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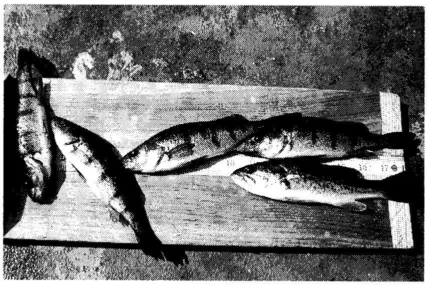
Fish Population Dynamics in Max Lake, a Softwater Wisconsin Lake Subject to Ground-water Pumping

by **Sandy Engel**, DNR Bureau of Integrated Science Services, Woodruff
Michael H. Hoff, U. S. Geological Survey, Ashland
Michael T. Vogelsang Jr., DNR Service Center, Madison
Kent E. Bass and **Jeffrey S. Anderson**, DNR Bureau of Integrated Science Services, Woodruff



Abstract

The annual growth, abundance, biomass, mortality, and diet of yellow perch (*Perca flavescens*) and largemouth bass (*Micropterus salmoides*) were studied in Max Lake, a seepage lake in north-central Wisconsin. Ground water of pH 8.3 was pumped intermittently during ice-free times onto the 9.2-ha lake surface to study responses of the lake ecosystem to decreasing acidity. The pumping raised the pH of Max Lake water, averaged for April-November, from 5.2 (1988-89) to 5.6 (1990-92), 6.2 (1993), and 6.7 (1994-95).

Ground-water pumping failed to alter growth, abundance, biomass, or mortality of yellow perch and largemouth bass 3-7 years old. Compared with "statewide" and north-central Wisconsin populations, the mean total length by age of yellow perch stayed average to 58 mm (149%) above average while that of largemouth bass stayed 70-142 mm (64-78%) below average. The spring abundance and biomass of these yellow perch varied between years by 4-54% while that of largemouth bass declined 5-28% between years after 1991. Meanwhile, rates of total annual mortality *(A),* computed by sequential computations of stock size for fish 4-7 years old, exceeded 40% for yellow perch and decreased from 61% to 27% for largemouth bass.

The summer diets of yellow perch and largemouth bass 2-7 years old, compared for just three years, overlapped in number of prey taxa by 45% in 1992, 76% in 1994, and 42% in 1995. Both fish species ate larvae and pupae of midgeflies (Diptera: Chironomidae) and caddisflies (Trichoptera: Limnephilidae). But yellow perch ate more zooplankton in midwater, especially *Daphnia*, whereas largemouth bass ate more winged insects from the water surface, especially adult dragonflies (Odonata: Corduliidae). Some yellow perch stomachs had moss (*Drepanocladus*) leaves, indicating predation on moss-dwelling insects offshore. No fish were found in largemouth bass stomachs from 1992, but nearly half of the stomachs examined in 1994 and 1995 had remains of age-0 yellow perch or largemouth bass.

Adult yellow perch ate smaller prey, grew faster, and had greater population abundance and biomass than did largemouth bass throughout the study. To improve growth and biomass of largemouth bass in Max Lake, we recommend continued ground-water pumping while stocking minnows (Cyprinidae) as forage and planting native submersed vegetation as refuge.

Contents

Introduction

Fish growth, production, and recruitment can be poor in acidic, softwater lakes with few minerals and nutrients to sustain egg production, prey populations, and fish development (Rahel 1984). We hypothesize that growth of piscivores (fish eaters) will remain below average in softwater lakes deficient in suitable prey fish during summer. Yet alkaline ground water underlies all such lakes in north-central Wisconsin (Attig 1985). Can ground-water pumping improve fish growth and summer forage by raising lake pH and alkalinity?

Alkaline ground water was pumped intermittently for six years onto the open-water surface of Max Lake, a softwater lake without surface inlet or outlet. We studied the growth, abundance, biomass, mortality, and diet of yellow perch *(Perca flavescens)* and largemouth bass *(Micropterus salmoides)*—the lake's principal fish species—before (1989) and during (1990-95) ground-water pumping. We also recorded total lengths and weights of the lake's other fish species: central mudminnows *(Umbra limi)* and white suckers *(Catostomus commersoni).* We discuss how ground-water pumping could improve fish populations in softwater, seepage lakes like Max Lake, though a single year of pretreatment data and variations in fish year-class (cohort) strength limited our analysis of ground-water pumping effects.

Study Area

Located in Wisconsin's Vilas County, Max Lake (latitude 46°01' N; longitude 89°42' W) is a 9.2-ha seepage lake with a maximum depth of 5.8 m and a mean depth (total volume/surface area) of 2.9 m. The lake is surrounded by state forest and peatland, though public access is restricted by a gated private road north of County Road N and west of Highway 51. Beavers (*Castor canadensis*) have built four lodges and felled many trees near the shoreline; otherwise the entire lakeshore remains undisturbed.

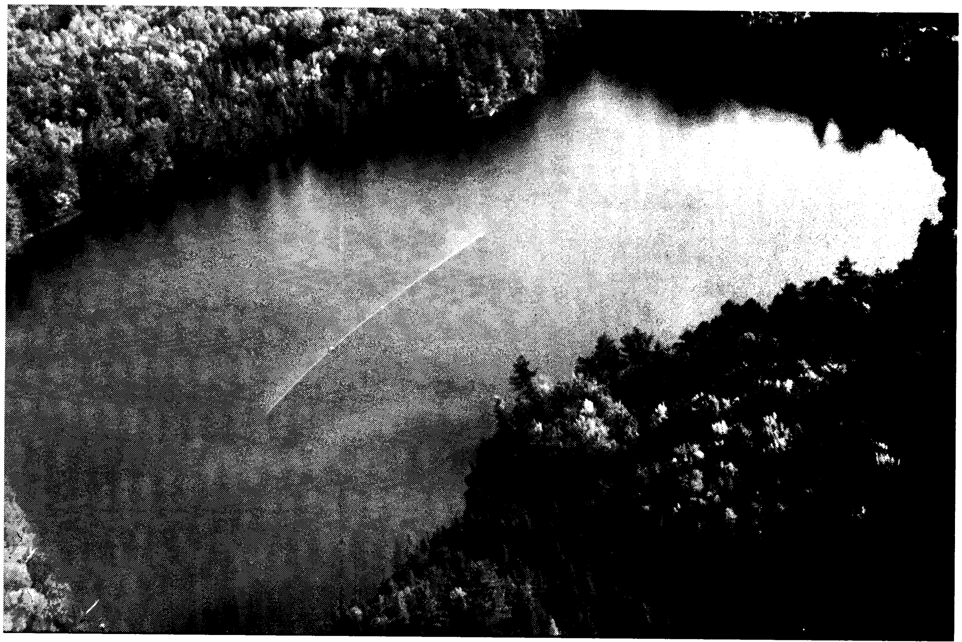


PHOTO: PAUL J. GARRISON

The sylvan watershed of Max Lake photographed from an airplane during October 1990.

Max Lake lies on about 40 m of Pleistocene sediment covering Precambrian bedrock (Attig 1985). Most of the lake is hydraulically mounded: Water moves from the lake to the ground. In 1990, before ground-water pumping began, less than 1% of the lake's water supply came from minor underground seepage along the north shore (Krabbenhoft and Babiarz 1992).

A treelined *Sphagnum* bog borders the north, west, and southwest shores. Lake sedge *(Carex lacustris),* leatherleaf *(Chamaedaphne calyculata),* soft rush *(Juncus effusus),* three-way sedge *(Dulichium arundinaceum),* and water arum *(Calla palustris)*—identified from Fassett (1957) and Gleason and Cronquist (1991)—grow at the water's edge. Patches of variable-leaf spatterdock *(Nuphar variegata)* and floating-leaf bur reed *(Sparganium angustifolium)* cover a sparse carpet of pipewort *(Eriocaulon septangulare)* and water lobelia *(Lobelia dortmanna),* dotted with quillwort *(Isoetes echinospora)* and dwarf watermilfoil *(Myriophyllum tenellum).* A few clumps of fern-leaf pondweed *(Potamogeton epihydrus)* grow off the west shore. Toothed water moss *(Drepanocladus angustifolium),* identified from Grout (1931) and Crum (1976), grows beyond a water depth of 1.5 m and forms a thick bottom turf in which dissolved oxygen becomes depleted (Paul J. Garrison, unpubl. data, 1996).


PHOTO: SANDY ENGEL

Alkaline ground water pumped onto the Max Lake water surface from four aerators connected by tubing to a lakeside well. (Photo taken in May 1993.)

Methods

Ground water was pumped intermittently during ice-free times from a well drawing water at 21-29 m beneath the north shore of Max Lake. The water was delivered through a plastic tube to four floating sprinklers stationed offshore 30 m apart in 1990-92 (Figure 1) and 7-8 m apart in 1993-95. The sprinklers helped disperse the water onto the lake surface, avoiding cold pockets of alkaline ground water.

