 24 h. One additional experiment with a 2% meal size indicated time for complete evacuation was about the same as for a 1% meal, meaning the average rate in $g \cdot g\ perch^{-1} \cdot d^{-1}$ was about double.

Walleye gastric evacuation rate was slower and more variable than that of yellow perch. A regression line fit to 1% meal data and forced through the origin (Figure 4) produced this equation for percent evacuation by walleye ($GE_w$):

$$GE_w = 1.297(\pm 0.045)\,H, \qquad (7)$$

where $H$ is time (hours) since ingestion, $N = 30$, ±1 SE in parentheses. This indicated 100% evacuation occurred in 77.1 h, and 50% evacuation in 38.6 h. These were about double the time estimates obtained for yellow perch. The average evacuation rate on a weight basis was slow, 0.0028 $g \cdot g\ walleye^{-1} \cdot d^{-1}$. A bluegill could be identified to species after 24 h but was not usually identifiable as a sunfish at 48 h. The transition point from sunfish to fish probably occurred near 39 h, when evacuation was 50% completed.

Percent evacuation for a 2% meal was similar to that for a 1% meal (Figure 4), indicating that the rate by weight was double (0.0057 $g \cdot g\ walleye^{-1} \cdot d^{-1}$). This tendency for percentage evacuation rate to be nearly independent of relative meal size was noted above for yellow perch, and has been observed previously in percids by Schneider (1973b) but not by Persson (1986).

## Gape and Body Depth

### *Methods*

We measured mouth gape of walleye and yellow perch and maximum body depth of bluegill to determine the largest bluegill that might be ingested by a given size of predator. We estimated gape (to the nearest 0.1 mm) of live or fresh walleye and yellow perch by two methods. For the first method, the mouth was opened to where it was judged to be fully open and the inside width was measured with vernier calipers. This is referred to as the estimated mouth width because of the subjectivity in forcing the mouth open to maximum width. In the second method, progressively larger bluegill were forced into the mouth (horizontally, the widest dimension) to determine the largest one which could be inserted. Body depth of the largest bluegill was then measured. This is referred to as the maximum mouth width, and clearly is the upper boundary on prey size. However, the throat opening may further constrain food particle size. Regressions were fitted to calculate gape from total length.

Maximum body depth (to the nearest 0.1 mm) and total length were measured on bluegill from the Saline ponds. Body depth was measured as the maximum distance from the top of the compressed dorsal fin to the bottom of the belly. Linear regressions were computed and used to estimate maximum body depth from total length. Estimated regression coefficients were reported ±1 SE.

### *Results*

For yellow perch ranging from 104 to 355 mm TL, estimated mouth width ($EM_p$, mm) is a linear function of perch total length ($TL_p$, mm):

$$EM_p = -1.59(\pm 0.49) + 0.1011(\pm 0.0027)\, TL_p\,, \quad (8)$$

$r^2 = 0.93$, $N = 104$ (Figure 5).

However, force-feeding ($MM_p$) indicated large yellow perch can stretch their mouth much wider than caliper measurements suggested (Figure 5). This explains the unexpectedly large bluegill found in stomachs of wild yellow perch (Figure 1). The equation is:

$$MM_p = -4.57(\pm 1.09) + 0.1518(\pm 0.0051)\, TL_p, \quad (9)$$

$r^2 = 0.97$, $N = 27$, for yellow perch 110-355 mm.

For walleye ranging from 84 to 527 mm, estimated mouth width ($EM_w$, mm) is a linear function of walleye length ($TL_p$, mm):

$$EM_w = -1.25(\pm 0.95) + 0.1208(\pm 0.0027)\, TL_w\,, \quad (10)$$

$r^2 = 0.97$, $N = 67$ (Figure 6). Bluegill actually found in wild walleye stomachs were within the expected size range (Figure 2).

Maximum mouth width ($MM_w$, mm) is also linear function of walleye length ($TL_w$, mm):

$$MM_w = 12.08(\pm 0.28) + 0.1072(\pm 0.0061)\, TL_w\,, \quad (11)$$

$r^2 = 0.98$, $N = 9$, for walleye 391-561 mm (Figure 6). $MM_w$ is about 10% higher than $EM_w$ over this restricted size range.

The maximum body depth ($D_b$, mm) of bluegill increases allometrically for total lengths ($TL_b$, mm) of 18.5 to 220 mm:

$$\log_{10} D_b = -0.863(\pm 0.021) + 1.190(\pm 0.003) \log_{10} TL_b\,, \quad (12)$$

$r^2 = 0.997$, $N = 416$ (Figure 7).

For bluegill larger than about 30 mm, body depths predicted by this equation are similar to those from the equation of Schramm and Zale (1985), but the equations produce quite different results when extrapolated to bluegill smaller than 20 mm (Figure 7). Likewise, the equation of Lawrence (1958) underestimates body depth compared to Equation 12 for bluegill smaller than about 40 mm.

Several studies have indicated that the largest prey taken by a predator has a maximum body depth equal to the predator's mouth width (Lawrence 1958; Johnson 1969; Schramm and Zale 1985; Hambright 1991). To estimate the size of bluegill that can be ingested by a given size of predator, one first estimates predator gape from predator length, and then bluegill length from bluegill body depth. For this calculation one needs Equation 8 (or 9) for yellow perch or Equation 10 (or 11) for walleye and an equation with bluegill body depth as the independent variable:

$$\log_{10} TL_b = 0.728(\pm 0.017) + 0.8383(\pm 0.0020) \log_{10} D_b\,, \quad (13)$$

$r^2 = 0.997$, $N = 416$, for bluegill from 18.5-220 mm TL, with maximum body depths from 4.1-89 mm.

In Michigan lakes with slow-growing bluegill populations, the mean bluegill length at first annulus (Figure 8) is often larger than the mean lengths used in our pond studies. In samples from 16 lakes over several years, most young bluegill were 25-60 mm TL during their first winter. A 25-mm bluegill is predicted to have a maximum body depth of 6.3 mm (Equation 12). Therefore, to ingest that bluegill a walleye needs to be at least 63 mm ($EM_w$) and a yellow perch needs to be at least 78 mm ($EM_p$) or 72 mm ($MM_p$). A 60-mm bluegill has a body depth (17.9 mm) equal to the estimated mouth width of a 158-mm walleye and a 193-mm yellow perch. However, the majority of age-0 bluegill are less than 50 mm and could be ingested by any walleye likely to be present and by any yellow perch over 158 mm.

## Discussion

Actual and potential consumption of bluegill by walleye and yellow perch were assessed by a combination of (a) lake observations on diet, (b) pond experiments on consumption rates, and (c) laboratory studies on consumption, maintenance ration, and stomach evacuation. These assessments, expressed as consumption in %BW/d (Figures 9-12), generally are in agreement. Typical consumption rates for yellow perch are about 0.3 %BW/d in winter and 0.8 %BW/d in fall/spring, while typical consumption rates for juvenile walleye are about 0.4 %BW/d in winter and 1.5 %BW/d in fall/spring. These winter consumption rates match the 0.4% BW/d rate projected from the literature analysis in the introduction. The most glaring discrepancy is the group of walleye lakes for which estimated consumption was much higher than average digestion capability, probably because by chance sampling occurred when feeding was intense.

Evacuation rate sets the upper limit on potential food consumption rate at about 1 %BW/d at winter temperatures and about 2.5 %BW/d at fall and spring temperatures. These estimates, based on a 2% meal, may change because evacuation rate can vary with meal size. There is a possibility that we underestimated evacuation rate (of walleye, especially) by force-feeding (see review by Persson 1986). However, that bias is believed to be minimal in our experiments because outlying data (all low) were dropped from our analysis, some of our experimental fish fed voluntarily between tests, and our previous experiments (Schneider 1973b) indicated similar results can be obtained from force- and voluntary-fed yellow perch. Our estimated winter evacuation rate for juvenile walleye was 3 times higher than for adult walleye (Hofman 1969) and was the same as for juvenile European perch *Perca fluviatilis* at the 90% point (Persson 1979). Our estimate of evacuation rate for adult yellow perch was comparable to that for European perch up to the 50% point, then continued in a rapid linear fashion whereas the evacuation rate for European perch tailed off exponentially. The European perch were smaller (about 24 g) and had fed on *Gammarus* instead of fish. Maintenance rations provide an estimate of minimal food requirements. Our estimates were 0.1-0.4 %BW/d in winter and about 0.5-1.0 %BW/d in fall and spring, with main-tenance requirements for walleye exceeding those for yellow perch of comparable weight.

Maintenance ration does not set a firm lower boundary on short-term consumption, however, because both species can live long periods of time - perhaps all winter - without feeding. All 40 of our laboratory fish (in four groups) that were not fed for 98-112 d showed no ill effects. In addition, many fish in the ad-libitum groups did not eat enough to maintain body weight. Newsome and Leduc (1975) reported that unfed, stunted yellow perch can survive over 200 days at winter temperatures. In contrast, Sullivan (1986) found that 82-165 mm yellow perch could not survive winter without feeding.

