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Ecological factors affecting muskellunge (Esox masquinongy)

reproduction in midwestern lakes

by

Michael Paul Dombeck

An Abstract of

A Dissertation Submitted to the

Graduate Faculty in Partial Fulfillment of the

Requirements for the Degree of

DOCTOR OF PHILOSOPHY

Approved:

In Charge of Major Work

For the Major Department

For the Graduate College

Iowa State University
Ames, Iowa
1984

Ecological factors affecting muskellunge (*Esox masquinongy*) reproduction in midwestern lakes

Michael Paul Dombeck

Under the supervision of Bruce W. Menzel
From the Department of Animal Ecology
Iowa State University

Natural reproduction of muskellunge *Esox masquinongy* has failed in many waters that formerly supported self-sustaining populations. Laboratory studies showed high muskellunge egg mortality associated with high biological oxygen demand (BOD) substrates where hypoxic conditions developed at the substrate-water interface. Measured dissolved oxygen concentration (DO) at the substrate-water interface in muskellunge spawning sites in eight midwestern lakes showed that four lakes had high DO (mean, 6.0-8.4 mg/liter) and little microstratification, and support self-sustaining muskellunge populations. The remaining four lakes showed extreme DO microstratification and hypoxia (mean, 0.4-2.4 mg/liter) at the substrate-water interface. Populations of the latter are almost solely supported by stocking.

Qualitative and quantitative observations of spawning areas in the eight lakes showed that suitable spawning area characteristics include low BOD substrates, dense stonewort *Chara* sp. beds, or reservoirs where water level is lowered annually, resulting in substrate

aeration. Reproductive failure is associated with spawning areas characterized by deep organic matter accumulations and dense macrophyte growth. Improvements of spawning habitat to prevent or alleviate DO depletion are among the options available to manage this species.

A method to obtain DO measures within 8 mm of the bottom was developed using oxygen-permeable dialysis tubing to obtain a sample, followed by a modification of the micro-Winkler technique. In controlled experiments, results showed that DO within dialysis tubing reach 99% equilibrium (via diffusion) with environmental DO within 3 hours in flowing water and 5 hours in stagnant water.

Statistical analysis of ecological information on 117 selected lakes showed that nine variables accounted for 57% of the variability in natural muskellunge reproduction. Conditions identified as most strongly promoting reproduction were limited northern pike abundance, rising springtime water level, high alkalinity, and high shoreline development factor in drainage lake systems. When organized by discriminant function analysis, 58% of the lakes were classified identically to manager-estimated reproductive level, and 91% were classified within ± 1 reproductive level.

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GENERAL INTRODUCTION

The muskellunge (Esox masquinongy) is a prized gamefish in northern states and Canada. It is Wisconsin's official state fish and the feature fish species of the United States Forest Service-Eastern Region. The native range of the muskellunge is centered in the Great Lakes states with lesser extensions into the major drainages of the northeast (Crossman 1978). The muskellunge occupies about 1% of the total freshwater area in North America, compared to 54% occupied by the northern pike Esox lucius and 32% by the walleye Stizostedion vitrium (Carlander et al. 1978). It is estimated that the majority of this water lies within National Forest boundaries in the Great Lakes states. On many of these waters, the Forest Service is the sole or primary landowner. Various management practices affect this species. A recent report submitted to the Chief's office by the Eastern Region cited the importance of the muskellunge and concern for its habitat.

Despite its widespread popularity, the muskellunge faces an uncertain future. In many areas where the species once maintained healthy natural populations, it has been extirpated or is sustained only through artificial propagation and stocking. Over the long term, a more desirable approach to muskellunge management would be to identify ecological factors contributing to the species decline followed by corrective measures. Several hypotheses have been advanced to account for the decline: (1) competitive superiority of the congeneric northern pike when the two species occur syntopically (Inskip and Magnuson 1983;

Oehmcke et al. 1974); (2) overharvest (Bimber and Nicholson 1981); and (3) reproductive failure due to loss or alteration of habitat (Trautman 1981).

The focus of this research concerns the last hypothesis; however, the first hypothesis is also addressed to a lesser extent. The impacts of man's activities on the muskellunge are innumerable, some being quite obvious while others remain very subtle or completely unapparent. The damming of streams has blocked migrations to spawning habitat. Activities such as draining marshes and channelizing rivers and streams have eliminated vast spawning areas (Trautman 1981). Improper water level management can result in high egg and fry mortality. Increased sedimentation can cause egg mortality and reduces spawning habitat through the siltation of formerly clean substrates and the elimination of weed beds (Muncy et al. 1979). Additionally, the invasion of formerly exclusive muskellunge waters by northern pike has been associated with declining muskellunge populations (Inskip and Magnuson 1983; Johnson 1981).

The economic value of the muskellunge is substantially higher than most freshwater gamefishes. The large size to which this species grows, its excellent fighting ability, and the difficulty encountered in catching a legal-sized fish all contribute to its trophy status (Miles 1978). The average economic value of a warm water angler-day in Michigan was estimated to be $25 by Talhelm et al. (1979). An average of 20 angler days of effort is required to catch a legal-size fish, placing the economic value of each muskellunge over 76 cm at $500 or more. Taylor and Irwin (1980) estimated 1.42 million muskellunge angler days in Wisconsin in 1980 and projected 1.56 million in 1985. Taylor and Irwin also stated that a fewer number of fish will be available for harvest by 1985 with increasing demand and declining habitat as prime factors. They projected that by 1990 muskellunge harvest in Wisconsin will increase by 17% while 8% of the present habitat will be lost. Communities such as Cass Lake, Minnesota, Hayward and Eagle River, Wisconsin, and many others have substantial economic dependence upon nearby muskellunge fisheries. Both the economic and biologic implications of muskellunge habitat management are, therefore, far reaching.

The maintenance of muskellunge fisheries through stocking programs alone appears increasingly economically questionable. Muskellunge have proven difficult to rear on artificial diets (Graff 1978) and hatchery costs are high. The present cost of 25-35 cm muskellunge is $7.50 each (Kalepp Fish Farms, Dorchester, Wisconsin, USA) not including stocking costs. Furthermore, survival of stocked hatchery reared muskellunge to legal size is typically 10% or less (Johnson 1978). Using these data, the net investment in a 76 cm muskellunge from hatchery stock is $75.

Detailed descriptions and analyses of muskellunge spawning and early life habitat are limited in the literature. Muskellunge spawning habitat protection or enhancement is difficult or impossible without such information. This study was sponsored by the United States Forest Service and facilitated through a cooperative agreement between the Forest Service and State of Wisconsin. It was designed to provide a basis for the development of muskellunge spawning habitat management guidelines through a synthesis of information obtained from this study and the literature.

Explanation of Dissertation Format

The general design of the research was a product of Dombeck with the assistance of the Program of Study Committee. All laboratory and field data were generated by Dombeck. Program of Study Committee members provided expertise in data analysis and manuscript preparation as follows: Roger W. Bachmann, limnology; Paul N. Hinz, statistics; and Bruce W. Menzel, biology.