Water chemistry and chlorophyll samples were collected with a peristaltic pump and vinyl plastic tubing every few weeks from water depths of 0, 3, and 5 m in the ice-free lake. The samples were analyzed for pH by using a pH meter with combination electrode (±0.01) without stirring, acid neutralizing capacity (ANC) by modified Gran titration (U. S. Environmental Protection Agency 1987), calcium and magnesium by inductively coupled plasma (ICP) emission spectroscopy (American Public Health Association 1989), dissolved silica (SiO_2) by automated oxalic acid-molybdate colorimetry (Fishman and Friedman 1989), sulfate by ion chromatography (U. S. Environmental Protection Agency 1983), total phosphorus by persulfate-digestion automated ascorbate colorimetry (U. S. Environmental Protection Agency 1983), and monochromatic chlorophyll *a* by spectrophotometry after membrane filtration, cell wall maceration, and pigment extraction in 90% v/v acetone (Scournia 1978). Sample measurements were volume-weighted for differences in water depth and averaged for each April-November.

Annual growth, abundance, biomass, and mortality were estimated for yellow perch and largemouth bass each spring of 1989 and 1991-95. Within 1-2 days of ice-out in April, we set 4-6 fyke nets (1.2 by 1.5-m frames and 9.5-mm square mesh) perpendicular to the shoreline to catch spawning yellow perch. These fish were released after they were marked by clipping the lower lobe of their tail fin. The nets were set for 2 days in 1989, 3 days in 1991, 4 days each in 1992-94, and 7 days in 1995. We recorded daily captures of marked and unmarked yellow perch to estimate population size and biomass by the Schnabel method (Ricker 1975).

A few weeks later in May, when the inshore water temperature reached 15.6°C, we set 4-8 of the same fyke nets perpendicular from shore to catch and mark largemouth bass before most of them spawned. (A few nests were built before fyke netting ended, when the lake shallows warmed above 18.9°C.) Netting lasted 4-5 days in 1989-94 but was extended to 11 days in 1995 because of low catches. Largemouth bass were released after they were marked by clipping the lower lobe of their tail fin. Marked and unmarked largemouth bass were recaptured a few evenings later by electrofishing with alternating current to estimate population size and biomass by the Bailey-modified Petersen method (Ricker 1975).

Electrofished largemouth bass were held overnight in screened live boxes by shore before being measured, weighed, and sampled for scales: Fewer than 2% of them died overnight. During electrofishing, the inshore water had a mean specific conductance (adjusted to 25°C) of 15 µS/cm before (1989) and 20 µS/cm after (1991-95) ground-water pumping began.

Central mudminnows were caught in the 4-6 fyke nets set for yellow perch in April and in 24 wire minnow traps, some baited with bread, set throughout the lake in April and May. All captured fish were measured, weighed, and released after they were marked by clipping the lower lobe of their tail fin. Sex was determined by color, markings, and fin size (Becker 1983).

All fish caught in fyke nets were measured each spring for total length (±1 mm). To determine age, we removed some scales from up to 10 yellow perch of each sex and 10 unsexed largemouth bass in each 12.7-mm (0.5-inch) total length group. After 1991, we also measured the whole body weight (±2 g) of each fish sampled for scales. Biomass in 1989 and 1991 was estimated from individual fish weights *(W)* computed from simple linear regressions (least-squares method) involving total lengths *(L)* of 114 male yellow perch, 70 gravid and 74 spent female yellow perch, and 99 unsexed largemouth bass all sampled in spring 1992:

Male yellow perch: $\text{Log}_{10} W = -5.2098 + 3.1076 \text{ Log}_{10} L$; $r^2 = 0.960$

Female yellow perch: $\text{Log}_{10} W = -3.9251 + 2.5581 \text{ Log}_{10} L$; $r^2 = 0.720$

All largemouth bass: $\text{Log}_{10} W = -5.1108 + 3.0516 \text{ Log}_{10} L$; $r^2 = 0.967$

Condition factor *(K)*, an index of plumpness (Lagler 1956), was computed from the fresh total lengths and body weights of all fyke-netted fish, assuming a regression coefficient of 3.0: $K = (W/L^3) \times 10^5$.

Population size and biomass were estimated for each year class and 12.7-mm (0.5-inch) total length group. These separate year-class or length-group estimates were summed to compute total population size and biomass by species each spring. Fish sex was ignored in these computations.

Fish age at capture (expressed in years) was determined by counting annuli on scales magnified with a microfiche projector; no ages were back calculated. Pigmented scales were impressed on acetate slides to discern annuli. All scales aged before 1993 were later re-examined to reduce bias in age estimates.

Rates of total annual mortality *(A)* were computed by sequential computations of stock size (Ricker 1975), modified by using abundance estimates instead of catch numbers. We computed mortality rates of cohorts in successive years by dividing the population size of fish age $x + 1$ (say, age 4) by that of fish age x (say, age 3) until each

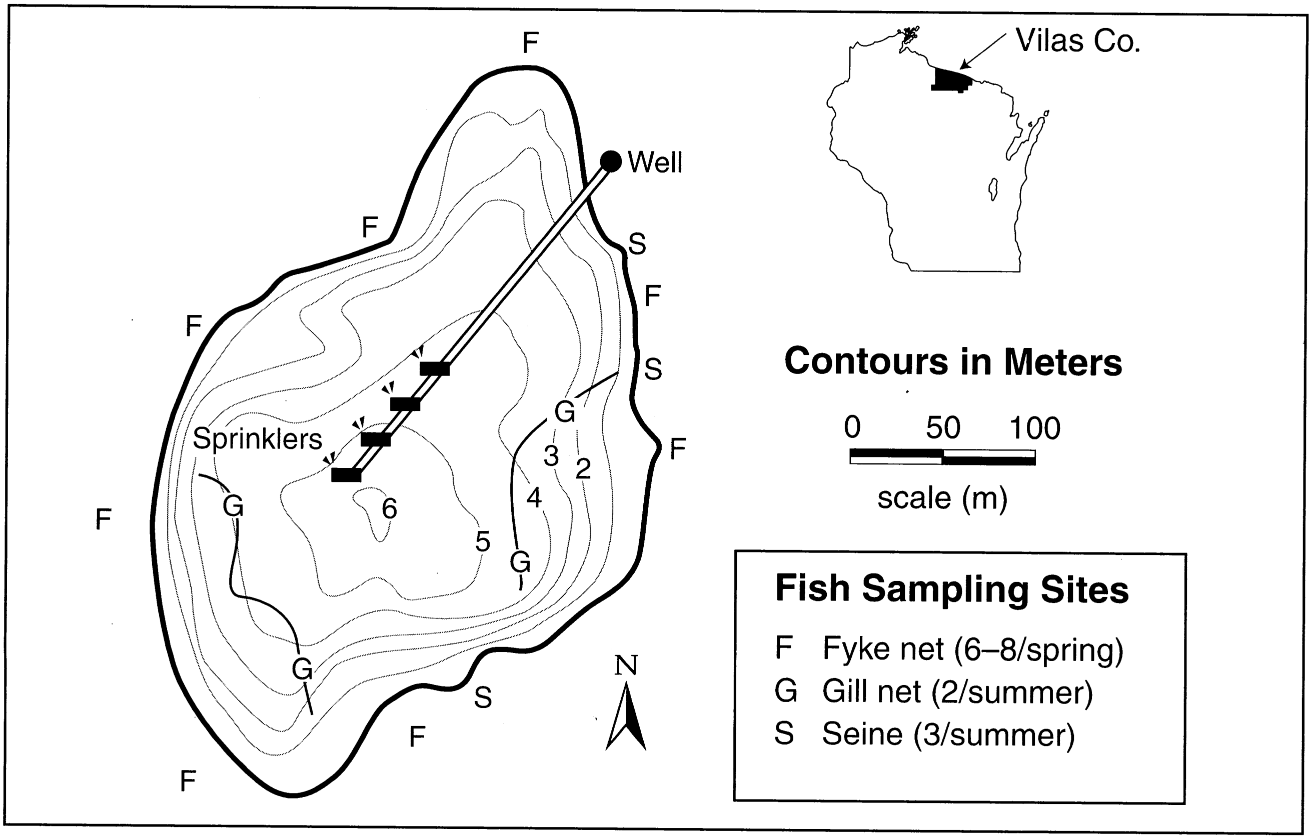


***Figure 1.** Locations of fish sampling sites and ground-water sprinklers on Max Lake, Vilas County, Wisconsin. The entire lakeshore was electrofished.*


PHOTO: SANDY ENGEL

Each spring a fyke net along the shaded south shore of Max Lake had to be set beneath lake ice and lifted the next day by cutting a boat channel over the net.

cohort disappeared from the spring catch. Unlike mortality computations by least-squares regression analysis of catch curves, our method is less biased by year-class and recruitment changes but can be affected by sample size differences among age groups (Jensen 1985).

Stomach contents were examined from yellow perch and largemouth bass that were 1-7 years old. The fish were seined or gill netted in June, July, and August of 1992, 1994, and 1995. Two monofilament nylon gill nets, each 91 m by 1.8 m with five panels of square mesh (25, 38, 51, 64, and 76 mm), were set off the east and west shores in a meandering pattern to catch fish swimming parallel or perpendicular to shore. Both nets were set 4-6 times between an hour before sunrise and an hour after sunset and fished for 1-2 hours. During each gill-netting period, a nylon bag seine (12 m by 3 m with 6.4-mm square mesh) was dragged along the south shore for 30 m, the east shore for 55 m, and the northeast shore for 61 m. Lakeside bog and woody debris kept us from seining more of the shoreline.