We anticipated that walleye and yellow perch fed bluegill ad libitum in laboratory tanks would exhibit the highest consumption rates, but this was not always true because certain fish (especially walleye) were reluctant to feed. We anticipated that predation on bluegill in ponds would be higher than in natural lakes because lakes contain alternative foods for predators, more opportunity for spatial separation, and more cover for prey. However, there was good agreement between lake and pond data for yellow perch in winter (Figure 9). For lakes with the highest incidence of predation on bluegill (Cedar and Cassidy), total food consumption rates were estimated at 0.49 and 0.31 %BW/d, and bluegill consumption rates at

0.43 and 0.24 %BW/d, respectively. These are similar to the rates in ponds, and imply that bluegill were readily available to yellow perch in these two lakes. The estimates of consumption in ponds were more variable and less precise than those in tanks because the number of bluegill actually eaten was estimated indirectly and would be in error to the extent that non-predatory bluegill mortality varied among ponds.

Consumption rates and maintenance rations varied with predator size more than anticipated. Among juvenile walleye, consumption rate was highest for smaller fish (Figures 10 and 12). In previous experiments (Kelso 1972), maintenance ration was reported to be a constant 0.4 %BW/d for walleye larger than 170 g. Previous work with small (11 g) yellow perch suggests they have higher rates than we estimated for adult perch (Schneider 1973a).

It is clear that in some lakes small bluegill are an important food of yellow perch in winter, and to a lesser extent in cool months. Rarely have bluegill been found in yellow perch stomachs from Michigan lakes during summer (Laarman and Schneider 1972; Schneider 1993 and unpublished data), but Beard (1982) reported a frequency of 6.7% for one Wisconsin lake and calculated that yellow perch ate considerable numbers of bluegill in summer. Yellow perch prey on young bluegill which are 20-50 mm long, the size typical of Michigan lakes in fall and winter (Figure 8). Walleye diet is less well known for those months, but pond and laboratory experiments in winter confirmed walleye too could be important predators in lakes where they co-occur with bluegill. Walleye, by virtue of their large size, are not restricted to eating only the smallest bluegill (Figure 2). Nonetheless, young bluegill will be preyed on more because they are more abundant and because small walleye usually outnumber large walleye. In summer, bluegill can make up a substantial proportion of the walleye diet if more preferred forage is not available (Schneider 1975; Santucci and Wahl 1993).

For percid predation to be effective at controlling bluegill recruitment and the bluegill stunting problem, a number of factors come into play:

(a) Small bluegill must occur in the same habitats as yellow perch or walleye;

(b) Predators must be agile enough to catch bluegill;

(c) Size of bluegill eaten will be limited by gape of predator;

(d) The predator population must be relatively abundant so that even a low rate of daily consumption - as occurs in winter due to low metabolism - adds up to a significant number of bluegill eaten;

(e) The significance of this predation to bluegill population dynamics depends on how many small bluegill began the winter, how many would have survived the winter if they hadn't been eaten, and the number of yearling and older bluegill the lake is capable of supporting at a satisfactory growth rate.

Factors (a)-(c) are operative at a number of lakes as indicated by the presence of bluegill in stomachs; factor (d) can be evaluated, with difficulty, by also estimating predator population size; factor (e) is very difficult to evaluate, but insights can be gained by looking at certain correlations.

Sufficient data on both incidence of yellow perch predation on bluegill and density of yellow perch has been obtained at two lakes to calculate total bluegill consumption from December to March. At Blueberry Pond, where incidence of predation is low and density of yellow perch is relatively high, the estimated December-March consumption was 3,460 bluegill/ha (Schneider 1993). At Cassidy Lake, incidence of predation is high and density of yellow perch is relatively high. Based on Schneeberger's (1988) population data, we estimated the average perch population in winter at 1,300, and calculated total December -March consumption at 8,640 bluegill/ha. Estimates for both lakes seem impressive, but it is difficult to evaluate their significance to bluegill population dynamics because fall and spring densities of young bluegill and optimal levels of yearling recruitment are not precisely known. For Blueberry Pond, winter consumption by yellow perch is roughly 75% of the fall population of young bluegill. But, the only way to conclusively measure the significance of yellow perch predation in these two lakes would be to remove all perch and monitor changes in bluegill recruitment and growth. Since bluegill are already growing at desirable rates in Cassidy Lake and Blueberry Pond, it is very likely that perch removal would have a negative effect on bluegill dynamics.

The importance of yellow perch predation on bluegill dynamics can be inferred from other sources. Among 102 southern Michigan lakes sampled with large seines (Schneider 1981), the lakes with higher proportions of large bluegill and faster bluegill growth also had larger and faster growing yellow perch. The impression gained from sampling stunted bluegill lakes over the last 30 years is that they rarely contain good yellow perch populations. The same observation has been made in Minnesota (Goeman et al. 1990). Similarly, Snow and Staggs (1994) noted that slow bluegill growth usually does not occur in Wisconsin lakes with good populations of walleye.

Management implications from this study are that yellow perch and walleye may, in certain situations, control or prevent bluegill stunting. The role of yellow perch as a beneficial predator in the fish community has been undervalued in particular. High exploitation of yellow perch is encouraged in Michigan by very liberal angling regulations, including high bag limits (50/d), no minimum size limit, and no closed season. Yellow perch are easily caught in some lakes, especially during winter. At Blueberry Pond, 15-30% of the adult yellow perch were caught by a few anglers on two winter weekends (Schneider 1993). At Cassidy Lake, perhaps 50% of the population is caught each winter by an intensive perch fishery. At Mill Lake, 61% of the yellow perch were caught in 3 summer days of intensive fishing (Schneider 1973c). Therefore, we recommend a reduction in bag limit, to 10 or 15/d, for southern Michigan lakes dominated by bluegill to prevent overharvest of yellow perch. Stocking of yellow perch to enhance perch and bluegill populations appears to be impractical, at least in lakes with abundant and slow-growing northern pike populations, based on a Minnesota experiment (Goeman et al. 1990).

Stocking of walleye to increase predation on bluegill has been widely attempted. Hope is offered by the results of this pond experiment and another (Schneider 1975), plus observations in Wisconsin (Snow and Staggs 1994) and Minnesota (Goeman et al. 1990) that walleye lakes rarely have stunted bluegill. In addition, walleye maintained satisfactory growth of bluegill and yellow perch in Jewett Lake, Michigan (Schneider, 1995). Based on gape estimates, walleye need be only 63 mm long to ingest 25-mm bluegill and be potentially effective overwinter predators. However, initial mortality of stocked walleye in many bluegill-dominated lakes is so high that no improvement of bluegill size is achieved (Beyerle 1978; Schneider 1989; Goeman et al. 1990). Only very large (and expensive) fingerling walleye are likely to succeed in bluegill-dominated lakes or lakes with complex fish communities (Laarman and Schneider 1986; Santucci and Wahl 1993).

## Acknowledgments

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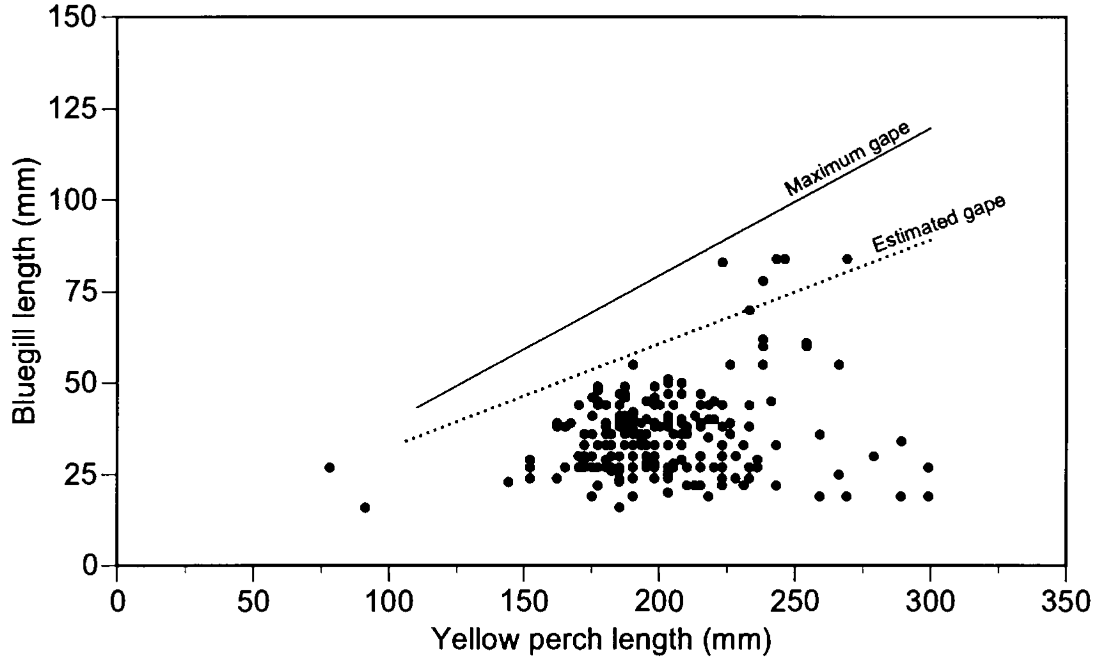

Figure 1.—Estimated total lengths of 239 bluegill (adjusted for 9% shrinkage) eaten by different sizes of yellow perch collected from Michigan lakes during fall and winter. The two lines indicate the largest bluegills expected based on two types of measurements of perch mouth gape (Figure 5 and Equations 8 and 9) and the bluegill length-depth relationship (Figure 7 and Equation 13).