The dissertation follows the alternate format with each part representing a manuscript for publication with authorship, title, and publication status as follows: (1) Dombeck, M. P., B. W. Menzel, and P. N. Hinz. 1984. Muskellunge spawning habitat and reproductive success. Transactions of the American Fisheries Society 113:205-216; (2) Dombeck, M. P., R. W. Bachmann, and B. W. Menzel. A method for measuring oxygen in aquatic microzones. Submitted to the Journal of Freshwater Ecology; and (3) Dombeck, M. P., B. W. Menzel, and P. N. Hinz. Natural muskellunge reproduction in midwestern lakes. Submitted to the Proceedings of the International Muskellunge Symposium. The General Introduction reviews the problem in general, provides background justification and the overall project objective. The General Summary is, in part, an abridged version of a fourth manuscript:

Dombeck, M. P. Muskellunge habitat management with emphasis on reproductive habitat, submitted to the Proceedings of the International Muskellunge Symposium. It is designed to provide the resource manager with a foundation for implementing muskellunge habitat management measures based upon a synthesis of the literature and results of this study in a non-technical format.

MUSKELLUNGE SPAWNING HABITAT AND REPRODUCTIVE SUCCESS

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PART I. MUSKELLUNGE SPAWNING HABITAT AND REPRODUCTIVE SUCCESS

Abstract

Reproduction of muskellunge *Esox masquinongy* has failed in many waters that formerly supported self-sustaining populations. Laboratory experiments were conducted to isolate causes of such failures. Differential mortality was observed in lots of muskellunge eggs incubated in jars of unaerated lake water over substrates of sand, gravel, silt, aquatic macrophytes, wood, tree leaves, polyethylene screen, and bare glass. High and rapid early mortality (days 1-2), attributable to low dissolved oxygen (DO) concentrations (0-0.1 mg/liter), occurred among eggs incubated on leaves and macrophytes. After day 3, *Saprolegnia* sp. fungus was implicated in high egg mortalities in jars with inorganic substrates and moderate DO (3.8-4.1 mg/liter). Lowest mortality rates occurred on organic substrates (silt and wood) amidst intermediate DO concentrations (0.4-1.7 mg/liter) and limited fungal infestation. Measured DO at the substrate-water interface in eight midwestern lakes showed that four lakes had high DO (mean, 6.0-8.4 mg/liter), little microstratification, and support self-sustaining muskellunge populations. The other four showed extreme DO microstratification and virtual anoxia (mean, 0.4-2.4 mg/liter) at the substrate-water interface. Populations of these four lakes are almost solely supported by stocking. Qualitative and quantitative observations of spawning areas in the eight lakes showed that suitable spawning area characteristics include substrates with low biological oxygen demand, dense stonewort *Chara* sp.

beds, or reservoirs where water level is lowered annually, resulting in substrate aeration. Reproductive failure is associated with spawning areas characterized by deep accumulations of organic matter and dense macrophyte growth. Improvements of spawning habitat to prevent or alleviate hypoxia are among the options available to manage this species.

Introduction

Despite its widespread popularity as a northern gamefish, the muskellunge (*Esox masquinongy*) faces an uncertain future. In many areas where the species once maintained healthy natural populations, it has been extirpated or is sustained only through artificial propagation and stocking. Several hypotheses have been advanced to account for this decline: (1) competitive superiority of the congeneric northern pike *Esox lucius* when the two species occur syntopically (Inskip and Magnuson 1983; Oehmcke et al. 1974); (2) overharvest (Bimber and Nicholson 1981), and (3) reproductive failure due to loss or alteration of habitat (Trautman 1981).

Our focus here concerns the last hypothesis. Major human habitat modifications leading to dammed streams, drained marshes, and altered water levels unquestionably have eliminated substantial areas of muskellunge spawning habitat (Scott and Crossman 1973; Trautman 1981). Evidence from lake populations in Wisconsin (Oehmcke 1969) and New York (Bimber and Nicholson 1981) further suggests that even more subtle environmental changes can seriously jeopardize the species' reproductive success. Hatchery experiences imply that early life stages of muskellunge are very sensitive to environmental variables (Hess and Heartwell 1978). In nature, reproductive failure may be associated with the unusual physical properties of muskellunge eggs. Eggs of other esocids are adhesive and cling to vegetation and debris, but those of muskellunge are non-adhesive (Hess and Heartwell 1978) and stay in direct contact with bottom materials throughout embryonic development. Environmental hazards posed to benthic fish embryos and larvae are numerous (Peterka and Kent 1976) and have been implicated as a major ecological factor determining reproductive strategies among fishes (Balon 1975). In lakes, muskellunge eggs often are broadcast over bottoms covered by detritus and silt (Dombeck 1979). In such areas, dissolved oxygen can become depleted at the substrate-water interface (Peterka and Kent 1976), and L. D. Johnson, from preliminary laboratory and field investigations, attributed high muskellunge egg and fry mortalities to adverse conditions in lakes (Wisconsin Conservation Department, Federal Aid in Fish Restoration Project F-83-R job progress reports, 1967-1969, Madison, Wisconsin, USA).

These considerations suggest that the microhabitat where embryonic development occurs may be an important factor related to muskellunge reproductive success. In this study, we established a variety of egg-incubation habitats in the laboratory to (1) assess substrate influence on dissolved oxygen concentrations in the eggs' microhabitat, (2) determine if differential egg mortality occurs in the various microhabitats and, if so, to (3) evaluate causes of egg mortality.

To evaluate conditions existing in nature, muskellunge spawning sites in eight midwestern lakes were studied to determine if microhabitat conditions observed in the laboratory occurred in nature. The field phase of this study had the following objectives: (1) to determine if microstratification of dissolved oxygen occurs at the substrate-water interface in muskellunge spawning areas, (2) to describe biological and physical characteristics of spawning areas, and (3) to relate habitat features to reproductive success of local populations.

Laboratory Methods

Substrates

Incubation vessels were 1.8 liter glass jars containing substrates of sand, gravel, organic silt, living plants, wood, dead leaves with polyethylene screen support, bare glass (control), or polyethylene screen (control). Natural substrate material and water were collected from Little Miller's Bay, West Lake Okoboji, Iowa, immediately after the 1982 spring thaw and placed in the experimental jars for a 10-day stabilization period before the addition of eggs. Little Miller's Bay is thought to be a potential muskellunge spawning site (Miller, M. L. 1982. Behavior of the muskellunge (*Esox masquinongy*) in West Lake Okoboji, Iowa as determined by ultrasonic telemetry. M.S. Thesis, Iowa State University, Ames, Iowa, USA). The bay is typical of spawning sites in Wisconsin lakes identified by Dombeck (1979), being shallow with bottom materials of organic mucks, detritus, and wood, and thawing earlier than the remainder of the lake.

Jars with sand, gravel, wood, and silt contained similar amounts of substrate (about 5 cm. thick; 65 ml). Wood was a 5 x 13 cm cross section of water-soaked log. Plant and leaf materials were 25 g wet weight of coontail *Ceratophyllum* sp. and willow leaves *Salix* sp., respectively. In an effort to keep all eggs in full view, 2-mm mesh polyethylene screen was placed over the leaves, and three to six leaves were placed on top of the screen. After substrates were in place, the jars were filled to the top level with lake water.

Muskellunge eggs

Fertilized muskellunge eggs were obtained from the Iowa Conservation Commission (ICC) Spirit Lake Hatchery. Adult muskellunge were netted from Spirit Lake by ICC personnel as part of their annual spawn-taking operation. The fish were transported to the hatchery and placed in holding tanks. Females were injected with pituitary hormone to induce gonadal maturation. Eggs were stripped by using standard spawn-taking techniques approximately 72 hours after injection and fertilized dry. All eggs used in the experiment came from a single female and sperm from 2 males so as to reduce genetic variance.