All seined and gill-netted fish except fry were measured for total length (±1 mm) and whole body weight (±2 g); scales were sampled to determine age at capture. Fish caught in 1992 were preserved for 72 hours in 10% formalin before being measured; correction factors (Engel 1974) were used to convert these measurements to fresh total lengths and body weights. Fish caught in 1994 and 1995 were measured live and penned in a screened box near shore for up to 7 days to assess handling stress, mainly from gill netting: 65% of yellow perch and 58% of largemouth bass died after the 1994 netting; 43% of yellow perch and 7% of largemouth bass died after the 1995 netting. Pumping stomachs allowed at least some fish to survive.

Fish stomach contents were obtained by dissection in 1992 and flushing in 1994 and 1995. We used a submersible bilge pump to squirt filtered lake water through tubing into the gullets of fish inverted over a funnel. The prey were flushed through the funnel into nylon cloth bags, which then were labeled, tied shut, and stored in a jar of preservative. A forceps was sometimes used to dislodge food items in the gullets. Stomach contents were preserved in 10% formalin (1992) or 70% ethanol (1994 and 1995) until examination.

To assess pumping effectiveness, stomachs in 1994 were also dissected from 32% of yellow perch and 14% of largemouth bass whose stomachs had been flushed: Only 13% of yellow perch stomachs and 25% of largemouth bass stomachs retained any zooplankton or insect larvae after being pumped.

The entire contents of dissected or pumped stomachs were first blotted dry with filter paper and weighed on an analytical balance (±0.0001 g), calibrated with standard weights. The contents were then placed in a petri dish to be identified and counted. Genera of zooplankton and other noninsects were identified with keys in Edmondson (1959), Pennak (1989), and Thorp and Covich (1991); families or genera of aquatic insects were identified with keys in Wiggins (1977), Hilsenhoff (1981), and Merritt and Cummins (1984); and families or genera of terrestrial insects were identified with keys in Borror and DeLong (1964). Prey items were weighed separately by size or taxa after being counted. Stomachs with 0.010 g or less of food were judged empty.

For each prey taxon, food habits were expressed as *percent by stomach* (percentage of total stomachs with > 0.010 g of food), *percent by number* (percentage of the total number of prey eaten), and *percent by weight* (percentage of the total blotted wet weight of prey eaten). These three percentages were summed to compute *absolute importance values*, which were divided by the sum of all importance values to give *relative importance values* (George and Hadley 1979). *Percent dietary overlap* was calculated as the percentage of prey taxa common to both diets (Odum 1971:144).

PHOTO: SANDY ENGEL

A fyke net being lifted in April 1992 on Max Lake by Michael T. Vogelsang Jr. (left) and Daniel E. Jacoby (right).

Unpaired Student's *t*-tests, Pearson product-moment correlations *(r),* and 95% confidence limits *(CL)* around means were calculated with Statistix® version 4.1 (Anonymous 1994) to compare annual changes in growth (mean total length by age), abundance, biomass, and mortality rates of each species and yellow perch sex. Differences between sample means were judged significant at an α-level of 0.05. Test assumptions of approximate normality and equal variances were evaluated on raw and $\log_{10}$– or square root-transformed data with the Shapiro-Wilk cumulative frequency distribution (Shapiro and Wilk 1965) and Bartlett's test of homogeneous variances with X^2 approximation (Snedecor and Cochran 1989). Outliers were identified from box plots (Anonymous 1994) and the data rechecked for typographical or calculation errors. Some tests were repeated without the outliers to assess their effect on the particular database.

Results

Water Chemistry Changes

Beginning in 1990, ground water was pumped from April to November for six years. Annual pumping delivered 3.8-23.4 million liters of alkaline water at 1.0-1.6 L/sec (Table 1). Because the pH of Max Lake water decreased each winter, from supersaturation of CO_2 (Garrison et al. 1996), water had to be pumped for a few weeks after ice-out and then intermittently during summer and fall to keep the pH at target level. To reach a target pH of 7.0, however, we had to run the pump longer and at a higher rate.

Prior to the initial pumping, Max Lake had water high in acids (pH 5.2) and low in minerals and nutrients (Table 2). After four years of pumping, mean pH of the ice-free lake water increased to 6.7 while mean ANC increased 15 times to 73.7 μeq/L. Meanwhile, the concentrations of calcium, magnesium, and total cations nearly doubled. Mean pH for April-November remained below target pH, because decrease in pH of the lake water during ice cover required more ground-water pumping than expected.

The lake water also became more fertile from the ground-water pumping (Garrison et al. 1996). Concentrations of total phosphorus and especially dissolved silica increased while that of sulfate decreased. Phytoplankton responded with a 2.3-fold increase in monochromatic chlorophyll *a* from 1990 to 1995. Floating-leaf bur reed dramatically spread along the east, west, and north shores in 1995; fern-leaf pondweed become more common off the west shore. No changes were seen in other macroscopic plants, so any relation between ground-water pumping and growth of such plants remains obscure.

Fish Population Dynamics

Growth. Fish growth in Max Lake differed by age and species. Mean total length by age for largemouth bass remained significantly below the Department of Natural Resources (DNR) "statewide" and north-central Wisconsin averages (Anonymous 1990), significantly above these averages for yellow perch ages 2-5, and near these averages for yellow perch ages 6-8 (Figure 2). Age-3 yellow perch in spring 1995 averaged 206 mm—54 mm longer than yellow perch "statewide" and 39 mm longer than age-3 largemouth bass in Max Lake. Even yearling (age-1) yellow perch averaged more than half the mean total length of age-3 largemouth bass. Annual growth slowed after age 4 for yellow perch and after age 3 for largemouth bass, though such older bass rarely grow more than 76 mm/year in Wisconsin (Bennett 1937).

As largemouth bass in Max Lake aged, their mean total length fell below average for the species. Max Lake bass were 70-142 mm (64-78%) short of the north-central Wisconsin average by age 7 (Figure 3). Growth was far below that of largemouth bass from larger and more alkaline lakes of northern Wisconsin, such as nearby Big Muskellunge Lake (Bennett 1937).

Only 11 of 837 largemouth bass fin clipped in Max Lake during 1989-95 had grown at least 356

Table 1. *Duration and volume of ground-water pumping at Max Lake.*

		Duration of Pumping		Water Volume Pumped	
Year	Target pH[a]	Dates	Total Days	Million Liters	L/sec
1990	5.6	18 Apr - 15 Nov	96	8.4	1.0
1991	5.6	8 May - 3 Aug	44	3.8	1.0
1992	6.1	6 May - 1 Oct	47	4.1	1.0
1993	7.0	7 May - 23 Nov	198	20.8	1.0 - 1.6
1994	7.0	5 May - 8 Nov	138	18.5	1.5 - 1.6
1995	7.0	19 Apr - 12 Dec	176	23.4	1.5 - 1.6

[a] Target pH is the pH of ice-free Max Lake water to be achieved by ground-water pumping.

Table 2. *Mean chemistry of ground water and lake water during ice-free times at Max Lake.*

		Lake Water (April-November Means)						
Measure	Groundwater	1988-89[a]	1990	1991	1992	1993	1994	1995
pH	8.3	5.2	5.5	5.6	5.7	6.2	6.7	6.8
ANC (μeq/L)	1,213	-4.9	4.2	9.5	12.6	26.7	63.7	105.1
Calcium (μeq/L)	848	51	63	60	55	59	88	103
Magnesium (μeq/L)	494	31	37	37	35	36	46	52
Mon. chlorophyll *a* (μeq/L)	—	1.8	1.9	3.6	2.2	2.1	4.6	4.4
Silica dioxide (μeq/L)	20	0.05	0.09	0.09	0.11	0.13	0.21	0.32
Sulfate (μeq/L)	41	108	105	91	82	76	67	65
Total cations (μeq/L)	1,467	101	125	123	118	121	165	191
Total phosphorus (μg/L)	95	8	7	10	9	12	12	11

[a] Lake water prior to ground-water pumping.

mm. The three longest largemouth bass—498 mm, 508 mm, and 511 mm—were fyke netted only in spring 1989.

Female yellow perch grew faster on average than males, being significantly longer and heavier each year at ages 2-7 (Figure 4). Such females outgrew males as well in east-central Wisconsin's Lake Winnebago (Weber and Les 1982). Gravid and spent females together averaged 41 mm longer and 58 g heavier than males of combined ages 2-8 in 1992-95. Gravid females, however, averaged 29 g heavier than spent ones without any significant difference in mean total length. Mean condition factor, however, was not found to differ significantly between the sexes for most age groups.

Abundance. The spring population size of yellow perch ages 3-7 averaged 2,144 ± 230 fish (mean ± 1 SE) for the six years studied, varying between estimates by 10-17% in 1989-93 and 54% each in 1993-94 and 1994-95 (Table 3). The population size of largemouth bass ages 3-7, in contrast, averaged 1,230 ± 267 fish for these years, rising 159% in 1989-91 and falling 37% in 1992-93 and 26-27% in subsequent years. Although yellow perch remained 1.1-3.0 times as numerous as largemouth bass within years, no significant correlation was found between years of high yellow perch abundance and those of high or low largemouth bass abundance. The estimated spring abundances of fish ages 3-7 and those 150-405 mm long were not found to differ significantly among years for yellow perch ($P = 0.09$) or largemouth bass ($P = 0.89$).