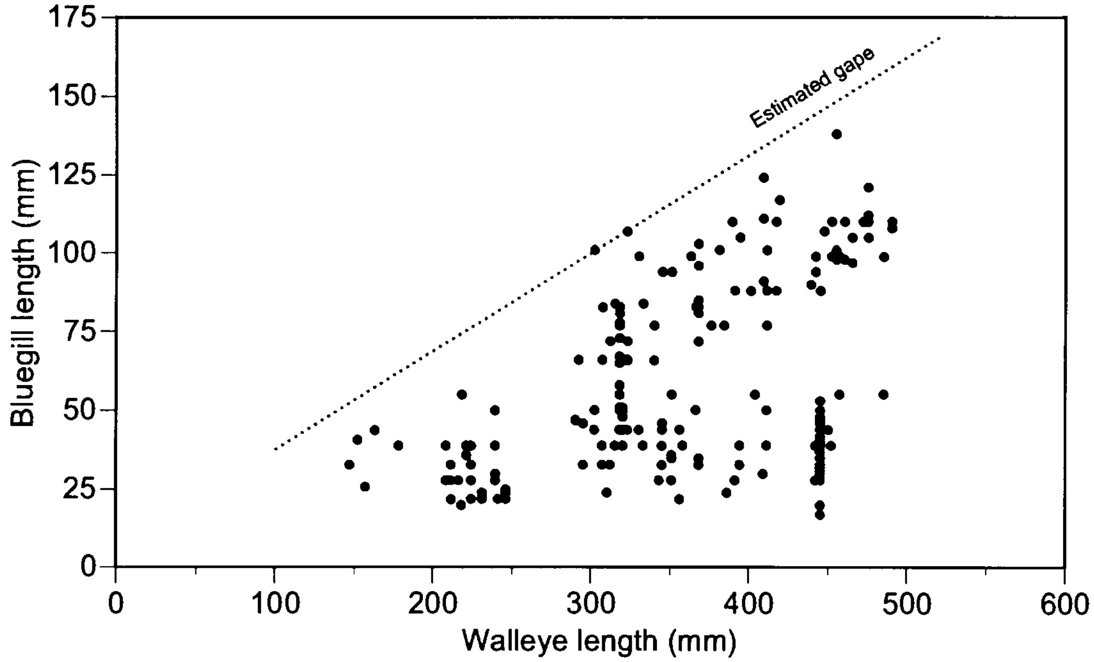

Figure 2.—Estimated total lengths of 219 bluegill (adjusted for 9% shrinkage) eaten by different sizes of walleye collected from lakes during fall. Most walleyes were from Jewett Lake. The line indicates the largest bluegills expected based on an estimate of walleye mouth gape (Figure 6 and Equations 10 and 11) and the bluegill length-depth relationship (Figure 7 and Equation 13).

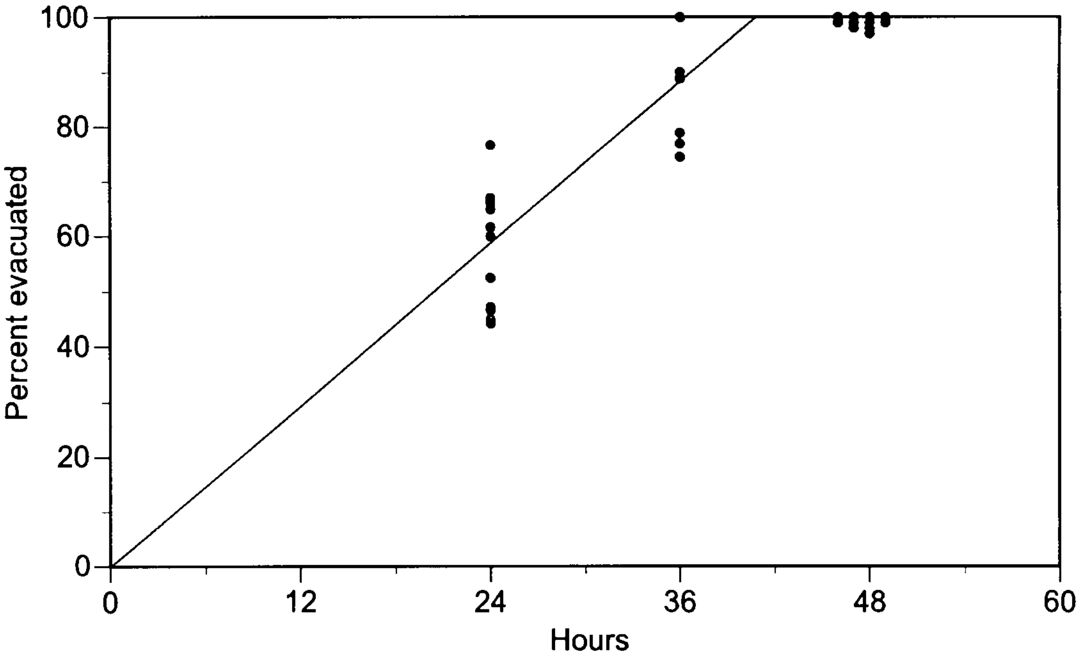

Figure 3.—Percent stomach evacuation for yellow perch fed a 1% meal of bluegill at 2.2-5.0°C. Regression line is from Equation 6.

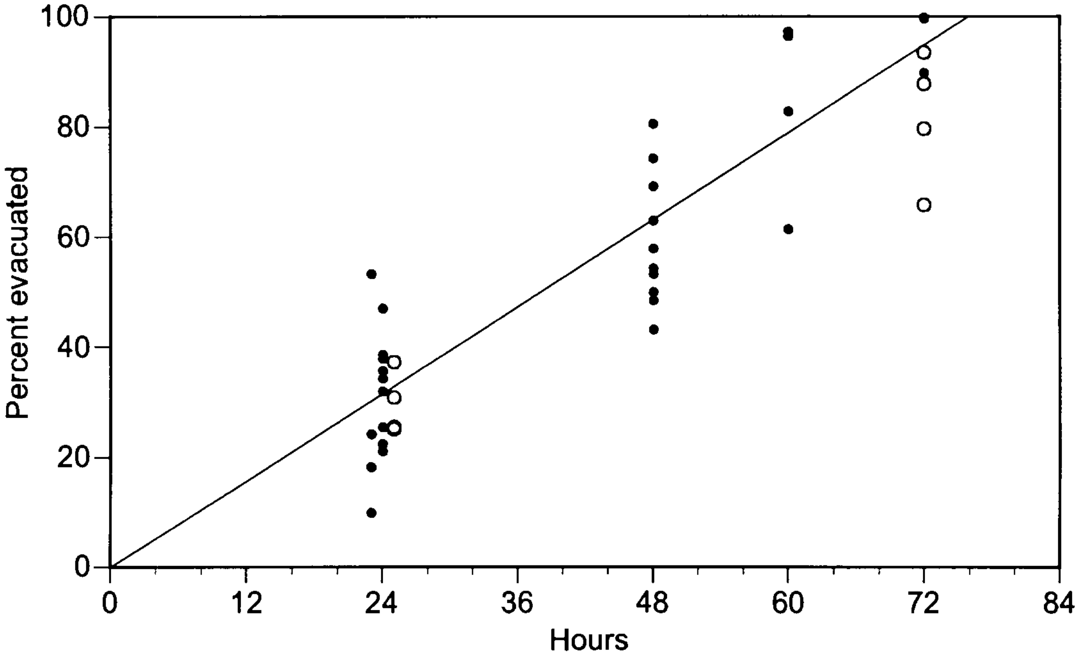

Figure 4.—Percent stomach evacuation for walleye fed a 1% meal of bluegill at 2.8-5.0°C (solid circles). Also shown are data for a 2% meal at 3.9-4.4°C (open circles). Regression line is for 1% data (Equation 7).