After 3 hours of water-hardening, the eggs were placed in a plastic bag filled with water and oxygen and transported to the laboratory at Iowa State University, a 3.5 hour trip. Eggs were examined for deformities and shell breakage, and 50 presumably fertilized and viable eggs were pipetted into each jar. Jars were placed and kept in a controlled environment chamber with a 12-hour light:12-hour dark cycle and a constant temperature of 13 C. This photoperiod and temperature regime approximates conditions during the natural egg development period (Scott and Crossman 1973). Water in jars was not circulated or aerated because we sought to establish which substrates are related to highest egg mortality.

A randomized-block design was used, a block (replication) being an individual shelf in the environmental chamber and each substrate type being a treatment. There were six blocks of the eight treatments. In addition, two randomized replicates of treatments were set up to measure dissolved oxygen concentrations in the water column above each substrate twice during the study.

Viability of eggs was checked daily throughout the 9-day study period. A translucent egg was considered alive, whereas an opaque or fungus-covered egg was considered dead. In living eggs, the primitive streak was first observed on day 4, and eyespots became evident on day 6. Casual observations were made of developmental rates between and within treatments, but detailed analyses of developmental features were not a study objective. All egg observations and counts were made with a 5X hand-held lens and a high-intensity lamp. Duplicate counts of dead and live eggs were made daily for each jar. When there was disagreement, additional counts were made to resolve the difference. The experiment was terminated after day 9 because almost total mortality had occurred. After fungus (*Saprolegnia* sp.) infection was first noted on inorganic substrates in some jars on day 3, the presence and extent of fungal growth in each jar was recorded during days 4-9.

Dissolved oxygen (DO) concentration

Because measurement of DO in egg-count jars would have disturbed oxygen stratification therein, DO conditions were determined from a separate set of jars. These represented two replicates of each treatment, including a full complement (50) of eggs in each jar. To determine if microstratification occurred, DO was measured at two levels in the water column above the substrate-water interface. Oxygen-permeable dialysis tubing (16 x 100 mm) was filled with distilled water and tied off with rubber bands to form a bag holding approximately 12 ml. On day 0 and day 2, six bags were placed in each of the 16 (8 treatments x 2 replicates) oxygen test jars. Three bags were laid on the substrate to obtain measures of DO from 0-16 mm (mean, 8 mm) above the substrate-water interface. This interval represents "close proximity" to muskellunge eggs, which are about 3 mm in diameter (Galat 1973). Additionally, three bags were suspended with ends resting on the substrate surface to obtain a measure of DO from 0 to 100 mm (mean, 50 mm) above the substrate-water interface.

On the basis of recommendations by Fremling and Evans (1963) and a pilot study of the system, bags were left in each jar for 2 days to allow the DO of the water within the bags and ambient water to reach equilibrium. Immediately upon removal of a bag from a jar, a 10-ml water sample was extracted with a hypodermic syringe. Dissolved oxygen concentration was determined by a modified micro-Winkler technique that gives experimental errors of less than 2% (Burke 1962). Dissolved oxygen concentration of each treatment was determined on day 2 and day

4 of the study. For each jar, DO was taken as the average concentration in the three bags at each level. Analysis of variance procedures were used to analyze DO data.

Analysis of mortality

For each treatment, daily mortality was analyzed as (1) cumulative mean percentage mortality and (2) mortality rate. The latter was calculated as the slope of the regression of cumulative percentage mortality versus time. Mortality rates were calculated over 1-day intervals and also for days 1-4.

Regression and analysis of variance procedures would ordinarily be used to obtain standard errors and to test for significant differences among slopes (mortality rates). However, measurements made on a single jar over several days are repeated measurements and can be correlated in a way that violates the usual independence assumptions required for these procedures. This difficulty can be overcome by calculating a separate slope for each jar and using slopes as data in an analysis of variance. A numerically equivalent way of analyzing the slopes is to regard the days as a split-plot factor in the analysis of percentage mortality (Table 1). The variance or experimental error for the slope of an individual jar is calculated by dividing the mean square for "Linear x Replication (Treatment)" by $\Sigma(x-\bar{x})^2$, x being the days on which the measurements were made. The variance for the average slope of a given treatment is the variance of the slope for an individual jar divided by the number of replications, six. This procedure accounts for the repeated-measure nature of egg counts of a single jar over days. Error estimates for daily mortality rates based on only two consecutive days of the data were calculated similarly.

Table 1. Analysis-of-variance table used to estimate errors for mortality rate of muskellunge eggs during test days 1-4

Source of variation	df	
Replications	5	
Treatments	7	
Replications X treatments	35	
Day	3	
Linear		(1)
Deviations		(2)
Day X treatments	21	
Linear X treatments		(7)
Deviations X treatments		(14)
Remainder	120	
Linear X replications (treatments)		(40)
Deviations X replications (treatments)		(80)

The variance of the difference between average slopes for two treatments is merely twice the variance of the average slope of a single treatment. This variance was used for the calculation of the least significant difference (LSD) for mortality rate (Snedecor and Cochran 1980).