Spring fyke nets caught many juvenile fish, nearly all of them yellow perch. Yellow perch catches were dominated by yearlings in 1989, 1994, and 1995 and by adults 3-5 years old in 1991-93 (Figure 5). Largemouth bass catches, however, included fewer than 2% of fish under 3 years old or 150 mm long; none of the bass were under 2 years old or 125 mm long. Inshore fyke nets, as well as electrofishing, can be ineffective at catching juvenile fish that remain off-

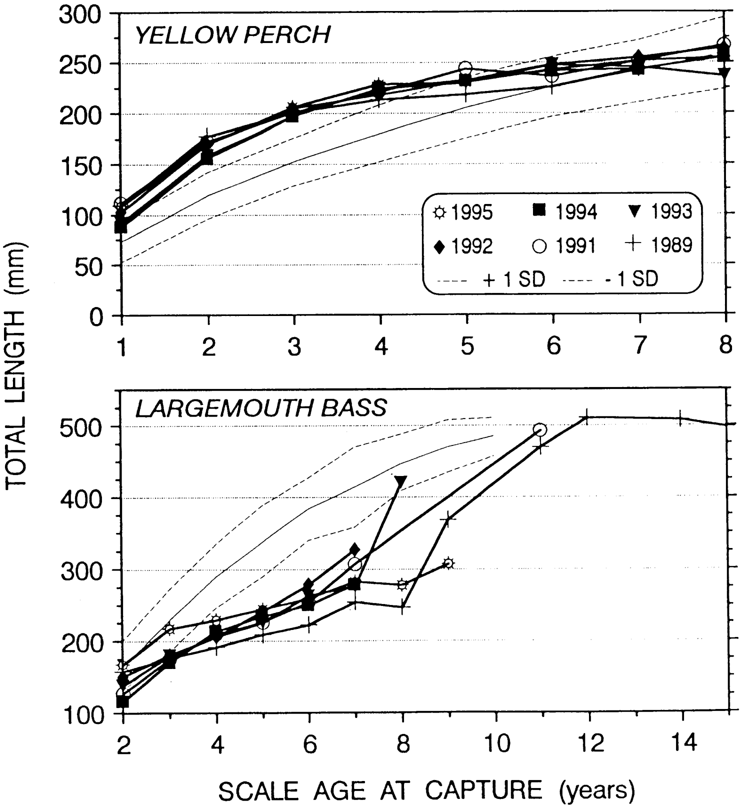


Figure 2. Growth (mean total length by age) of yellow perch and largemouth bass in Max Lake, compared with "statewide" averages in the DNR Fisheries Management Handbook (Anonymous 1990). Note differences in scales between panels.

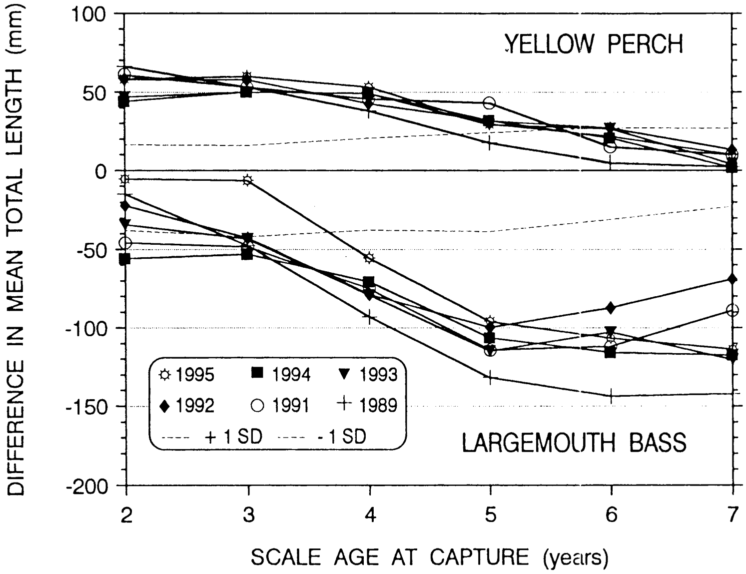


Figure 3. Differences in mean total length by age of yellow perch and largemouth bass between Max Lake and averages for these species in north-central Wisconsin (Anonymous 1990). Mean length differences above the 0-mm line (positive values) indicate fish of larger average length for their age; those below this line (negative values) indicate fish of smaller average length. Dashed lines join sample standard deviations (SD) for yellow perch (+1 SD above 0-mm line) and largemouth bass (-1 SD below 0-mm line) in these north-central Wisconsin populations.

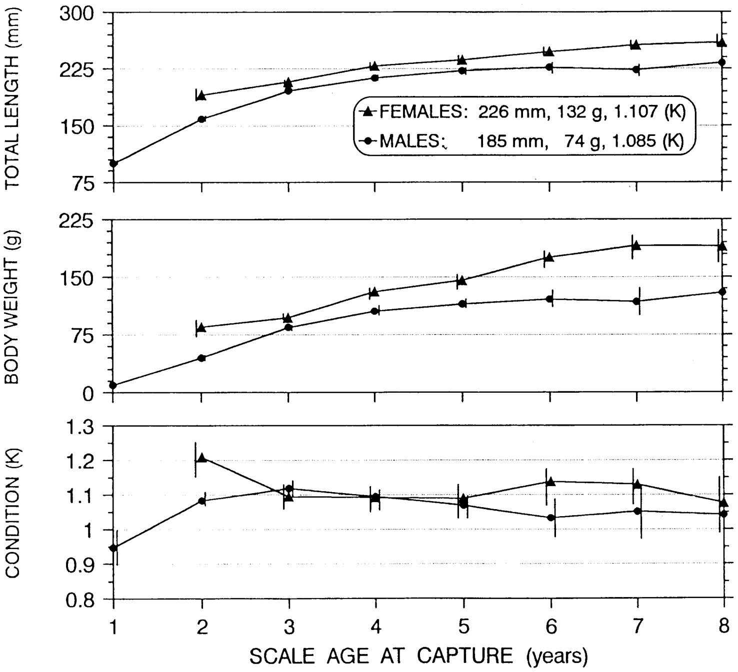


Figure 4. *Total length, body weight, and condition factor by age of yellow perch sampled each April from 1992 to 1995 in Max Lake. The legend notes mean values for ages 2-8. Vertical bars denote 95% confidence intervals offset to the right (females) or left (males) of each mean value.*

shore or inactive in spring (Maraldo and MacCrimmon 1981), though poor survival and recruitment can also reduce juvenile catches.

Few old fish were marked. Fyke nets caught only 8% of all yellow perch and 12% of all largemouth bass older than 5 years; fewer than 1% of both species were older than 7 years. Although fyke nets and electrofishing can catch such older fish (Lagler 1956), natural mortality and distribution offshore—especially of old (large) female yellow perch—could have reduced the number caught.

Spring fyke nets caught significantly more male than female yellow perch, though the sex ratio of fyke net catches varied by age. Males accounted for 73% of the total yellow perch catch for 1989-95, though 74% of all males were 1-3 years old whereas only 39% of all females were this young (Figure 6). Female yellow perch sexually matured by age 3, a year after males, and were

Table 3. *Abundance, biomass, and total annual mortality for yellow perch and largemouth bass in Max Lake (estimate ± 95% confidence limits) by year sampled and pH of lake water.*

Year (Apr or May)	pH Range (Apr-Nov)	Abundance Ages 3-7	Biomass (kg) Ages 3-7	Mortality (%) Ages 4-7
Yellow perch				
1989	4.9 - 5.4	2,322 ± 94	248 ± 31	—
1991	5.3 - 5.8	2,718 ± 102	257 ± 31	—
1992	5.5 - 6.2	2,305 ± 94	248 ± 31	54.7
1993	5.5 - 6.7	2,534 ± 99	305 ± 34	—
1994	6.5 - 7.0	1,173 ± 67	140 ± 23	64.3
1995	6.3 - 7.1	1,811 ± 83	190 ± 27	42.9
Largemouth bass				
1989	4.9 - 5.4	931 ± 60	73 ± 17	—
1991	5.3 - 5.8	2,407 ± 96	169 ± 26	—
1992	5.5 - 6.2	1,514 ± 76	133 ± 23	60.7
1993	5.5 - 6.7	1,120 ± 66	116 ± 21	35.2
1994	6.5 - 7.0	811 ± 56	92 ± 19	27.3
1995	6.3 - 7.1	597 ± 48	87 ± 18	27.2

[a] Mortality rates could not be computed for either species in 1989 and 1991 owing to missing abundance estimates for earlier years, or for yellow perch in 1993 owing to increased estimated abundance with age.

mostly larger than 178 mm when fyke netted. In spring, males are more vulnerable to fyke nets, because males move inshore earlier than females, linger on the spawning grounds, and spawn more than once during the season (Craig 1987).

Yellow perch spawning began a few days before complete ice-out (Figure 7), especially in spring 1993 when ice-out was nearly a week later than in spring 1995. (Ice was still present along the south shore of Max Lake when fyke nets were first set each April.) When netting began, spent females made up 0% of all females (196 mm or longer) caught in 1992, 30% in 1993, 0% in 1994, and 6% in 1995—most spawning had yet to occur. When netting ended 4 days later, spent females made up 64% of all females (196 mm or longer) in 1992 and 93% in 1993—most spawning had ended. These spawning runs lasted about 8 days centered around complete ice-out. But the spawning runs in 1994 and 1995 continued after our fyke nets were removed: Spent females on the last day of netting made up only 7% in 1994 and 26% in 1995 of the total female catch.