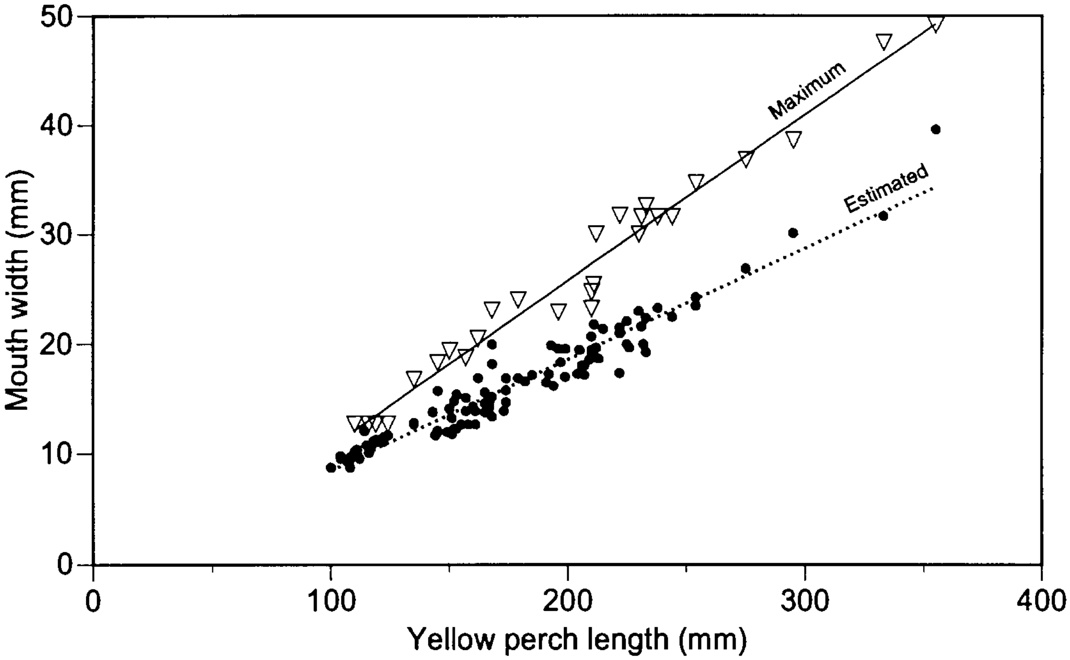

Figure 5.—Yellow perch mouth width is a linear function of total length. Gape was determined by estimating mouth width with calipers (circles and Estimated line, Equations 8), and by determining the deepest bluegill which would fit into the perch's mouth (triangles and Maximum line, Equation 9).

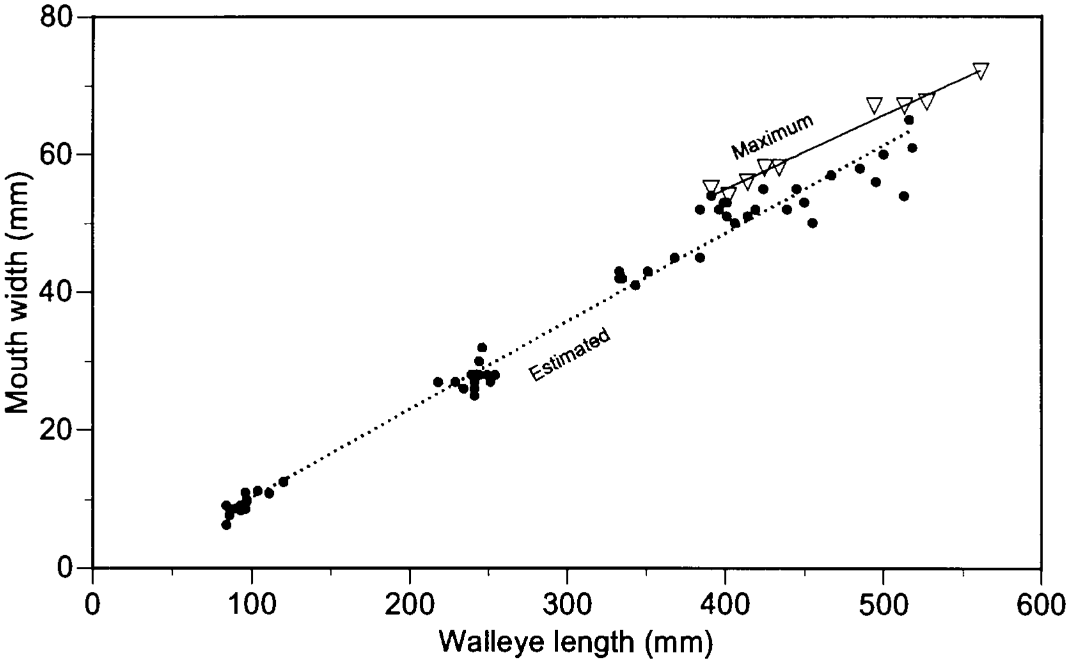

Figure 6.—Walleye mouth gape is a linear function of total length. Gape was determined by estimating mouth width with calipers (circles and Estimated line, Equation 10), and by determining the deepest bluegill which would fit into the walleye's mouth (triangles and Maximum line, Equation 11).

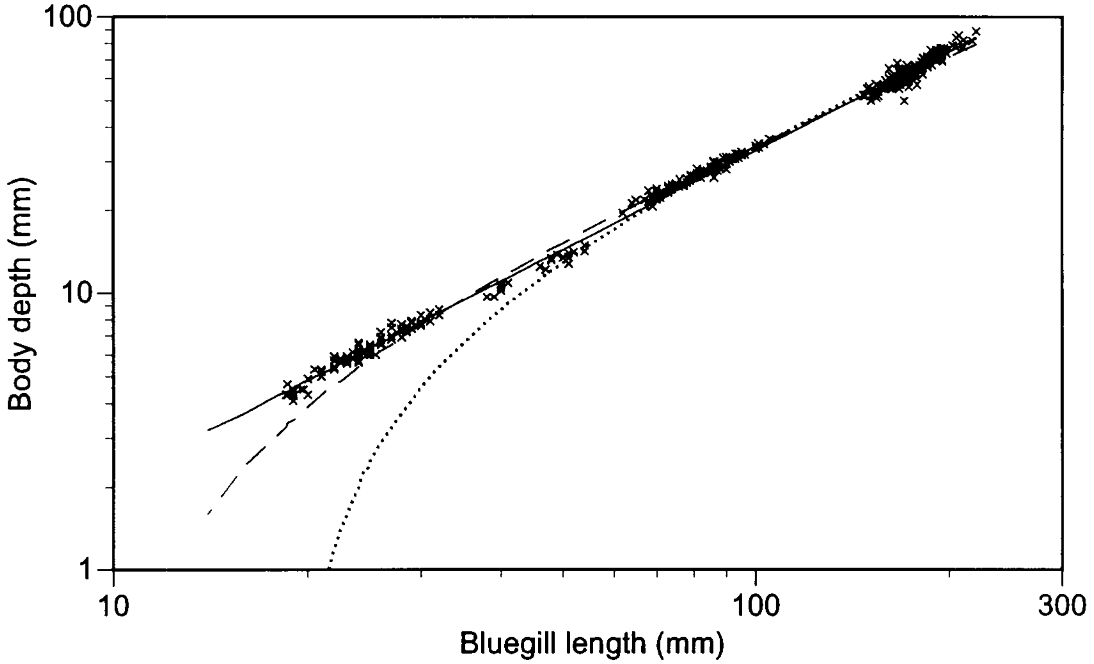

Figure 7.—Bluegill maximum body depth has an allometric relationship with total length. The solid line is computed with Equation 12. The dashed line uses the equation of Schramm and Zale (1985) and the dotted line uses the equation of Lawrence (1958).