Laboratory Results

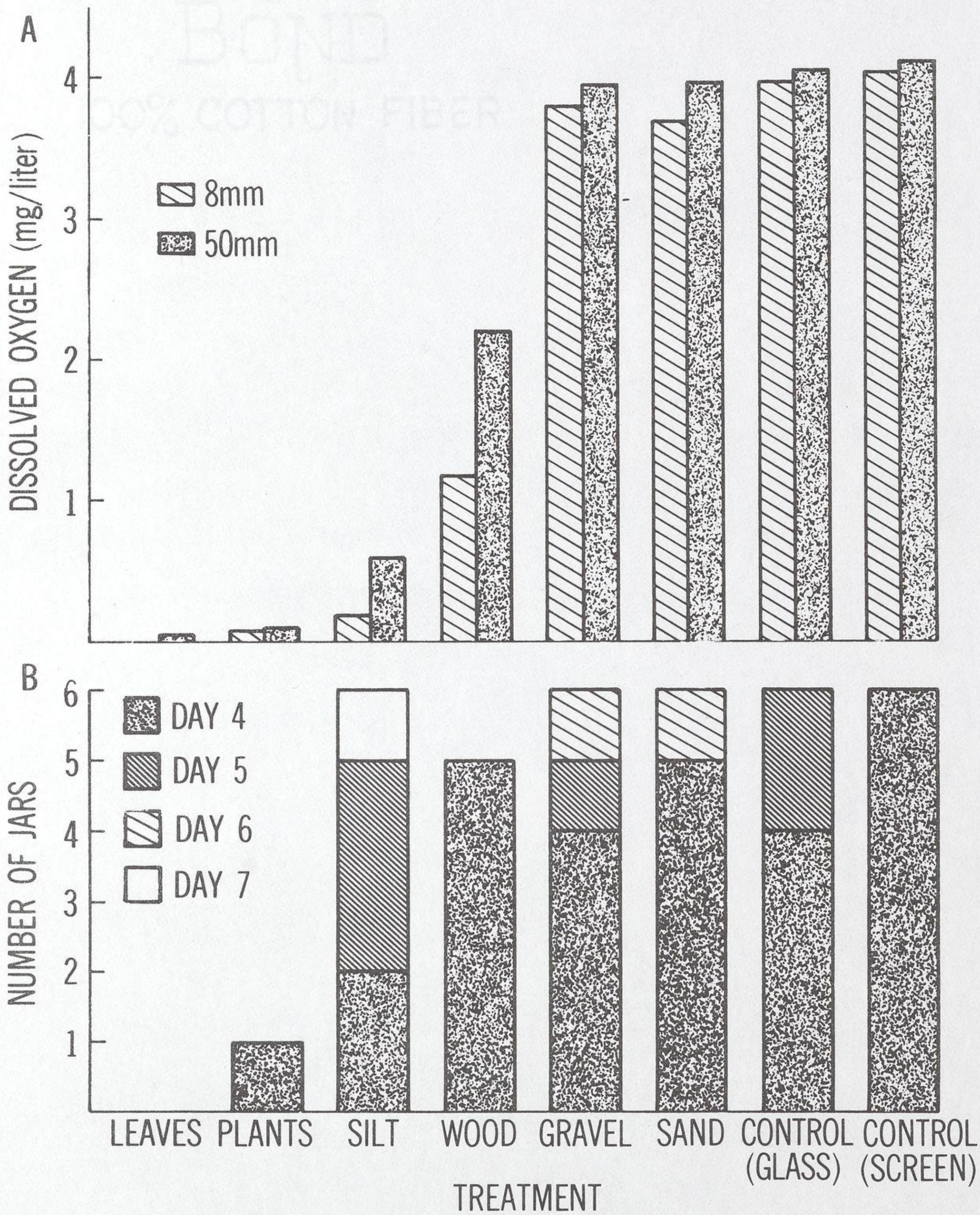
Dissolved oxygen concentration

Measured DO in 16 test jars did not differ significantly between day 1 and day 4; therefore, DO values for the 2 days were averaged for analysis by treatment and by depth within treatment (Fig. 1A). Close to the substrate (mean, 8mm), DO concentrations were lowest over leaves, plants, and silt (0.0-0.2 mg/liter). They were slightly higher over wood (1.3 mg/liter) and highest over sand, gravel, glass control, and screen control (3.8-4.1 mg/liter). Concentrations were greater in the upper (mean, 50 mm) than lower stratum in every treatment; greatest DO stratification occurred over wood and silt (Fig. 1A). The DO concentration LSD at the 0.05 level was 0.12 mg/liter between treatments and levels within treatments (N=12).

Fungus infection

Lowest incidence of fungus infection occurred on organic substrates (Fig. 1B). No fungus was observed in jars containing leaves, and one jar with plants had a minor infection during the study period. Among jars with silt substrate, two were infected by day 4, but at the end of the study period, fungus occurred to some extent in all replicates. Five jars with wood substrate were infected on day 4, and the other remained free of fungus for the duration. Profuse fungus growth did not occur on eggs over wood substrate, infestation usually being localized to a few eggs and not spreading to adjacent ones.

Figure 1--A, Mean dissolved oxygen concentration at the 8 and 50 mm above the substrate-water interface in jars containing muskellunge eggs. B, Number of jars with fungus infection in experimental treatments, days 4-7


A
DISSOLVED OXYGEN (mg/liter)
4
3
2
1
8mm
50mm
B
NUMBER OF JARS
6
5
4
3
2
1
DAY 4
DAY 5
DAY 6
DAY 7
LEAVES
PLANTS
SILT
WOOD
GRAVEL
SAND
CONTROL (GLASS)
CONTROL (SCREEN)
TREATMENT

In contrast to fungus on organic substrates, Saprolegnia in the inorganic and control jars spread quickly and grew profusely after its establishment in a jar. By day 4, 79% of the inorganic substrates were infected, and at the termination of the study, all were infected (Fig. 2). The incidence of infection was directly related to 8-mm DO among treatments on day 4 (r=0.80, P=0.02) (Fig. 2).

Egg mortality

Rapid mortality occurred in jars with lowest presumptive DO environments (leaves and plants) during days 2-4. After the onset of Saprolegnia infection on day 3, rapid mortality occurred in remaining jars as well, such that by day 6, more than 90% mortality had occurred in all jars, and mortality was virtually complete by day 9 (Table 2).

Table 2. Mean cumulative percentage mortality of muskellunge eggs incubated on different substrates. Initial egg number was 50; values are means of six jars

Day	Leaves	Plants	Sand	Glass control	Screen control	Wood	Gravel	Silt
1	16	7	8	7	8	5	3	8
2	85	35	16	14	19	12	10	17
3	99	76	38	39	31	36	31	33
4	100	87	75	60	65	58	50	55
5		97	90	90	92	86	89	86
6		97	91	93	96	91	91	94
7		98	95	96	98	94	95	95
8		99	97	98	99	95	97	96
9		100	99	100	100	97	99	97

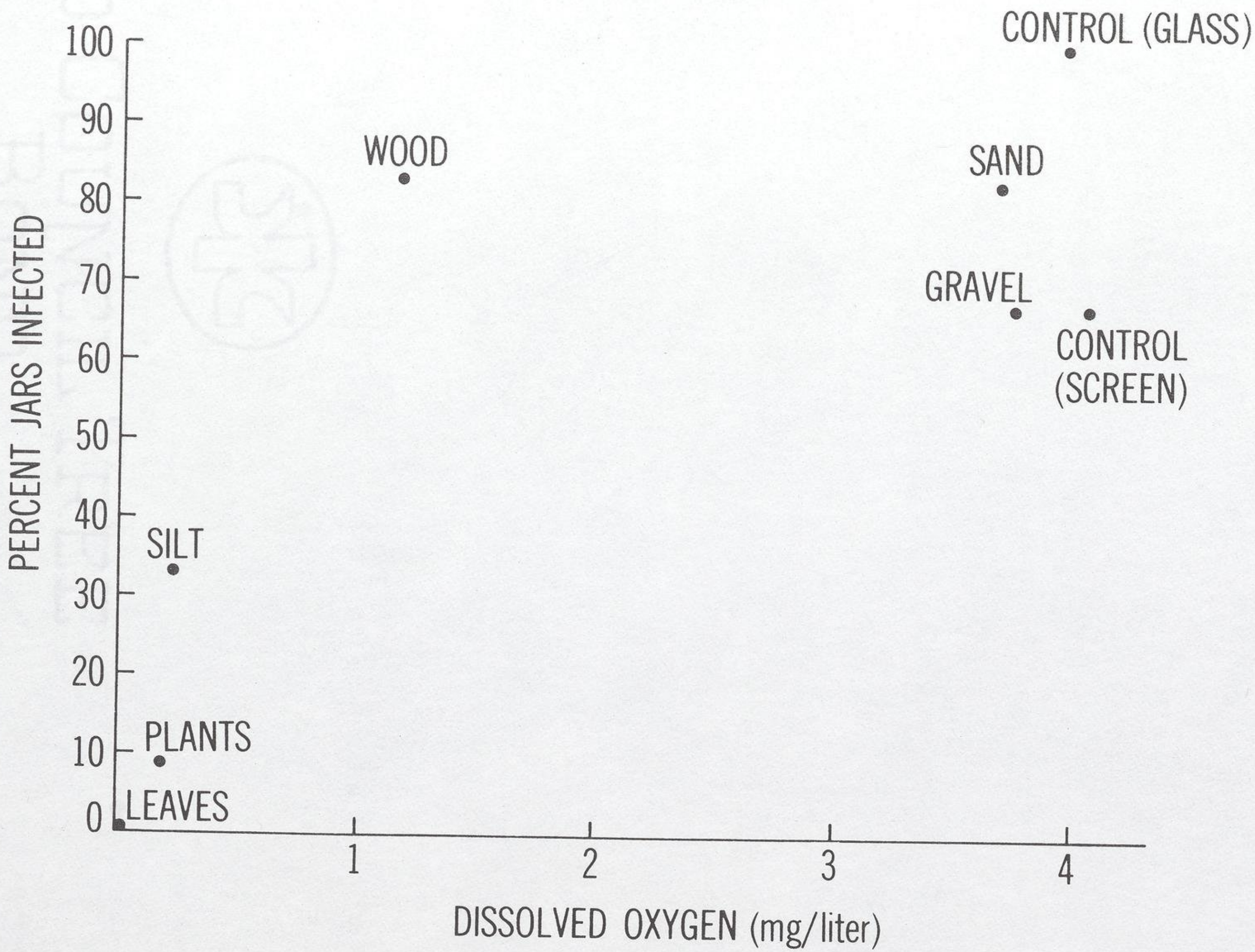
Significant differences in mean mortality rates among treatments occurred only for the first 6 days of the study, with greatest distinctions during days 1-4 (Table 3). Analysis of treatment mortality rates for days 1-4 revealed highest mortality rates on leaves and plants and lowest rates on gravel and silt (Table 3).