Yellow perch and largemouth bass that hatched in 1988 dominated the Max Lake fish community from 1991 until 1993 (Figure 8). This year class made up 56% (1991), 44% (1992), and 24% (1993) of the yellow perch population and 67% (1991), 46% (1992), and 32% (1993) of the largemouth bass population. The total estimated abundance of largemouth bass in 1991, for example, swelled to a significant 1.9 times the six-year average. By 1994, however, the 1988 year class made up only 5% of the yellow perch population and 7% of the largemouth bass population.

The 1989-92 hatches of yellow perch and largemouth bass were weaker than the 1988 hatches. But the 1993 and 1994 hatches of yellow perch became dominant, with age-1 fish making up 36% of all yellow perch in 1994 and 50% of all yellow perch in 1995; age-2 fish accounted for 18% of all yellow perch in 1995. Because of gear bias, the year-

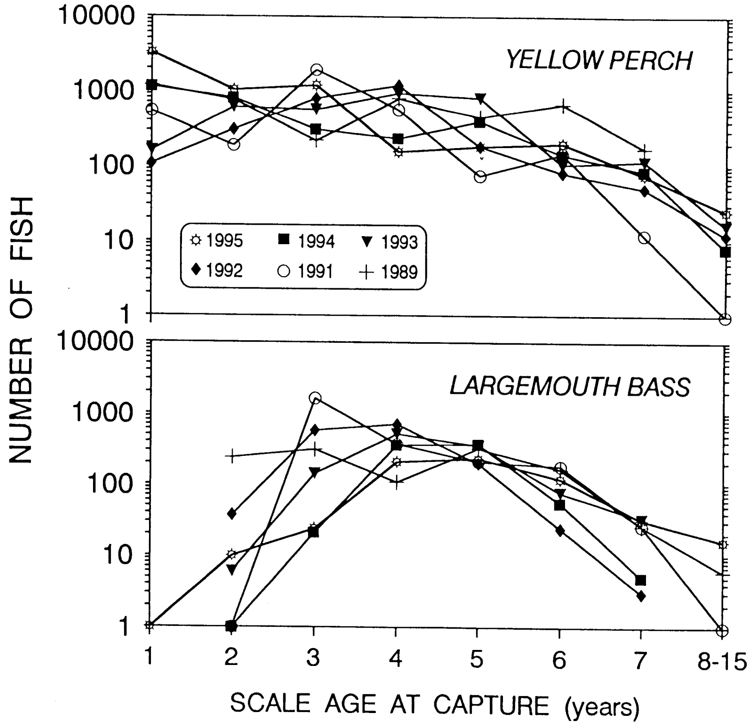


Figure 5. *Annual population size by age of yellow perch and largemouth bass estimated each spring in Max Lake.*

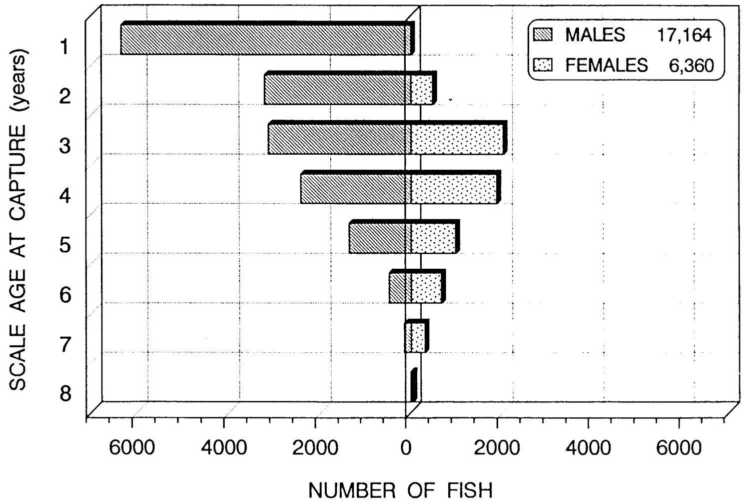


Figure 6. *Estimated abundance by age of male and female yellow perch sampled each April from 1989 to 1995 in Max Lake. The legend notes total abundance summed by sex for all years.*

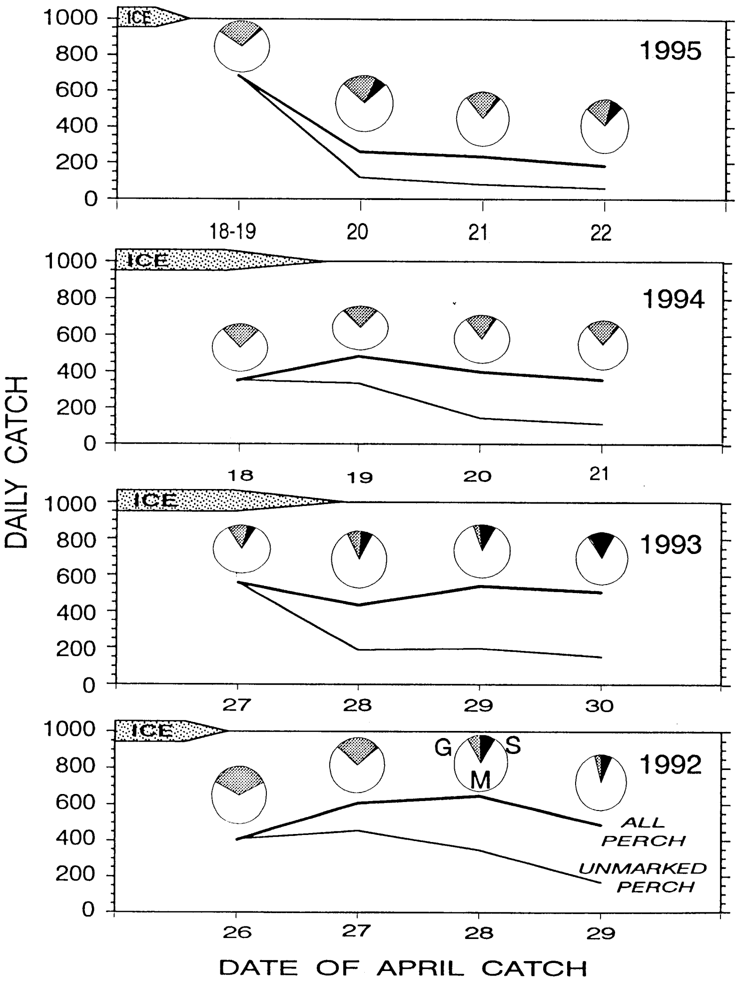


Figure 7. *Daily fyke net catch of marked and unmarked yellow perch (196 mm or longer) each April from 1992 to 1995 in Max Lake. Circles above graph lines show proportion of males (M) to gravid females (G) and spent females (S) in daily catch. Note differences in sampling dates among years.*

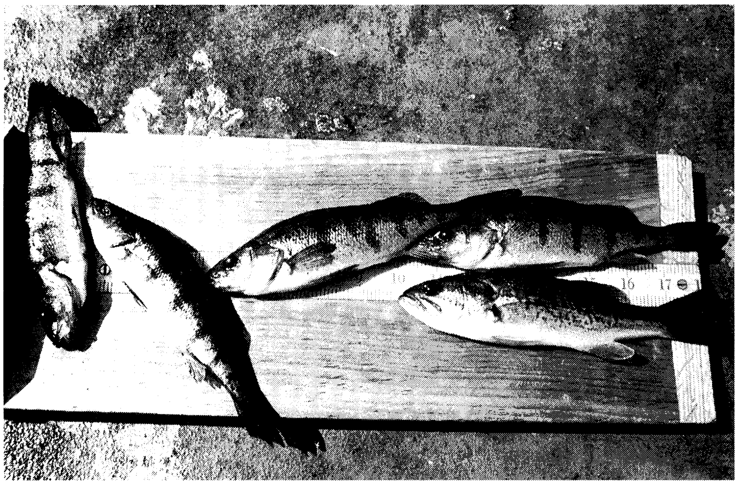


PHOTO: SANDY ENGEL

Four yellow perch and one largemouth bass (lower right) fyke netted in April 1992 are about to be measured and marked by fin clipping.

class strength of largemouth bass hatched after 1992 could not be assessed unless sampling had continued after 1995. Year-class strength, however, can be highly variable (Clady 1977) owing to yearly differences in spring warmup and wind action (Kramer and Smith 1962).

Not enough central mudminnows were fyke netted or minnow trapped to estimate total abundance for any year. The number of central mudminnows fin clipped after 4 days of fyke netting for yellow perch in April, as a measure of relative abundance, was 26 in 1992, 71 in 1993, 140 in 1994, and 98 in 1995. Few mudminnows were caught in baited or unbaited minnow traps, whether the traps were set in shallow or deep water. Captured fish had scale ages of 1-5 years.

Two white suckers, both males, were fyke netted one to several times each spring. We identified them from previous fin clips and dorsal markings. The fish hatched in 1987, probably escaped from a bait bucket before fyke netting began in 1989, and reached 500 mm and 533 mm long by April 1995.