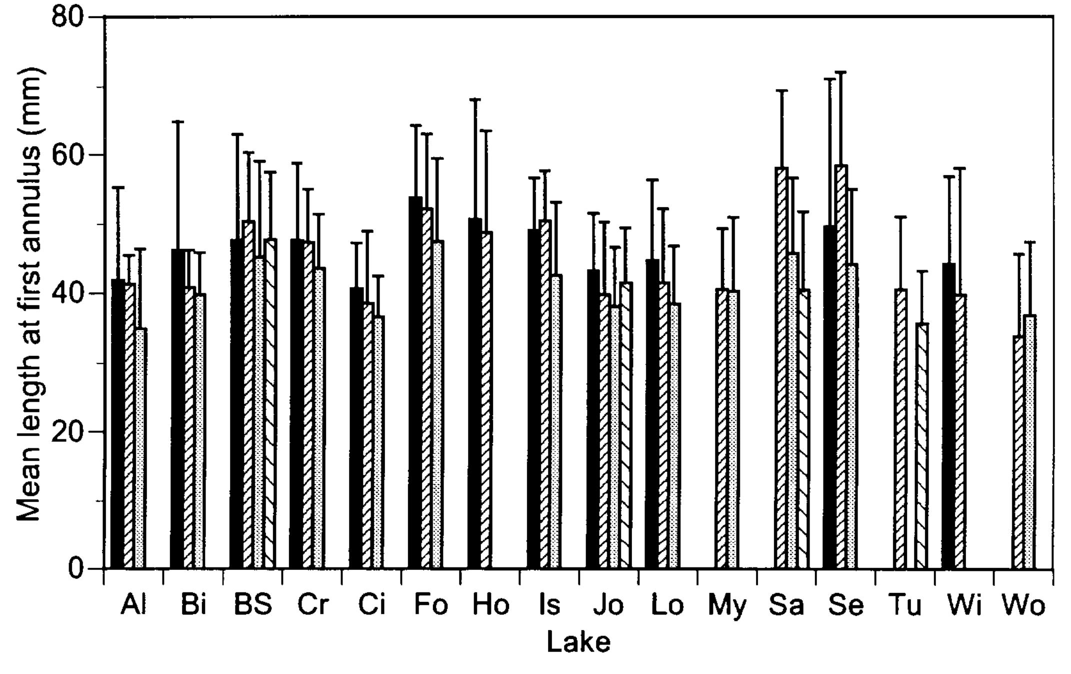

Figure 8.—Mean length at first annulus (±2 SD) backcalculated for bluegill from 16 slow-growing lake populations in southern Michigan, 1988-91 (Schneider and Lockwood unpublished). Each bar represents one year. The lakes are Algoe, Big, Big Seven, Crescent, Crispell, Fourteen, Horseshoe, Island, Joslin, Long, Myers, Saddle, Selkirk, Turk, Williams, and Woodard.

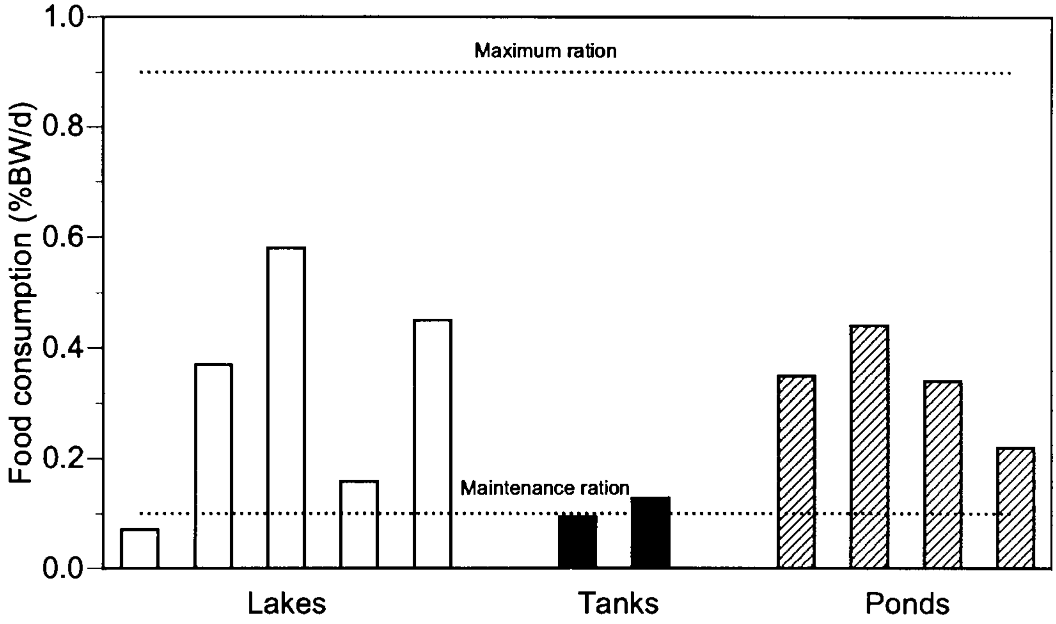

Figure 9.—Comparison of estimated average daily food consumption during winter (temperature about 4°C) by adult yellow perch in natural lakes (Table 1), and in experimental tanks and ponds with bluegill (Tables 4 and 5). Also shown are the rations required for maintenance of body weight (this study) and the maximum ration which could be evacuated (when fed a 2% meal—Schneider 1973b).

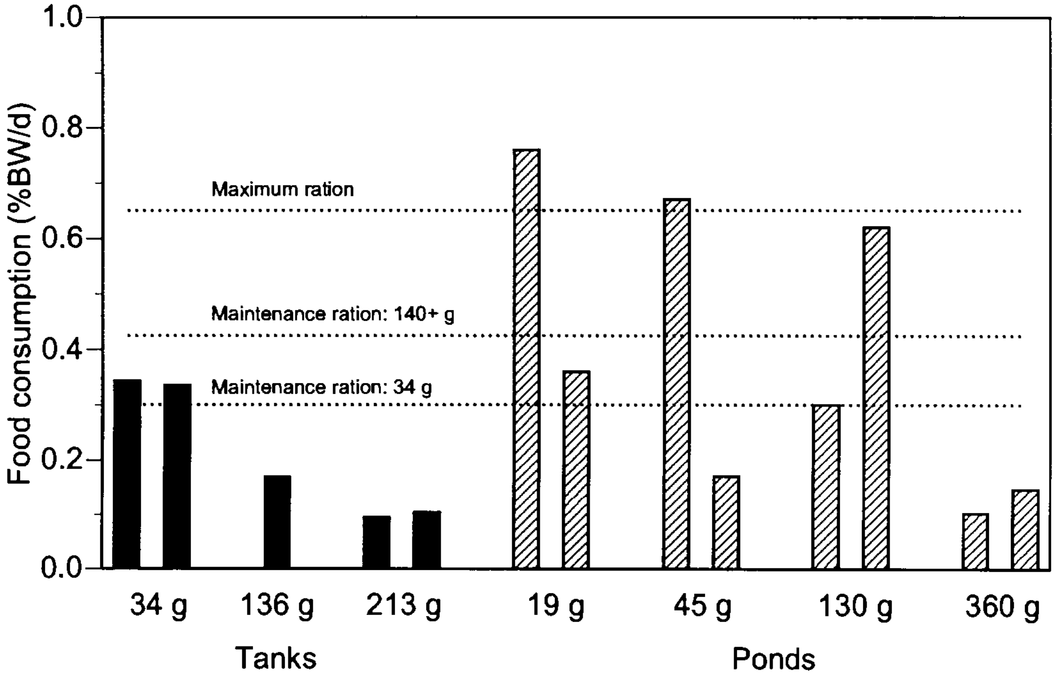

Figure 10.—Comparison of estimated average daily food consumption during winter (temperature about 4°C) by juvenile walleye of various sizes in experimental tanks and ponds with bluegill (Tables 4 and 5). Also shown are the rations required for maintenance of wet body weight for small (34 g—this study) and large (140+ g—Kelso 1972) walleye and the maximum ration which could be evacuated by 30-78 g walleye (when fed a 2% meal).

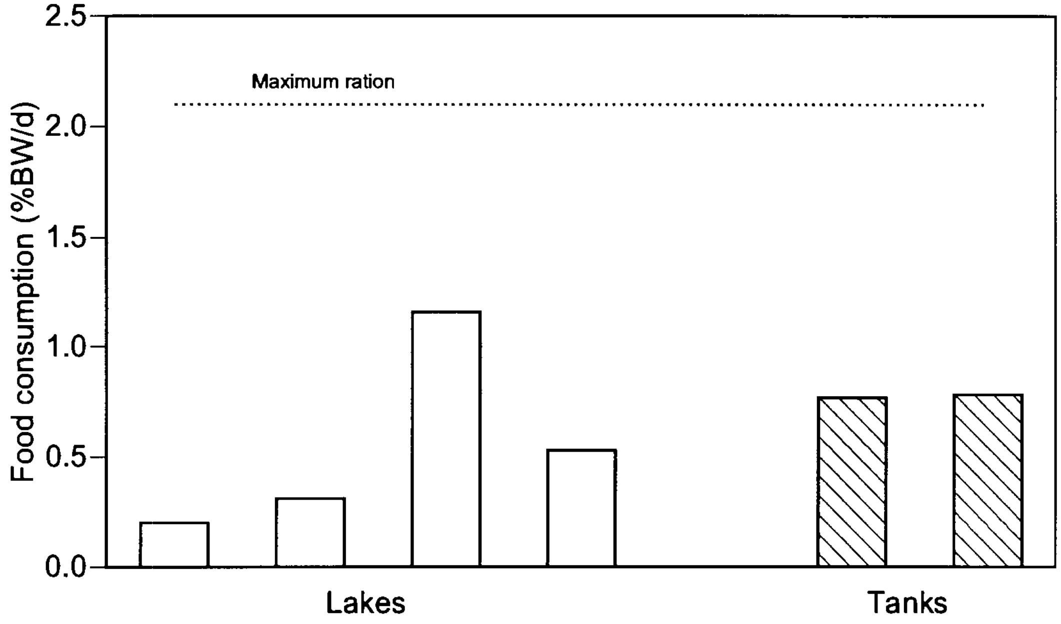

Figure 11.—Comparison of estimated average daily consumption during fall/spring (temperature about 15°C) by adult yellow perch in natural lakes (Table 1), and in experimental tanks with bluegill (Tables 4 and 5). Also shown is the maximum ration which could be evacuated (when fed a 2% meal—Schneider 1973b).