Table 3. Mean daily mortality rates of muskellunge eggs among substrate treatments for days 1-5 and the period days 1-4 of incubation in jars. Asterisk indicates peak mortality for the given treatment. Non-connected treatments are significantly different ($P < 0.05$, least significant difference (LSD) = 2.1)

Day	Leaves	Plants	Sand	Glass control	Screen control	Wood	Gravel	Silt	LSD
1	8.0	3.7	4.0	3.3	4.3	2.7	1.7	4.3	2.5
2	33.8*	13.7	4.0	3.3	5.2	3.7	3.2	4.2	4.3
3	7.8	20.8*	10.8	12.8	6.2	11.8	10.5	7.8	5.3
4	0.3	5.3	18.5*	15.5*	17.0*	11.0	10.2	11.2	4.9
5	0.0	5.2	7.8	10.2	13.2	13.8*	19.0*	15.5*	5.9
1-4	14.0	13.4	11.1	10.8	9.1	9.1	8.2	7.7	2.1

Of the eight treatments, the highest mean daily mortality rate observed throughout the study occurred on leaves on day 2 (Table 3). The mortality rate on plants peaked on day 3. On day 4, highest mortality rates occurred on sand and the two controls. Wood, gravel, and silt substrates were the last to show peak mortality rates, which occurred on day 5.

Figure 3--Relation of the incidence of fungus infection to dissolved oxygen (8 mm above substrate) in jars containing eggs on various substrates ($r=0.80$, $P=0.02$)

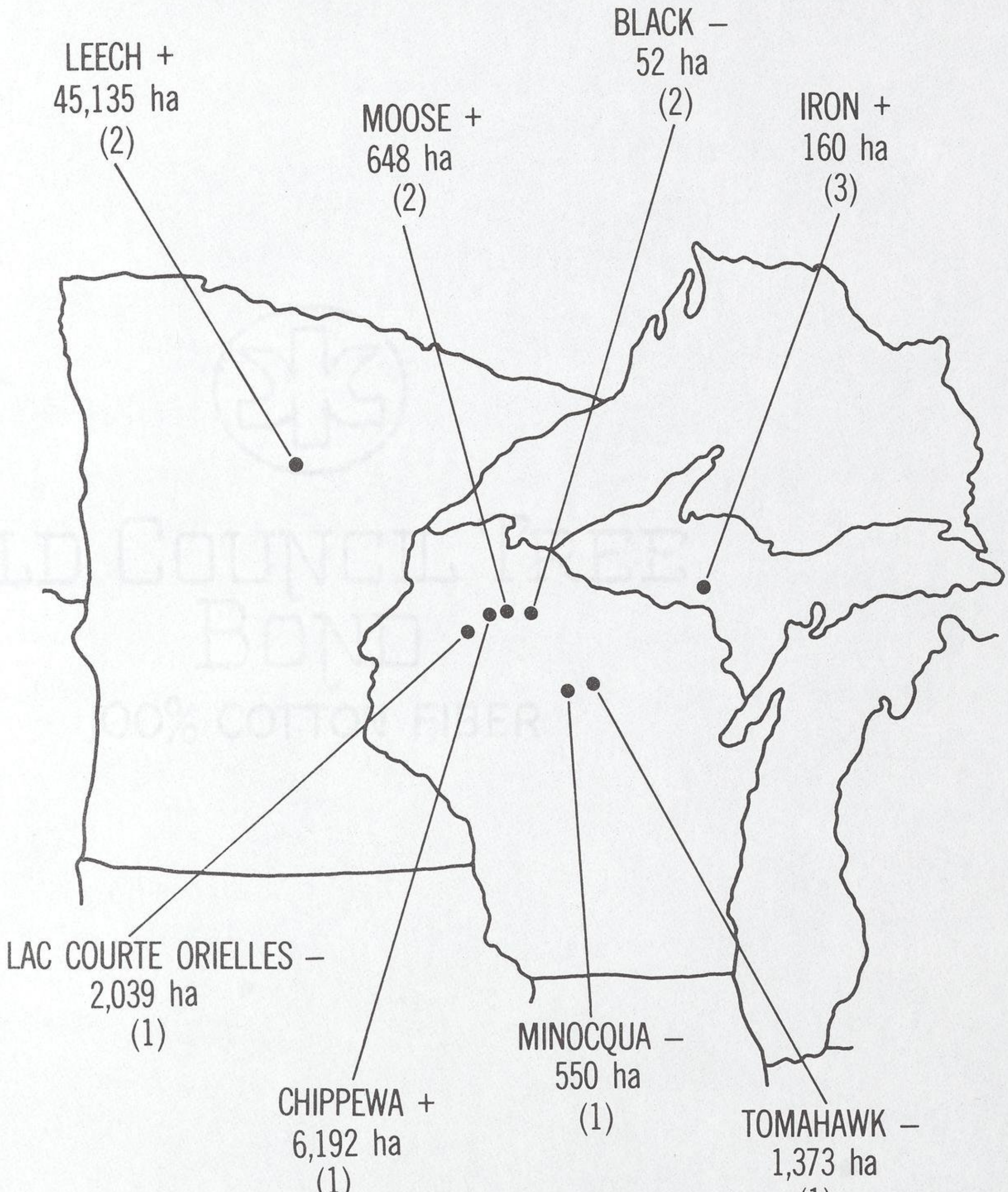

PERCENT JARS INFECTED
100
90
80
70
60
50
40
30
20
10
0
CONTROL (GLASS)
WOOD
SAND
GRAVEL
CONTROL
(SCREEN)
SILT
PLANTS
LEAVES
1
2
3
4
DISSOLVED OXYGEN (mg/liter)

Field Methods

Study lakes

Thirteen muskellunge spawning areas in eight midwestern lakes were studied (Fig. 3). Muskellunge populations inhabiting four lakes are self-sustaining, whereas the others were formerly self-sustaining but now have little or no natural reproduction being maintained primarily by the stocking of hatchery produced fish. Black, Leech, Minocqua, and Tomahawk Lakes are natural lakes whose water level has been raised by a dam. Lac Courte Orielles and Iron Lakes are unmodified natural lakes, and Chippewa and Moose Lakes are reservoirs whose water levels are lowered more than 2 m in late fall and are filled immediately after ice-out each spring. Muskellunge spawning areas on Moose and Black Lakes were located by Dombeck (1979) and on Leech Lake by Strand (1983). The Lake Chippewa spawning area was located by Lyman O. Williamson (Fisheries Biologist, Hayward, Wisconsin, USA, personal communication), and spawning was observed by the senior author. The spawning areas on remaining lakes were located by respective Departments of Natural Resources (DNR) fisheries biologists by visual observations and/or netting during spring spawn-taking operations. The status of natural muskellunge reproduction was determined by the respective DNR fisheries biologists.