Biomass. Because yellow perch ages 3-7 were significantly more numerous and grew faster than largemouth bass of this age range, their population biomass (collective weight) in spring was 1.4-3.4 times that of all largemouth bass within years (Table 3). The spring population biomass of yellow perch ages 3-7 averaged 231 ± 24 kg (mean ± 1 SE) for the six years studied, rising between estimates by 4-23% in 1989-93, falling 54% in 1993-94, and rising 36% in 1994-95. The spring population biomass of largemouth bass, in contrast, averaged 112 ± 14 kg for the six years, rising between estimates by 132% in 1989-91 and falling 5-21% between estimates in 1991-95. No significant correlation was found among spring population biomass estimates of these species.

Male and female yellow perch fyke netted in spring differed in mean size, with females significantly heavier and longer than males (Figure 9). This size difference could be due to sampling bias:

Males mature and move inshore to spawn at an earlier age than females (Craig 1987). Nearly two-thirds of all spent females marked in fyke nets were at least 229 mm long, indicating that smaller (younger) females were scarce or waited to spawn when longer (or older).

Dominance of the 1988 year classes had opposite effects on the biomass of these populations after 1991. As young yellow perch dominated the fish community, their fast growth eventually increased population biomass, whereas slow growth of aging largemouth bass kept weight gain to a minimum, dampening changes in population biomass.

Mortality. Despite almost no angling, rates of total annual mortality for yellow perch and largemouth bass ages 4-7 varied between 27% and 64% in 1992-95 (Table 3). Natural mortality rates for adult largemouth bass, however, were higher in two acidic, softwater lakes of Upper Peninsula Michigan (Clady 1977). Mortality rates for largemouth bass in Max Lake decreased by more than one-half after 1992, perhaps because of poor recruitment from year classes formed after 1988.

Diet. The summer diets of yellow perch and largemouth bass ages 2-7 overlapped in number of prey taxa by 45% in 1992, 76% in 1994, and 42% in 1995. Larval and pupal midgeflies (Diptera: Chironomidae and some Ceratopogonidae) and caddisflies (Trichoptera: Limnephilidae and some Polycentropodidae, Phrygaenidae, and Leptoceridae) were common to both diets (Figure 10). Zooplankton (Crustacea), mayfly nymphs (Ephemeroptera), and spiders (Arachnida) at times were common to both diets.

Yellow perch ate more zooplankton in midwater, whereas largemouth bass ate more aerial insects from the water surface (Table 4). Zooplankton made up 70-88% of all prey abundance in the yellow perch diet, especially *Daphnia* and some *Holopedium*, *Ophryoxus*, and *Polyphemus*. Only yellow perch ingested *Drepanocladus* leaves and thus ate moss-dwelling prey in deep water,

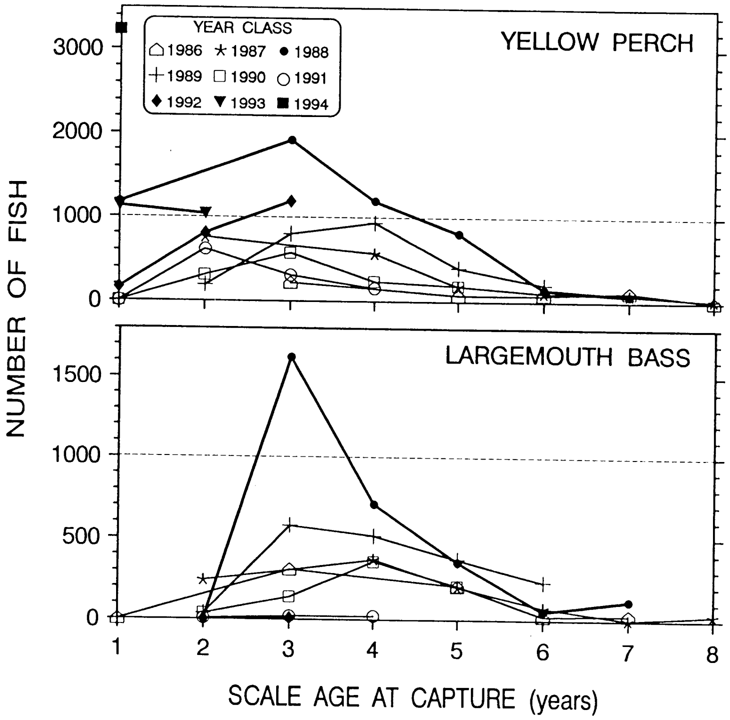


Figure 8. *Year-class abundance by age of yellow perch and largemouth bass in Max Lake. Year classes with at least one age group above 1,000 fish are shown by solid symbols. Lines of increasing year-class abundance with age are sampling artifacts. Note identical x-axes (scale age at capture) but different y-axes (number of fish).*

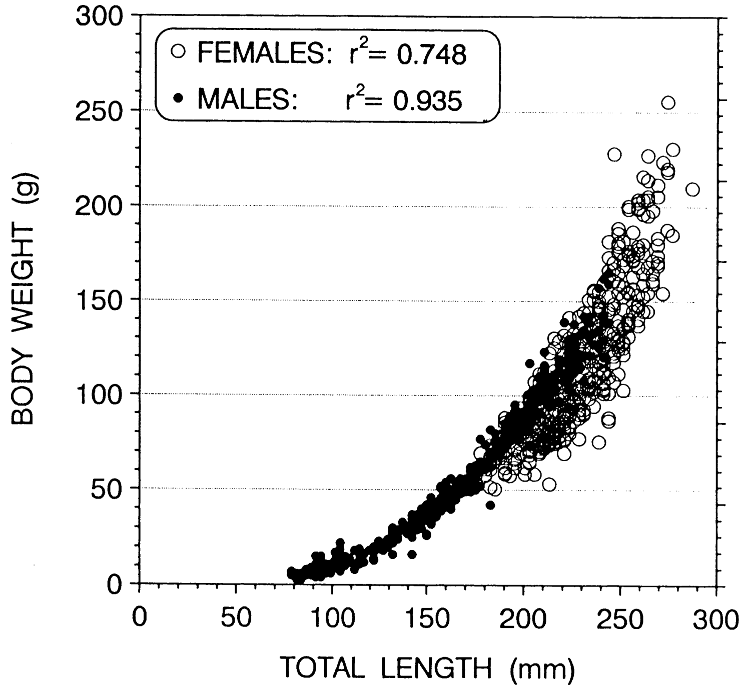


Figure 9. *Weight-length relations of male and female yellow perch fyke netted each April from 1992 to 1995 in Max Lake, based on fresh total lengths and body weights of 493 males and 497 females.*

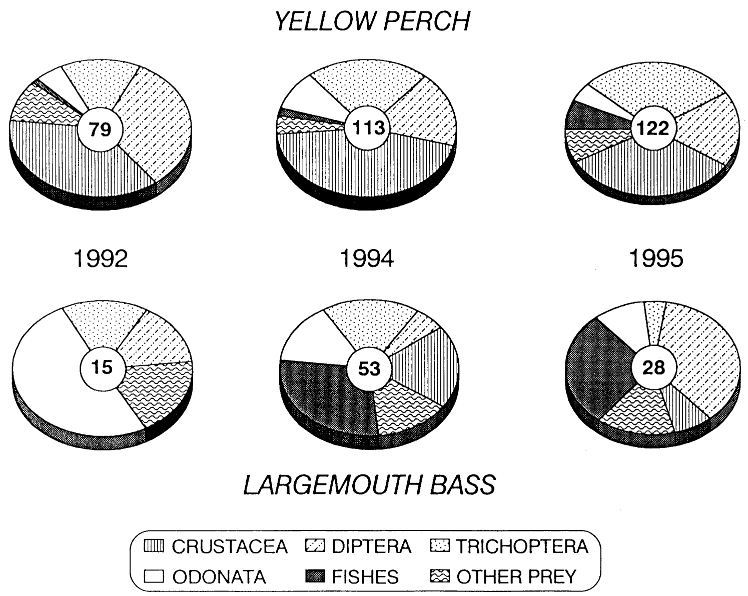


Figure 10. *Relative importance values of prey in stomachs of Max Lake yellow perch (top half) and largemouth bass in the summers of 1992, 1994, and 1995. The number of stomachs with >0.010 g of food is given within each pie chart. See Table 4 for list of other prey.*

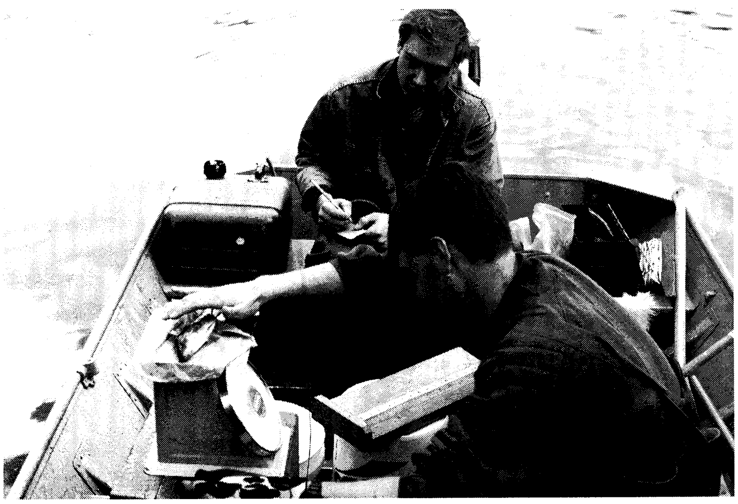


PHOTO: SANDY ENGEL

Christopher N. Hornung (rear) and Kent E. Bass (front) measuring and weighing yellow perch fyke netted in April 1993.

especially larvae of midgeflies and caddisflies. Insects made up 44-99% of all prey abundance in the largemouth bass diet, especially dragonfly nymphs and adults (Anisoptera: Aeshnidae, Corduliidae, Libellulidae, and Cordulegastridae) and some damselfly nymphs (Zygoptera: Coenagrionidae), beetles (Coleoptera: Dytiscidae), true bugs (Hemiptera: Corixidae and Gerridae), and treehoppers (Homoptera: Membracidae).