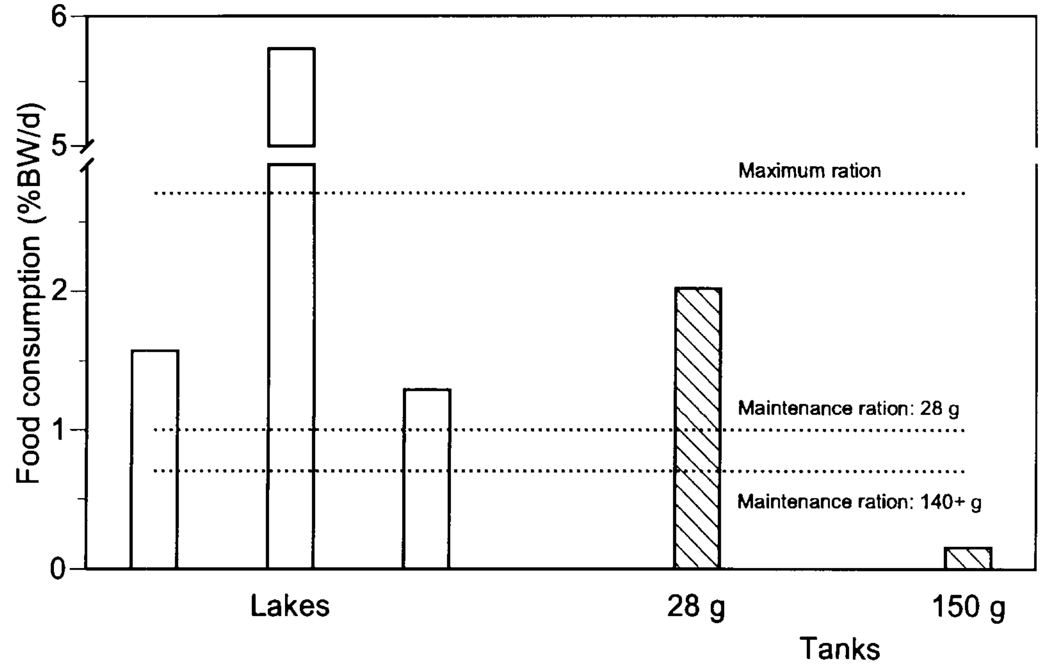

Figure 12.—Comparison of estimated average daily consumption during fall/spring (temperature about 15°C) by walleye in natural lakes (Table 1) and in experimental tanks with bluegill (Table 5). Also shown are the rations required for maintenance of wet body weight for small (28 g—this study) and large (140+ g—Kelso 1972) walleye, and the maximum ration which could be evacuated by 40-570 g walleye (when fed a 2% meal—Swenson and Smith 1973).

Table 1.–Occurrence of sunfish (*Lepomis* spp.) in stomach samples of adult yellow perch collected in winter and fall, and of juvenile and adult walleye collected in fall.

| Lake and county | Predator length (mm) | Dates/ years | *N* Pred. | Void (%) | Sunfish in diet: Freq.[a] (%) | Sunfish in diet: Average /pred.[a] | Sunfish in diet: Identifiable[b](%) | Diet by weight: Total (%BW) | Diet by weight: Sunfish (%) |
|---|---|---|---|---|---|---|---|---|---|
| | | | | **Perch, Winter (December-March)** | | | | | |
| Blueberry Livingston | 152-277 | 17/5 | 184 | 39 | 14 | 0.250 | 92.0 | 0.12 | 59 |
| Cassidy Washtenaw | 152-282 | 33/5 | 587 | 34 | 49 | 1.036 | 94.1 | 0.63 | 77 |
| Cedar[c] Washtenaw | 152-279 | 8/1 | 37 | 5 | 84 | 1.460 | 98.0 | 0.98 | 88 |
| Mill Washtenaw | 152-254 | 17/5 | 165 | 64 | 13 | 0.182 | 50.0 | 0.27 | 54 |
| Sugarloaf Washtenaw | 152-335 | 11/4 | 128 | 41 | 6 | 0.086 | 26.2 | 0.77 | 8 |
| | | | | **Perch, Fall (September-October)** | | | | | |
| Blueberry Livingston | 152-269 | 10/4 | 55 | 11 | 2 | 0.073 | 36.4 | 0.20 | 8 |
| Gilead Branch | 152-295 | 1/1 | 43 | 47 | 0 | 0.000 | 0.0 | 0.31 | 0 |
| Jewett[d] Ogemaw | 152-305 | 12/7 | 208 | 50 | 11 | 0.178 | 61.7 | 0.53 | 58 |
| Marble Branch | 152-284 | 1/1 | 42 | 52 | 0 | 0.000 | 0.0 | 1.16 | 0 |
| | | | | **Walleye, Fall (September-October)** | | | | | |
| Jewett[d] Ogemaw | 203-521 | 12/7 | 671 | 37 | 20 | 0.484 | 42.2 | 1.18 | 36 |
| 6 lakes Northern | 117-340 | 6/2 | 47 | 13 | 8 | 0.128 | 12.5 | 4.31 | 6 |
| 3 lakes Southern | 147-282 | 3/1 | 17 | 18 | 35 | 0.529 | 69.2 | 0.97 | 37 |

[a] Includes all yellow perch and walleye examined, both with and without food.

[b] The percentage of all fish in stomachs which could be identified as *Lepomis* spp.

[c] Resummarized data of Moffett and Hunt (1943).

[d] Restricted prey availability because only bluegill, yellow perch, and walleye occurred in this lake.

Table 2.–Walleye pond experiments during the winters of 1988-89, 1991-92, and 1992-93: summary of initial conditions and resulting survival and growth.

| Treatment and pond number | Pond volume ($m^3$) | Exp. duration (days) | Stocked[a] Walleye (*N*) | Stocked[a] Walleye (g) | Stocked[a] Bluegill (*N*) | Stocked[a] Bluegill (g) | Results Bluegill Survival (%) | Results Bluegill Length change (mm) | Results Walleye Survival (%) | Results Walleye Specific growth (%BW/d) |
|---|---|---|---|---|---|---|---|---|---|---|
| Control | | | | | **1988-89** | | | | | |
| 11 | 1100 | 158 | 0 | 0 | 2200 | 471 | 22 | — | — | — |
| 12 | 1600 | 167 | 0 | 0 | 3200 | 685 | 24 | — | — | — |
| 13 | 2000 | 161 | 0 | 0 | 4000 | 856 | 12.5 | — | — | — |
| Small Walleye | | | | | | | | | | |
| 2 | 1770 | 154 | 30 | 581 | 3400 | 728 | 5.8 | — | 70 | — |
| 3 | 1660 | 144 | 30 | 583 | 3400 | 728 | 0.2 | +17.0 | 100 | -1.805 |
| Large walleye | | | | | | | | | | |
| 7 | 2534 | 155 | 7 | 903 | 5100 | 1091 | 3.9 | — | 100 | -0.839 |
| 8 | 2599 | 148 | 7 | 909 | 5100 | 1091 | 2.5 | — | 43 | — |
| Control | | | | | **1991-92** | | | | | |
| 12 | 1600 | 111 | 0 | 0 | 2527 | 599 | 88 | +0.1 | — | — |
| 14 | 2130 | 112 | 0 | 0 | 3595 | 852 | 92 | +2.2 | — | — |
| Walleye | | | | | | | | | | |
| 7 | 2534 | 110 | 17 | 866 | 4277 | 1014 | 79 | +1.6 | 100 | -0.0599 |
| 13 | 2000 | 111 | 18 | 677 | 3376 | 800 | 47 | +2.6 | 89 | 0.0555 |
| Control | | | | | **1992-93[b]** | | | | | |
| 3 | 1660 | 106 | 0 | 0 | 530 | 285 | 92 | -0.7 | — | — |
| | | | | | 53 | 472 | 89 | +0.7 | | |
| Walleye | | | | | | | | | | |
| 5 | 3536 | 111 | 9 | 3310 | 1200 | 646 | 60 | -1.0 | 78 | -0.0557 |
| | | | | | 120 | 1069 | 78 | -1.8 | | |
| 16 | 2301 | 107 | 6 | 2101 | 800 | 430 | 47 | +1.6 | 100 | -0.0377 |
| | | | | | 80 | 713 | 73 | +0.2 | | |

[a] Average sizes of fish at stocking were: **1988-89 small walleye**--132 mm and 19.4 g; **1988-89 large walleye**--245 mm and 129.5 g; **1988-89 bluegill**--27.8 ± 6.5 mm and 0.214 g; **1991-92 walleye**--189 mm and 51.0 g (Pond 7), 182 mm and 37.6 g (Pond 13); **1991-92 bluegill**--28.3±4.2 mm and 0.24g; **1992-93 walleye**--353 mm and 367.8 g (Pond 5), 349 mm and 350.1 g (Pond 16); **1992-93 bluegill**-- 34.9±3.3 mm and 0.538 g (age-0, first row), 85.7 ±3.6 mm and 8.9±1.3 g (age-1, second row).