Figure 3--Geographic locations of lakes, surface area in hectares (ha), number of muskellunge spawning areas studied ( ), and status of natural muskellunge reproduction: +=self-sustaining, -=little or none


LEECH +
45,135 ha
(2)
BLACK –
52 ha
(2)
MOOSE +
648 ha
(2)
IRON +
160 ha
(3)
LAC COURTE ORIELLES –
2,039 ha
(1)
CHIPPEWA +
6,192 ha
(1)
MINOCQUA –
550 ha
(1)
TOMAHAWK –
1,373 ha
(1)

Ecological parameters studied

The field studies were conducted during the muskellunge spawning seasons (May) of 1982 and 1983. A stratified sampling technique was used to establish transects within each spawning area and also to establish sample sites along each transect (Cummins 1962). Dissolved oxygen concentration was measured at two levels in the water column (mean, 8 and 50 cm) above the substrate-water interface at each sample site by using the technique previously described in Laboratory Methods. Three replicate DO measures were taken at each level at each site in early morning hours so as to obtain daily low DO. The replicate measures at each level were averaged to obtain a composite DO measure for each of the two levels at a sample site.

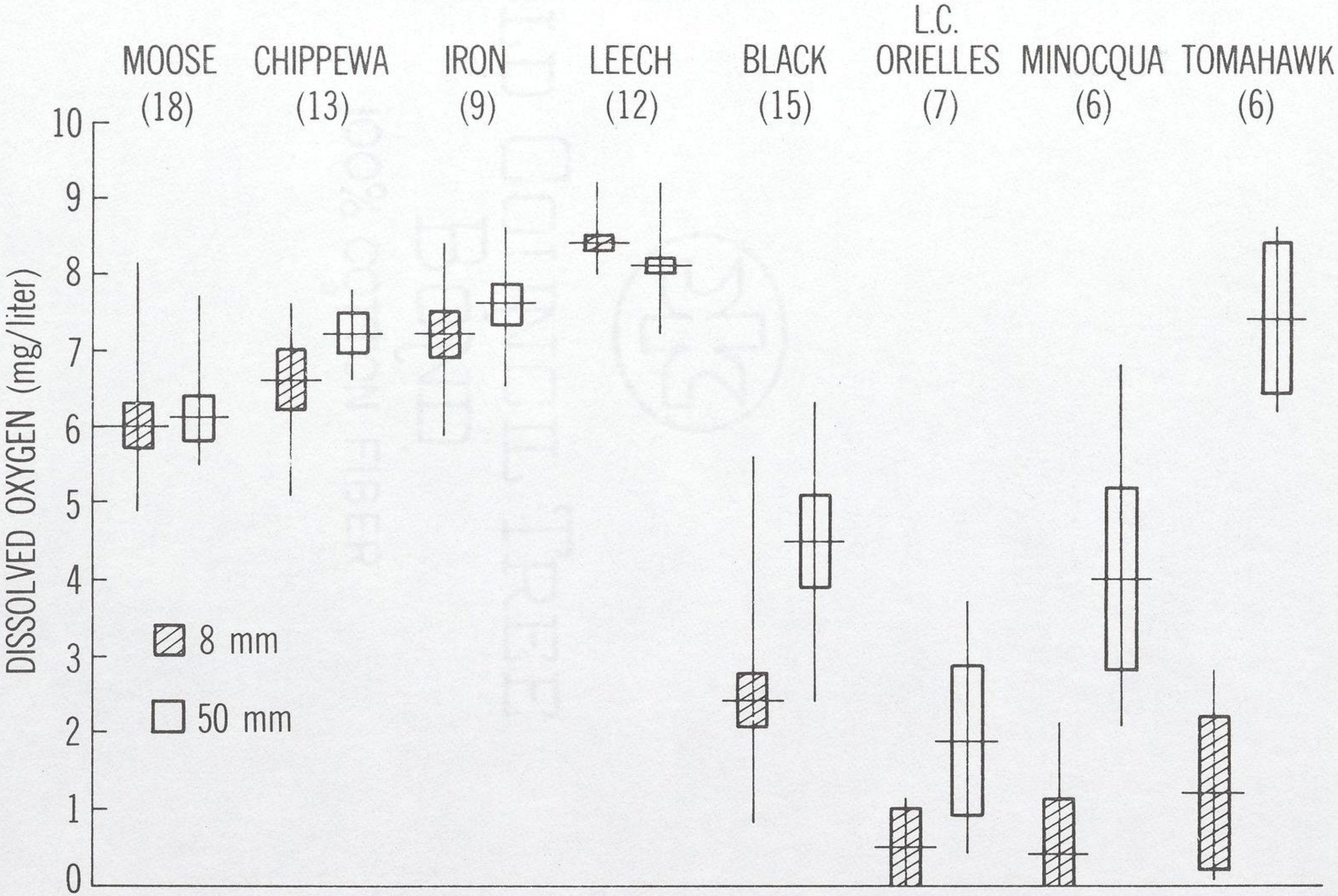
The percentage rock (greater than 2 mm), wood, detritus, and vegetation cover was estimated at each sample site by using a one-half meter square Daubenmire quadrat. The quadrat was randomly placed at three locations about the sample site and percentages were averaged to obtain a mean value for each site. Dominant macrophytes were identified and their height was estimated to the nearest 5 cm at three locations by using a Robel stick and averaged (Mueller-Dombois and Ellenberg 1974). Major detritus components were identified. Mean depth was determined by averaging three measures randomly taken about the sample site, and distance to shore was measured at all sites except Leech Lake. Substrate samples were collected at each site by using a hand-held core sampler, or an Eckman dredge (at depths greater than 1.5 m). Replicate substrate samples were collected at three randomly selected locations at each site and mixed to form a composite sample. Substrate analysis was performed by the Iowa State University Agronomy Laboratory. Percentage organic matter was determined by using the Walkley-Black method (Allison 1965). Carbonate content was determined using the Chittick apparatus (Dreimanis 1962). Inorganics were size fractioned as follows: sand (2.0-0.5 mm), silt (50-2 um), and clay (less than 2 um) by using a modified pipette method (Walter et al. 1978). Additionally, a subjective determination of substrate texture (firm or flocculent) was made. Analysis of variance procedures were used to analyze the results.

Field Results

Dissolved oxygen concentration

Measured DO at two levels in the water column (mean, 8 and 50 mm) above the substrate-water interface at spawning area sample sites indicated that the eight lakes constituted two distinct groups (Fig. 4). Moose, Chippewa, Iron, and Leech lakes had high DO (mean, 6.0-8.4 mg/liter) at the 8-mm level with similar DO (mean, 6.2-8.0 mg/liter) at the 50-mm level. In contrast, the sites in remaining lakes had considerably lower DO (mean, 0.4-2.4 mg/liter) at the 8-mm level and significantly higher DO (mean, 1.9-7.4 mg/liter) at the 50-mm level, indicating DO microstratification. Greatest microstratification occurred on Tomahawk Lake where the difference between mean upper and lower DO was 5.1 mg/liter.