The diets varied among years, with both fish species eating significantly more insect taxa and zooplankton after 1992. Yellow perch ate twice as many prey items in 1994 as in other years; largemouth bass ate 4 times as many items in 1994 and 9 times as many items in 1995 as they ate in 1992. More largemouth bass ate midgefly larvae in 1995 (84% of all stomachs with food) than in earlier years when the diet was more varied. Yellow perch continued to eat few fish, but largemouth bass increased their intake of fish from 0% in 1992 to 54-58% of all stomachs with food in 1994-95. Largemouth bass ate mainly age-0 yellow perch and largemouth bass, plus a few central mudminnows. With each year, therefore, yellow perch became more planktivorous while largemouth bass became more piscivorous.

Discussion

The fish community of Max Lake is typical of "centrarchid" (Rahel 1984) or *"Umbra-Perca"* (Tonn and Magnuson 1982) lakes of northern Wisconsin: Low acidity excludes darters (Percidae) and minnows (Cyprinidae), but adequate winter aeration (dissolved oxygen remained > 2.0 mg/L in Max Lake) permits yellow perch and largemouth bass to survive despite the acidity. Even with adequate aeration, acidic lakes have fewer fish species than more alkaline ones (Graham 1993), especially when pH stays below 6.2 (Wiener et al. 1984).

Standing crops of largemouth bass can be low in softwater lakes (Moyle 1956) and show a positive correlation with carbonate concentration (Carlander 1955). Low calcium levels (Max Lake calcium averaged only 51-63 μeq/L during April-November of 1990-93) can limit egg production, bone development, and survival of invertebrate prey. But a sparse community of submersed vascular plants can also be limiting, by providing little habitat in shallow water for macroinvertebrate or fish prey. Together, low calcium and sparse plants can severely limit largemouth bass growth and production (Kelso and Johnson 1991).

Unlike largemouth bass, yellow perch can survive and grow well in these softwater lakes. The perch hatch early in

Table 4. *Percentage of the prey abundance in yellow perch and largemouth bass stomachs from Max Lake during the summers of 1992, 1994, and 1995.*

	Yellow Perch			Largemouth Bass		
Prey 1992	**1994**	**1995**	**1992**	**1994**	**1995**	
Crustacea	70.4	92.3	88.5	0.0	27.9	3.7
Insects	27.2	7.5	11.3	98.6	43.9	92.5
Aerial and surface insects	0.1	<0.1	0.5	52.7	16.5	5.6
Diptera (adults)	0.0	<0.1	<0.1	12.2	1.3	0.8
Trichoptera (adults)	0.0	<0.1	<0.1	6.8	0.8	0.3
Coleoptera (adults)	0.1	0.0	<0.1	1.4	0.5	0.0
Hemiptera (Gerridae)	0.0	0.0	<0.1	4.1	0.5	1.7
Odonata (adults)	0.0	<0.1	0.0	24.3	1.4	0.6
Hymenoptera (adults)	0.0	<0.1	0.0	1.4	3.2	0.0
Homoptera (adults)	0.0	<0.1	0.4	2.7	8.5	2.1
Submersed insects	27.1	7.5	10.8	45.9	27.4	85.9
Diptera (larvae, pupae)	23.1	5.3	4.2	6.8	1.9	85.4
Trichoptera (larvae, pupae)	2.5	1.8	5.1	6.8	19.5	<0.1
Ephemeroptera (larvae)	1.3	0.1	0.9	5.4	0.1	0.2
Coleoptera (larvae)	<0.1	<0.1	<0.1	5.4	1.3	0.3
Hemiptera (except Gerridae)	<0.1	<0.1	0.0	2.7	0.8	0.0
Odonata (larvae)	0.2	0.2	0.5	17.6	3.8	0.7
Megaloptera (larvae)	<0.1	0.0	0.0	1.4	0.0	0.2
Neuroptera (larvae)	0.0	<0.1	0.0	0.0	0.1	0.0
Arachnids	2.3	0.2	<0.1	1.4	0.6	0.2
Fish	<0.1	<0.1	0.1	0.0	27.6	3.5
Total Diet						
Prey items	11,577	45,112	16,743	74	1,021	1,311
Prey items/stomach with food	145	399	137	5	19	47
Stomachs examined	83	113	139	16	56	31
Stomachs with food	79	113	122	15	53	28
Prey taxa ingested	21	26	34	19	32	27

PHOTO: SANDY ENGEL

Jeffrey S. Anderson flushing the stomach contents from a largemouth bass through a funnel into a nylon mesh bag.

spring, consume zooplankton, and then browse macroinvertebrates such as midges, beetles, and amphipods on logs, rocks, and sediment (Lott et al. 1996). Rapid growth on an insect diet, in turn, permits an early shift to a fish diet—if suitable fish are available—when the perch reach a total length of about 150-200 mm (Clady 1974). A plethora of insect prey can also be found on branched underwater foliage with large surface areas (Krecker 1939, Mrachek 1966), though we found few insects on the sparse unbranched pipewort and water lobelia of Max Lake. Yet at least some yellow perch ate insects from the tufted moss *(Drepanocladus)* that covers much of the lake bed offshore. This moss may have served as a feeding station for the yellow perch, hastening their shift to an insect diet and contributing to rapid growth early in life.

Most largemouth bass, in contrast, hatch too late for predation on age-0 yellow perch or central mudminnows, yet the bass must store enough fat to survive their first winter (Keast 1985). Largemouth bass that hatch late are subject to cannibalism (DeAngelis and Coutant 1979) and slow growth before winter (Miranda and Hubbard 1994). Those shifting early to a fish diet improve their growth and first winter survival (Aggus and Elliott 1975). Such hatching and feeding differences create a bimodal length distribution by fall (Gutreuter and Anderson 1985), with the smaller size class disappearing in winter (Toneys and Coble 1979).

Fish typically increase in the diet as largemouth bass age (Snow 1971), though some insects are consumed throughout life (Kramer and Smith 1962). For example, as largemouth bass aged in a 4.2-ha southern Wisconsin lake they ate more fish and larger insects (Engel 1988). But growth slows when the bass fail to switch to a fish diet: Largemouth bass stocked in nearby Spruce Lake, a bog lake nearly three-fourths the surface area and maximum depth of Max Lake, mainly ate insects to grow above average for northwestern Wisconsin as juveniles but below this average as adults (Hoff 1986, Newman and Hoff 1994).

Largemouth bass growth, abundance, and biomass in Max Lake failed to improve with ground-water pumping through 1992, when pH of the ice-free lake water had increased to 5.7 and calcium levels were 55 µeq/L (averaged yearly during open water). Their poor growth coincided with weak year classes of yellow perch in 1989-92 rather than with ground-water pumping. Because spring fyke nets and electrofishing sampled few largemouth bass under age 3, year-class strength and growth of largemouth bass that hatched after 1992 can first be detected only in spring 1996, after pH of the ice-free lake water will have been raised to 6.8 and calcium levels to 103 µeq/L.

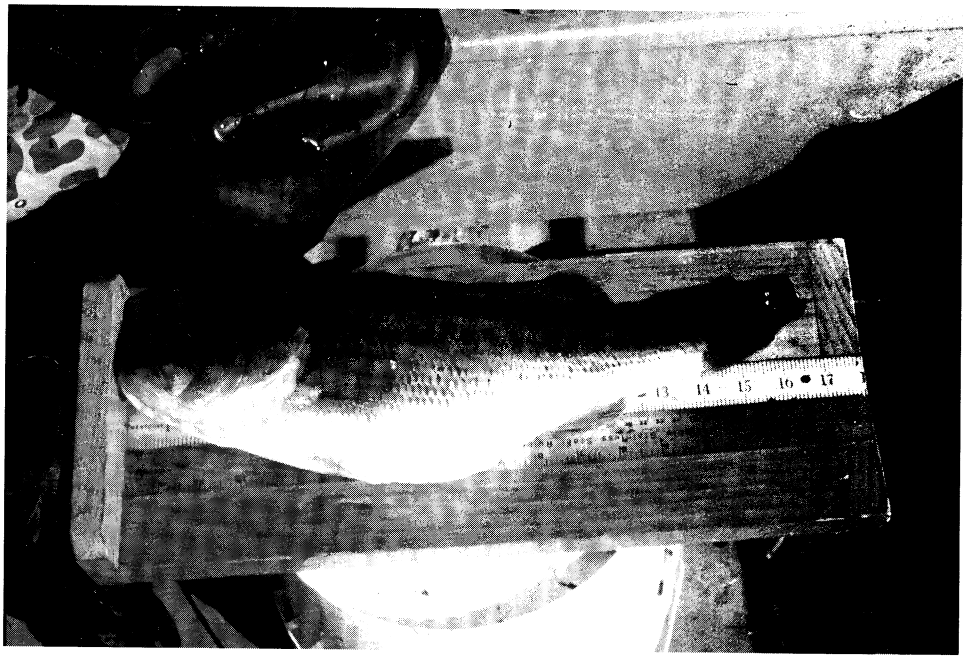


PHOTO: SANDY ENGEL

A largemouth bass 427 mm long—one of only 11 largemouth bass longer than 356 mm—that was fyke netted, marked, and released in Max Lake during May 1993.