[b] First row of bluegill data is for age-0, second row for age-1.

Table 3.–Yellow perch pond experiments during the winters of 1989-90 and 1990-91: summary of initial conditions and resulting survival and growth.

| Treatment and pond number | Pond volume ($m^3$) | Exp. duration (days) | Stocked | | | | Results | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Perch | | Bluegill | | Bluegill | | Perch | |
| | | | (*N*) | (g) | (*N*) | (g) | Survival (%) | Length change (mm) | Survival (%) | Specific growth (%BW/d) |
| Control | | | | | **1989-90** | | | | | |
| 11 | 1100 | 127 | 0 | 0 | 1130 | 253 | 83 | +1.0 | — | — |
| 17 | 2292 | 121 | 0 | 0 | 2450 | 549 | 82 | -0.8 | — | — |
| Adult perch | | | | | | | | | | |
| 2 | 1770 | 99 | 7 | 700 | 1820 | 408 | 57 | +2.9 | 86 | -0.0326[b] |
| 6 | 2826 | 103 | 13 | 1163 | 2900 | 650 | 93 | +0.7 | 62 | -0.1446[b] |
| 13 | 2000 | 103 | 10 | 832 | 2050 | 459 | 51 | +1.6 | 50 | -0.1529[b] |
| Control | | | | | **1990-91** | | | | | |
| 7 | 2620 | 114 | 0 | 0 | 4750 | 1197 | 100[d] | — | — | — |
| 14 | 2130 | 114 | 0 | 0 | 3850 | 970 | 91 | — | — | — |
| Adult perch | | | | | | | | | | |
| 12 | 1497 | 112 | 9 | 662 | 2700 | 680 | 53 | — | 89 | 0.1357[c] |
| 13 | 2000 | 115 | 11 | 893 | 3650 | 920 | 57 | — | 91 | 0.1222[c] |

[a] Average sizes of fish at stocking were: **1989-90 perch**--203 mm and 100 g (Pond 2), 195 mm and 89.5 g (Pond 6), 195 mm and 83.2 g (Pond 13); **1989-90 bluegill**--27.04±4.4 mm and 0.224 g; **1990-91 perch**--186 mm and 71.6 g (Pond 12), 192 mm and 83.2 g (Pond 13); **1990-91 bluegill**--0.252 g.

[b] Within replicated ponds 2,6 and 13, all 10 surviving males lost weight (mean, -0.146 %BW/d); whereas 3 out of 8 females gained weight (mean, -0.0628 %BW/d).

[c] All perch were females.

[d] Final number recovered was 1% greater than recorded number stocked; survival assumed to be 100%.

Table 4.–Overwinter nonpredatory mortality ($N_{np,t}$, number of bluegill), predatory mortality ($N_{p,t}$, number of bluegill), and consumption of bluegill by juvenile walleye or adult yellow perch in ponds calculated from instantaneous rates. The number of bluegill consumed by predators assumes a constant *proportion* of the population died each day due to nonpredatory mortality and a constant *number* of bluegill was consumed daily per predator (Appendix 1, Method #2). Consumption of bluegill is expressed as the daily number per predator ($N_c$), the daily number per gram of predator ($N_{cg}$), and %BW/d ($C_g$). Average predator density for a pond was the geometric mean of the initial and final number present.

| Pond | | Estimated consumption of bluegill | | | |
|---|---|---|---|---|---|
| number | $N_{np,t,t}$ | $N_{p,t}$ | $N_c$ | $N_{cg}$ | $C_g$ |
| **1988-89: Small walleye** | | | | | |
| 2 | 2,391 | 811 | 0.21 | 0.011 | 0.36 |
| 3 | 2,076 | 1,316 | 0.31 | 0.016 | 0.76 |
| **1988-89: Large walleye** | | | | | |
| 7 | 3,502 | 1,397 | 1.29 | 0.010 | 0.30 |
| 8 | 3,339 | 1,631 | 2.41 | 0.020 | 0.62 |
| **1991-92: Walleye** | | | | | |
| 7 | 386 | 498 | 0.27 | 0.0054 | 0.17 |
| 13 | 251 | 1,533 | 0.81 | 0.0211 | 0.67 |
| **Age-0 bluegill, 1992-93: Large walleye** | | | | | |
| 5 | 81 | 399 | 0.45 | 0.0013 | 0.069[a] |
| 16 | 47 | 380 | 0.59 | 0.0017 | 0.092[b] |
| **Age-1 bluegill, 1992-93: Large walleye** | | | | | |
| 5 | 13 | 13 | 0.014 | 0.00004 | 0.034[a] |
| 16 | 8 | 14 | 0.021 | 0.00006 | 0.055[b] |
| **1989-90: Yellow perch** | | | | | |
| 2 | 279 | 498 | 0.78 | 0.0077 | 0.22 |
| 6 | 198[c] | 0[c] | 0[c] | 0[c] | 0[c] |
| 13 | 314 | 686 | 0.94 | 0.0132 | 0.34 |
| **1990-91: Yellow perch** | | | | | |
| 12 | 95 | 1,183 | 1.25 | 0.016 | 0.44 |
| 13 | 136 | 1,420 | 1.18 | 0.013 | 0.35 |

[a] The total walleye consumption of both sizes of bluegills is 0.103 %/d for Pond 5.

[b] The total walleye consumption of both sizes of bluegills is 0.147 %/d for Pond 16.

[c] Based on the average mortality rate for the two control ponds, 546 bluegills were predicted to die due to nonpredatory mortality in Pond 6. Because only 198 bluegills were lost from this pond, no deaths need to be attributed to predation.

Table 5.–Winter and early spring laboratory experiments on consumption of bluegill and growth of walleye and yellow perch, 1988-93.

| Date | Days | Avg. temp. (°C) | Tank | Food | No. preds. | Specific growth (% BW/d) | | | Bluegill consumption[a] | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Dry | Wet | | No. | g/ | |
| | | | | | | average | Average | Max/pred | pred/d | pred/d | (%BW/d) |
| | | | | **Winter walleye, small (176 mm, 34g)** | | | | | | | |
| 4 Dec 91- | | 5.3 | N | Ad lib | 10 | -0.0151 | 0.0018 | 0.0450 | 0.495 | 0.117 | 0.344 |
| 25 Mar 92 | 112 | | S | Ad lib | 9 | -0.0136 | 0.0156 | 0.0700 | 0.496 | 0.118 | 0.336 |
| | | | R | None | 10 | -0.1556 | -0.1111 | -0.0712 | 0.000 | 0.000 | 0.000 |
| | | | | **Spring walleye, small (162 mm, 28 g)** | | | | | | | |
| 24 Apr 92- | 34 | 15.0 | N | Ad lib | 10 | 0.2618 | 0.2889 | 0.4856 | 1.838 | 0.595 | 2.017 |
| 28 May 92 | | | R | None | 5 | -0.5633 | -0.3132 | -0.2145 | 0.000 | 0.000 | 0.000 |
| | | | | **Winter walleye, large (283 mm, 193g)** | | | | | | | |
| 4 Nov 88- | 105 | 5.2 | S | Ad lib | 8 | — | -0.1233 | — | 0.162 | 0.198 | 0.095 |
| 17 Feb 89 | | | | | | | | | | | |
| 22 Dec 92- | 111 | 4.5 | S | Ad lib | 3 | — | 0.0496 | -0.0132 | 0.366 | 0.217 | 0.104 |
| 12 Apr 93 | | | N | Ad lib | 4 | — | 0.0414 | 0.0329 | 0.464 | 0.250 | 0.160 |
| | | | | **Spring walleye, large (273 mm, 156g)** | | | | | | | |
| 24 Apr 92- | 34 | 15.0 | S | Ad lib | 10 | — | -0.1589 | -0.0915 | 0.340 | 0.225 | 0.154 |
| 28 May 92 | | | R | None | 5 | — | -0.1984 | -0.1756 | 0.000 | 0.000 | 0.000 |
| 19 Apr 89- | 5 | 14.4 | S | Ad lib | 8 | —[b] | —[b] | —[b] | 1.450[c] | 1.325[c] | 0.747[c] |
| 24 Apr 89 | | | | | | | | | | | |
| | | | | **Winter yellow perch (184 mm, 70g)** | | | | | | | |
| 10 Dec 90- | 98 | 4.4 | S | Ad lib | 10 | — | 0.0102 | 0.0338 | 0.295 | 0.068 | 0.095 |
| 18 Mar 91 | | | N | Ad lib | 10 | — | 0.0335 | 0.0834 | 0.400 | 0.093 | 0.129 |
| | | | R | None | 10 | — | -0.0442 | -0.0186 | 0.000 | 0.000 | 0.000 |
| | | | | **Spring yellow perch (184 mm, 70g)** | | | | | | | |
| 18 Mar 91- | 14 | 10.8 | S | Ad lib | 10 | —[b] | —[b] | —[b] | 2.357 | 0.556 | 0.769 |
| 1 Apr 91 | | | N | Ad lib | 10 | —[b] | —[b] | —[b] | 2.421 | 0.571 | 0.782 |
| | | | R | None | 10 | —[b] | —[b] | —[b] | 0.000 | 0.000 | 0.000 |

[a] Average number and weight of bluegills voluntarily eaten per predator per day.