Figure 4--Mean dissolved oxygen concentration at 8 and 50 mm above the substrate-water interface in muskellunge spawning sites. Horizontal lines are means, boxes enclose ± 2 SE, and vertical lines are ranges. Sample sizes are indicated in parentheses. Each sample is a mean of three values


MOOSE (18)
CHIPPEWA (13)
IRON (9)
LEECH (12)
BLACK (15)
L.C. ORIELLES (7)
MINOCQUA (6)
TOMAHAWK (6)
DISSOLVED OXYGEN (mg/liter)
0
1
2
3
4
5
6
7
8
9
10
8 mm
50 mm

Environmental characteristics of spawning sites

Table 4 provides a summary of environmental characteristics of muskellunge spawning sites. In seven of eight lakes studied, spawning areas were located in shallow areas (mean, 74 cm) nearshore with a wide variety of bottom components. Leech Lake was the exception where spawning areas were located in deeper (mean, 157 cm), offshore locations whose flocculent marl substrate was covered by dense patches of stonewort *Chara* sp. Densest macrophyte cover (mean, 76%) and greatest height (mean, 42 cm) was observed in Lac Courte Orielles, dominated by *Potamogeton Robbinsii*. The Minocqua Lake spawning area was the only one where the dominant vegetation was filamentous algae; it occurred over a flocculent organic substrate, giving the area a dystrophic appearance. Substrates of spawning site in Minocqua and Tomahawk lakes contained highest percentage organic matter (mean, 36 and 40%, respectively) while Moose and Leech lakes had the lowest (mean, 11, and 15%, respectively). Detritus components were primarily macrophyte fragments in various stages of decomposition, presumably from the preceding years' growth. Large water-soaked woody materials (logs and stumps) were present at one of the three areas in Iron Lake, one of the two areas in Black Lake, and in the two drawdown reservoirs (Moose and Chippewa).

Small influent streams were present at or near the spawning areas studied in Black Lake and at one area each in Moose Lake, Lac Courte Orielles, and Minocqua lakes. Observations showed that the spawning areas studied on all lakes except Leech, for which there were no observations, thawed earlier in spring than other shoreline areas

Table 4. Environmental characteristics of muskellunge spawning sites in study lakes

PARAMETER	Lake means ± 1 SE Moose (N=18)	Chippewa (N=13)	Iron (N=9)	Leech (N=12)
Depth (cm)	72 ± 6	58 ± 5	48 ± 5	157 ± 5
M to shore	10 ± 2	11 ± 2	22 ± 5	
Vegetation				
species[b]	a,d,f	a,e,j	a,d,f,g	h
Height (cm)	8 ± 3	4 ± 1	4 ± 3	8 ± 2
% cover	2 ± 1	13 ± 4	4 ± 2	67 ± 14
Surficial materials				
% rock	2 ± 1	0	1 ± 1	0
% wood	8 ± 2	5 ± 2	10 ± 10	0
% detritus	3 ± 1	45 ± 2	17 ± 10	0
Detritus components[b]	d,n	a,n	a,f,n	
Substrate composition				
% organic	11 ± 4	24 ± 3	18 ± 8	15 ± 1
% carbonates	0	0	0	67 ± 1
% sand	71 ± 4	26 ± 8	62 ± 15	7 ± 2
% silt	22 ± 3	18 ± 5	2 ± 1	69 ± 7
% clay	8 ± 1	10 ± 3	1 ± 1	16 ± 2
Substrate texture[c]	1	1	1	2

[a]Excluding Leech Lake.

[b]Vegetation and detritus: a = bulrush (Scirpus), b = bushy pondweed (Najas), c = coontail (Ceratophyllum), d = horsetail (Equisetum), e = pondweed (Potamogeton), f = rush (Juncus), g = sedge (Carex), h = stonewort (Chara), i = waterlily (Nuphar, Numphaea), j = milfoil (Myriophyllum), k = watershield (Brasenia), l = waterweed (Anacharis), m = deciduous tree leaves, n = small wood chips, o = filamentous algae.

[c]Substrate texture: 1 = firm, 2 = flocculent.

Black (N=15)	Lac Courte Orielles (N=7)	Minocqua (N=6)	Tomahawk (N=6)	All Lakes (N=86)
64 ± 6	71 ± 5	51 ± 5	43 ± 2	74 ± 4
11 ± 4	3 ± 1	13 ± 3	13 ± 4	11 ± 1 [a]
b,c,i,k	c,e,j,l	c,e,j,p	b,e,f,g	
11 ± 3	42 ± 4	7 ± 4	11 ± 4	10 ± 1
33 ± 12	76 ± 17	2 ± 1	8 ± 3	23 ± 4
0	0	0	0	1 ± 0
2 ± 1	0	0	0	3 ± 1
7 ± 3	18 ± 18	27 ± 17	93 ± 3	20 ± 3
c,j,m	c,e	e,g	e,f,g	
21 ± 4	25 ± 19	36 ± 2	40 ± 5	21 ± 2
0	0	0	0	
54 ± 6	78 ± 18	1 ± 1	9 ± 9	42 ± 4
30 ± 4	4 ± 1	7 ± 7	2 ± 2	24 ± 3
16 ± 2	1 ± 0	8 ± 8	3 ± 3	9 ± 1
2	2	2	2	

of the lakes. The earlier thaw at the Lake Tomahawk spawning area seemed to be caused by water movement from a nearby seepage area. Groundwater seepage also may have influenced the Lac Courte Orielles spawning area. Reasons for the earlier thaw at other areas are unknown.

Discussion

Differential egg mortalities observed in this laboratory experiment are attributed to low DO conditions, fungal infestation, or both, depending upon treatment. Greatest early mortality rates (days 1-3) occurred over substrates of decaying leaves, which presumably exerted high biological oxygen demand (BOD), resulting in virtual anoxia in the proximity of the developing embryos. Somewhat lower early mortality rates occurred on living plant substrates amidst very low DO conditions (0.1 mg/liter), probably caused by plant respiration. Through day 3, mortality rates were similar and relatively low among the remaining treatments and over a DO range of 0.2-4.1 mg/liter at the 8-mm level.

Oxygen microstratification at the bottom-water interface of the hypolimnion of lakes is known to significantly affect the distribution and activity of benthic organisms (reviews by Brundin 1951; Mortimer 1971; Brinkhurst 1974). Less is known about the phenomenon of oxygen microstratification in shallow-water benthic zones. Fremling and Evans (1963) described bottom DO reductions associated with silt and wood fiber substrates in Rainy River, Minnesota. Peterka and Kent (1976) measured lowest DO concentrations within 1 cm of the bottom in northern pike spawning areas in a North Dakota marsh. Oxygen microstratification created over organic substrates in the present laboratory study were similar to conditions in nature at the water-bottom interface of the study lakes, where organic substrates and macrophytes are involved.

Results of lake DO measures (Fig. 4) demonstrated that little or no DO microstratification or depletion at the substrate-water interface in muskellunge spawning areas during the time of egg incubation in Moose, Chippewa, Iron, and Leech lakes. Each of these lakes supports a self-sustaining muskellunge population. Spawning substrates of the two drawdown reservoirs (Moose and Chippewa lakes) are aerated each winter and flooded about three weeks preceding the time of muskellunge egg deposition. The substrates in Iron (sand and gravel) and Leech (marl) lakes presumably exerted little BOD. On the other hand, in four lakes that no longer contain self-sustaining populations, severe DO microstratification and depletion were measured. Biological oxygen demand of organic substrate and detritus (Minocqua and Tomahawk lakes) and nighttime respiration (Black and Lac Courte Orielles lakes) were suspected causes of DO depletion. These comparisons suggest that DO depletion near the substrate-water interface, associated with eutrophic conditions, contributes to muskellunge egg mortality and, thus, is a factor limiting muskellunge reproduction in lakes. Concomitant elements of chemical microstratification such as hydrogen sulfide may be detrimental to embryonic development (Adelman and Smith 1970).