Summary

1. Ground-water pumping in April-November of 1990-95 delivered a total of 78.9 million liters of alkaline water to Max Lake. This raised the mean pH to 6.7 and mean ANC to 105.1 µeq/L in the ice-free lake. Total phosphorus and especially dissolved silica also increased with ground-water pumping. Phytoplankton standing crop, measured by chlorophyll *a* concentration, increased while fern-leaf pondweed and especially floating-leaf bur reed spread.
2. Yellow perch grew average to above average for populations "statewide" and in north-central Wisconsin, though growth slowed after age 4. Female yellow perch averaged longer and heavier than male yellow perch, though mean condition differed little between sexes for most ages. Largemouth bass grew much slower than average, lagging 70-142 mm by age 7. Largemouth bass averaged 200 mm long at age 4, a total length yellow perch averaged when age 3.
3. The spring abundance of yellow perch ages 3-7 varied between estimates by 10% in 1989-93 and 54% in the next two years. The spring abundance of largemouth bass ages 3-7, in contrast, rose 159% between 1989 and 1991 estimates and fell 26-37% in subsequent years. Adult yellow perch remained 1.1-3.0 times as abundant as adult largemouth bass. Spring fyke nets caught over 20% yearling yellow perch but no yearling largemouth bass, whereas fewer than 1% of largemouth bass and no yellow perch were 8 years or older.
4. Yellow perch spawned for about a week, starting a few days before complete ice-out. Females averaged 1-2 years older than males. Fyke nets caught 3-5 times as many males as females, though more females were caught as spawning progressed.
5. The spring population biomass of yellow perch varied 1.4-3.4 times that of largemouth bass ages 3-7 and differed between estimates by 5% in 1989-91, 22% in 1991-92, and 36-54% in the next two years. The spring biomass of largemouth bass ages 3-7, in contrast, rose between estimates by 132% in 1989-91 and fell 5-21% in subsequent years.
6. Rates of total annual mortality varied among years for yellow perch but decreased from 61% to 27% for largemouth bass.
7. The 1988 year classes of yellow perch and largemouth bass dominated until 1993, accounting for over 30% of the estimated spring abundance and biomass for fish ages 3-7. The 1993 and 1994 year classes of yellow perch also became dominant, increasing overall yellow perch abundance after 1994.

8. The summer diets broadly overlapped, although yellow perch fed mainly on midwater zooplankton or bottom-dwelling larvae of midgeflies and caddisflies, whereas largemouth bass fed mainly on larger insects at the water surface or lake bottom. Aerial and surface-dwelling insects accounted for fewer than 1% by number of the yellow perch diet but 6-53% of the largemouth bass diet. Fish remains were not found in largemouth bass stomachs in 1992 but occurred in 54-58% of bass stomachs with food in 1994-95.

Management Implications

Pumping ground water into softwater, seepage lakes to improve habitat for sportfish populations could fail unless the fish community is diversified and the plant habitat expanded. We suspect the forage fish in Max Lake became too big for newly hatched bass and too scarce for older bass. Pumping ground water to increase alkalinity, including calcium for egg production, cannot itself improve largemouth bass growth.

Hatching 4-6 weeks earlier than largemouth bass, yellow perch outgrew the young-of-year bass. Being gape-limited, largemouth bass have difficulty swallowing prey fish whose body depth exceeds the width of the bass mouth (Hambright 1991, 1994). Largemouth bass, therefore, are more effective predators on minnows than sunfish (Lagler and DeRoth 1952) and even prefer them to sunfish (Swingle 1949).

A forage fish species hatching later than yellow perch and growing more slowly may improve first-year growth and survival of largemouth bass in Max Lake. We recommend stocking bluntnose minnows (*Pimephales notatus*) or fathead minnows (*P. promelas*) while holding the pH of Max Lake water above 6.5 for normal hatching and growth of these prey species. These minnows occur in softwater lakes of northern Wisconsin and hatch in summer (Hubbs and Cooper 1936, Moyle 1973, Becker 1983)—about 4-8 weeks later than yellow perch and central mudminnows—providing small prey fish when young-of-year largemouth bass need to become piscivorous. Both species lay adhesive eggs on the undersides of submerged objects, such as sunken logs (Becker 1983), and thus would have ample spawning sites in Max Lake. Fathead minnows are especially hardy, survive handling well, and can be purchased from bait dealers (Dobie et al. 1956), but they need a pH above 5.9 for adequate reproduction and a pH above 6.5 for normal growth (Mount 1973). Such minnows failed to reproduce, for example, when stocked as prey for largemouth bass in acidic Spruce Lake nearby (Hoff 1986).

But reproducing populations of these minnow species in Max Lake could alter the size structure of the zooplankton community (Hambright and Hall 1992) and compete with yellow perch and largemouth bass for insect prey. Predation on minnows could also increase mercury concentrations in piscivores (Rask and Metsälä 1991, Futter 1994), though raising the pH of ice-free lake water would reduce the bioavailability of methyl mercury (Driscoll et al. 1994).

To expand refuge and foraging habitat for largemouth bass, as well as their fish and invertebrate prey, we recommend planting native underwater foliage such as purple-flowering bladderwort *(Utricularia purpurea),* clasping-leaf pondweed (*Potamogeton richardsonii*), variable-leaf pondweed *(P. gramineus),* and green watermilfoil *(Myriophyllum verticillatum).* These plants grow well in softwater lakes of northern Wisconsin (Wilson 1939, Nichols and Yandell 1995). Their branching foliage expands the surface area for invertebrate colonization (Engel 1988) and protects prey fish from overpredation by yellow perch and largemouth bass (Sullivan and Atchison 1978). Continued ground-water pumping can supply minerals and nutrients needed to encourage the growth of these plants.

Expanding the forage base of young-of-year largemouth bass with plant-dwelling invertebrates can improve largemouth bass growth after hatching and speed their shift to piscivory (Olson 1996). Macroscopic plants can also protect nests from wind action and allow maximum warmup of lake shallows in summer (Maraldo and MacCrimmon 1981). The plants can be collected from area lakes and planted in Max Lake as bundles of 3-5 shoots bound by rubber band with an 8-penny nail inserted for ballast.

Changing the water chemistry, fish community, and inshore habitat through continued ground-water pumping and judicious stockings of native fish and plants will mean a new and different ecosystem. Such intensive management, however, would be inappropriate for many lakes, and a lake management plan should be developed before stocking or planting. Yet experience gained from Max Lake could help managers improve sportfish production in other softwater, seepage lakes.

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We dedicate this report to the memory of Gregory I. Quinn, DNR water resources technician *extraordinaire* who, with partner Gerald D. Wegner, collected water chemistry and plankton samples on Max Lake.

About the Authors

All five authors studied Max Lake while working for the DNR Fish Research Section at Woodruff.

Sandy Engel trained in limnology and fishery biology at Indiana University- Bloomington and the University of Wisconsin-Madison. He worked on Max Lake after 1991 and continues to work as a DNR aquatic ecologist. He is stationed at the DNR Research Center, 8770 County Highway J, Woodruff, Wisconsin 54568. E-mail: engels@dnr.state.wi.us

Michael H. Hoff trained in fishery biology at the University of Wisconsin-Stevens Point and Tennessee Technological University at Cookeville. He worked on Max Lake in 1989-91 and is now a research fishery biologist with the Biological Resources Division of the U. S. Geological Survey, Lake Superior Biological Station, 2800 Lake Shore Drive East, Ashland, Wisconsin 54806. E-mail: michael_hoff@nbs.gov

Michael T. Vogelsang Jr. trained in fishery management at the University of Wisconsin-Stevens Point. He worked on Max Lake in 1991 and 1992 as a limited term employee and now works in the DNR Water Program as a fishery biologist on the Yahara River chain of lakes; he is stationed at the Madison Service Center, 3911 Fish Hatchery Road, Fitchburg, Wisconsin 53711. E-mail: vogelmj@dnr.state.wi.us

Kent E. Bass trained in water resources at the University of Wisconsin-Stevens Point. He worked on Max Lake in 1993 and 1994 as a limited term employee and can be contacted through Steven P. Newman, 8770 County Highway J, Woodruff, Wisconsin 54568.

Jeffrey S. Anderson trained in wildlife ecology at the University of Wisconsin-Madison. He worked on Max Lake in 1995 as a limited term employee and resides at 768 Clark Street, Hammond, Wisconsin 54015.

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Wendy M. McCown, Managing Editor
Patricia A. Duyfhuizen, Copy Editor
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Metric-U.S. Equivalents

1°C = (°C x 1.8) + 32°F
1 g = 0.035 oz (avoirdupois)
1 ha = 2.47 acres
1 kg = 1,000 g = 2.205 lb
1 L = 1.057 quarts = 33.8 oz (U. S. liquid)
1 m = 1,000 mm = 3.28 feet
1 mg $CaCO_3$/L = 19.6 μeq/L
1 mm = 0.10 cm = 0.039 inches

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