[b] Interval too short for a reliable estimate of growth.

[c] Only a 5-day interval representing a peak consumption rate.

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Alan D. Sutton, Graphics
Kathryn L. Champagne, DTP

Appendix 1.–Estimating predator consumption in ponds.

We used two methods to partition bluegill mortality among predatory and nonpredatory sources. The first method is similar to the Baranov catch equation (Ricker 1975), which is used to partition mortality between fishing and natural mortality. In this method we assume that the instantaneous mortality *rates* are constant during the experiment. In the second method we assume that the instantaneous nonpredatory mortality rate is constant, but that predators consume a constant *number* of prey each day (so that the instantaneous predatory mortality rate changes during the experiment). In both methods, nonpredatory mortality rates were estimated for the control ponds.

In the first method, total mortality rates were estimated for the ponds with predators. We subtracted the instantaneous *nonpredatory* mortality rate from the instantaneous *total* mortality rate to estimate the instantaneous *predatory* mortality rate. The number of bluegills lost to predators was estimated as the total number of bluegills lost multiplied by the ratio of the instantaneous rates of predatory and total mortality. The following paragraphs describe this method in detail.

Following Ricker (1975) and using 1 d as the unit of time, the actual total mortality rate for $t$ days ($A_t$) is:

$$A_t = 1 - e^{-Zt} = 1 - N_t/N_0\,, \qquad (1)$$

where $Z$ is the instantaneous total mortality rate ($d^{-1}$), $N_t$ is the number surviving to day $t$, and $N_0$ is the number stocked at $t = 0$. Because no fishing occurred in this experiment, the instantaneous total mortality rate is the sum of the instantaneous rates of predatory ($M_p$) and nonpredatory ($M_{np}$) mortality ($d^{-1}$):

$$Z = M_p + M_{np}\,. \qquad (2)$$

The fraction of the initial population dying by time $t$ due to predation ($v_{p,t}$) (or the expectation of predatory death) is (Ricker 1975):

$$v_{p,t} = A_t M_p/Z\,, \qquad (3)$$

and the fraction of the initial population dying by time $t$ due to nonpredatory causes ($v_{np,t}$) is:

$$v_{np,t} = A_t M_{np}/Z\,. \qquad (4)$$

The instantaneous rate of nonpredatory mortality ($M_{np}$, $d^{-1}$) can be estimated for each control pond:

$$M_{np} = (-1/t)\ ln(1-A_t)\,, \qquad (5a)$$

$$M_{np} = (-1/t)\ ln(N_t/N_0) \qquad (5b)$$

In 1990 and 1991 the predators and the bluegills were stocked on the same day. However, in 1988 and 1989 the predators were stocked 10 to 22 days after the bluegills. The number of bluegills present at the time of predator stocking ($N_s$) was estimated as:

$$ln(N_s) = ln(N_0) - M_{np}\, t_s\,, \qquad (6)$$

where $N_0$ is the number of bluegills stocked, $M_{np}$ is the average instantaneous nonpredatory mortality rate ($d^{-1}$) estimated from the control ponds, and $t_s$ is the number of days between bluegill and predator stocking.

Define $t'$ as the number of days after stocking the predators:

$$t' = t - t_s\,. \qquad (7)$$

Note that if the predators are stocked on the same day as the bluegills, then $t_s = 0$, $t' = t$, and $N_s = N_0$. The instantaneous total mortality rate ($Z$) can be estimated for the ponds with predators:

$$Z = (-1/t')\ ln(N_{t'}/N_s)\,, \qquad (8)$$

and then $M_p$ can be estimated from this $Z$:

$$M_p = Z - M_{np}\,, \qquad (9)$$

where $M_{np}$ is the average value for the control ponds. The estimated total number of bluegills consumed by predators by day $t'$ ($N_{p,t'}$) can be calculated using Equation 3 and $N_s$:

$$N_{p,t'} = v_{p,t'} N_s \, . \qquad (10)$$

This number can then be used to compute the daily number of bluegills consumed per predator or per gram of predator.

In the second method, we assume that predators take a constant total daily *number* of prey ($\Phi$) and that predation losses occur before nonpredatory losses each day. The number of prey surviving to the next day ($N_{i+1}$) is:

$$N_{i+1} = (N_i - \Phi) S_{np} , \qquad (11)$$

where $N_i$ is the number of prey on day $i$, $\Phi$ is the constant number of prey consumed daily by predators, and $S_{np} = e^{-M}$ is the proportion of the prey surviving predation that survive nonpredatory mortality. If both sources of mortality occur during $t$ days, then using Equation 11, the number of prey surviving on day $t$ ($N_t$) is:

$$N_t = N_0 S_{np}^t - \Phi X \qquad (12)$$

where $N_0$ is the initial number of prey, and

$$X = S_{np}^t + S_{np}^{t-1} + \ldots + S_{np}^2 + S_{np}^1 \ ,$$

which simplifies to:

$$X = S_{np}(1 - S_{np}^t) / (1 - S_{np}) \ , \qquad (13)$$

using the formula for the sum of a geometric series. Rearranging Equation 12 yields an equation for the constant daily number ($\Phi$) lost to predators, computed from the initial ($N_0$) and final ($N_t$) numbers of prey and the daily fraction surviving nonpredatory mortality ($S_{np}$):

$$\Phi = (N_0 S_{np} - N_t)(1 - S_{np}) / [S_{np}(1 - S_{np}^t)] \, . \qquad (14)$$

This total number of bluegills consumed per day can then be used to compute the number of bluegills consumed daily per predator or per gram of predator.

Appendix 2.–Weight-length regressions for bluegills used in the overwinter pond experiments, date of fish collection, and average weight predicted from the regression and the length-frequency distribution. The statistics reported are for the equation:

$$\log_{10} W = n + b \log_{10} TL \ ,$$

where $W$ is weight (g), and $TL$ is total length (mm).

| Pond | Date (m/d/y) | Intercept $n$±SE | Slope $b$±SE | $r^2$ | $N$ | Range (mm) | Predicted mean weight (g) |
|---|---|---|---|---|---|---|---|
| | | | **1988-89: Bluegills at stocking**[a] | | | | |
| 3 | 10/21/88 | -4.6890±0.0579 | 2.7098±0.1105 | 0.97 | 20 | 19-40 | 0.187 |
| | | | **1989-90: Bluegills at stocking** | | | | |
| 10 | 11/28/89 | -4.9145±0.0329 | 2.9809±0.0619 | 0.98 | 50 | 21-36 | 0.242 |
| | | | **1989-90: Yellow perch absent** | | | | |
| 11 | 04/04/90 | -5.1592±0.0413 | 3.1612±0.0864 | 0.97 | 46 | 22-38 | 0.284 |
| 17 | 03/29/90 | -4.8865±0.0477 | 2.9859±0.0976 | 0.96 | 44 | 21-37 | 0.242 |
| | | | **1989-90: Yellow perch present** | | | | |
| 2 | 03/29/90 | -5.2433±0.0416 | 3.2138±0.0787 | 0.97 | 50 | 22-40 | 0.343 |
| 6 | 04/02/90 | -5.1292±0.0351 | 3.1426±0.0756 | 0.98 | 42 | 22-37 | 0.274 |
| 13 | 04/02/90 | -5.1905±0.0485 | 3.1634±0.0986 | 0.96 | 46 | 22-39 | 0.283 |
| | | | **1990-91: Yellow perch absent** | | | | |
| 7 | 04/03/91 | -5.1384±0.0267 | 3.1605±0.0823 | 0.98 | 35 | 23-38 | 0.261 |
| 14 | 04/03/91 | -5.4579±0.0294 | 3.3831±0.1058 | 0.97 | 30 | 22-35 | 0.222 |
| | | | **1990-91: Yellow perch present** | | | | |
| 12 | 04/01/91 | -5.3014±0.0259 | 3.2615±0.0706 | 0.98 | 41 | 24-37 | 0.282 |
| 13 | 04/04/91 | -5.3445±0.0323 | 3.2727±0.0888 | 0.97 | 37 | 24-43 | 0.240 |

[a] This sample of bluegills was frozen for 6 days before thawing and measuring length and weight.