Published information on the oxygen requirements of muskellunge embryos and larvae are lacking, but inferences may be made on the basis of studies of the congeneric and ecologically similar northern pike. Inskip (1982) stated that eggs that fall to the bottom are unlikely to hatch because of anoxic conditions in the organic-rich sediments typical of pike spawning grounds. Peterka and Kent (1976) found that experimental exposure of pike eggs to DO levels below 0.6 mg/liter for 8 hours substantially increased mortality. Larvae suffered rapid mortality at exposures below 2.0 mg/liter and increased mortality remained at an exposure level of 4.0 mg/liter for 8 hours. Siefert et al. (1973) reported that at 15 C and 25% DO saturation (about 2.5 mg/liter), pike egg survival was not affected but that larval feeding was delayed 3 days, severe mortality occurred within 12 hours after the onset of feeding, and DO concentrations less than 33% (about 3.2 mg/liter) seemed unsuitable for embryos and larvae. Comparison of mortality observed here over organic silt versus leaves and plants might suggest that at least early embryonic development (days 1-3) of muskellunge eggs can progress without severe mortality under DO conditions as low as 0.2 mg/liter (see Fig. 1A, Table 2). Latent mortality might occur even if DO concentration is restored to higher levels and hatching occurred (Siefert et al. 1973). Additionally, as noted by Doudoroff and Shumway (1970) and demonstrated for northern pike by Peterka and Kent (1976) and Siefert et al. (1973), the development and survival of fish larvae can be more sensitive to oxygen depletion than are embryonic stages. Because of the confounding influences of fungus infestation and brief duration of the present laboratory study, little can be said here about influences of low DO levels on later embryonic and larval stages of muskellunge.

Under hatchery conditions, *Saprolegnia* infection often contributes to high mortality of cultured fish eggs (Brown and Gratzek 1980). Fungus infection has been observed on naturally deposited muskellunge eggs in lakes (James R. Gammon, DePauw University, Greencastle, Indiana, USA, personal communication), and L. D. Johnson, in an experimental study, observed fungus on muskellunge eggs incubating on sand and gravel substrates and noted that eggs on silt were fungus-free (Wisconsin Conservation Department, Federal Aid in Fish Restoration Project F-83-R job progress reports, 1967-1969, Madison, Wisconsin, USA). In the present study, fungus clearly contributed to mortalities in some jars after day 3, especially in those of higher DO environments, sand, and both control treatments (Fig. 2). The absence of fungus infection on decomposing leaves and its restricted growth over wood and silt imply fungus growth inhibition by low DO concentrations. Lower aquatic fungi, including *Saprolegnia* spp., are highly aerobic (Gleason 1976). Further, our observations suggest that physical isolation of the eggs from each other impedes fungus proliferation. The evidence for this is that, among high DO treatments, fungal infection did not spread rapidly to eggs isolated in interstitial spaces of coarse substrate (gravel). Rapid infestation occurred in those smooth bottom treatments where eggs were in direct contact or close proximity to each other (sand, both controls). Thus, fungus-caused mortalities resulted from interaction of treatment DO levels and morphologic structure of the substrate.

Balon (1975) has hypothesized that the oxygen regime of early-life environments is a major factor determining reproductive strategies of oviparous fishes. Bottom-spawning species may avoid deleterious DO conditions by behavioral adaptations of adults and larvae (e.g., selection of well-oxygenated spawning sites, egg-fanning by adults, phototaxic responses of larvae) or morphophysiological adaptations of embryos and larvae (e.g., buoyant, adhesive, and entangling eggs, special respiratory organs, cement glands). As a group, esocids are adapted for early life habitat conditions of dense plant growth, muddy bottoms, and low DO concentrations (Balon's A.1.5. reproductive guild of non-guarding, open substrate spawning phytophils). As exemplified by the northern pike, adaptations include deposition of small, highly adhesive eggs onto aquatic vegetation above the bottom. Immediately after hatching, larvae are temporarily active before attaching to vegetation by means of a cephalic cement gland, thus avoiding hypoxic conditions on the bottom (Inskip 1982). The broad circumpolar distributional range of the northern pike testifies to the ecological effectiveness of that strategy. Among the remaining North American esocids, there is reason to suggest at least a gross relationship between distributional range and early life history adaptations. The chain pickerel (*Esox niger*) occurs widely throughout Atlantic coastal drainages and the lower Mississippi River Valley (Crossman 1978). Its eggs are initially demersal and temporarily adhesive, but lose the latter characteristic after water-hardening and become semibuoyant to buoyant by the eyed stage (Mansueti and Hardy 1967). Like those of the northern pike, chain pickerel eleutheroembryos possess a cephalic cement gland, used for attachment to macrophytes during yolk sac absorption. The grass pickerel (*Esox americanus*) also exists widely in the eastern United States and southeastern Ontario but has suffered major historical range reduction west of the Mississippi River (Crossman 1978). Its eggs are thought to be demersal and slightly adhesive, and newly hatched larvae exhibit vegetation-attachment behavior (Scott and Crossman 1973). In contrast, the muskellunge occupies the most restricted range, occurring chiefly in the Great Lakes, St. Lawrence River, and upper Mississippi River drainages, extending south in large rivers of the Appalachians to Alabama (Crossman 1978). Throughout its range, the muskellunge seems to be most successful in more oligotrophic waters. Although it frequently spawns in vegetated areas, it broadcasts its demersal, non-adhesive eggs over the bottom. Newly hatched young lack the swim-up and vegetation-attachment behavior characteristic of other esocid larvae. Instead, they remain quiescent at the bottom, becoming active only after yolk sac consumption (Scott and Crossman 1973). Therefore, among the four North American esocid species, the muskellunge is unique in its apparent lack of early life adaptations to low DO conditions at the bottom. The paucity of detailed esocid early life history information indicates that additional study is needed.

Existing information concerning the environmental characteristics of muskellunge spawning habitat, for the most part, consists of qualitative descriptions. Oehmcke et al. (1974) reported that muskellunge in Wisconsin lakes spawn in shallow bays (1-3 feet deep) with muck bottoms covered with detritus and dead vegetation, whereas Nevin (1901) reported spawning in areas of greatest log, stump, and brush density in Wisconsin flowages. Scott and Crossman (1973) stated that spawning takes place in heavily vegetated flooded areas 15-20 inches deep. Our results showed that woody material occurred in the two Wisconsin flowages studied (Moose and Chippewa lakes), Iron Lake, and to a lesser extent in Black Lake. Earlier general spawning habitat descriptions are reinforced by our data, with the exception of Leech Lake. The somewhat deeper (mean, 157 cm), open-water spawning areas selected by muskellunge in Leech Lake more closely resemble spawning habitat used by muskellunge in Lake St. Clair, Michigan, where spawning reportedly occurs in open water over 3 m deep (Haas 1978). Shallow vegetated bays are present in Leech Lake; however, telemetry studies and intensive netting have shown that this type of habitat is not utilized by muskellunge for spawning (Strand 1983). Instead, they spawn over dense beds of stonewort growing over flocculent marl substrate. It seems that the structural features of the stonewort beds provide support for eggs and protection from predation, especially when compared with other spawning areas studied. Stonewort is also common in spawning areas in four upper peninsula of Michigan lakes that support self-sustaining muskellunge populations. Shrouder (1975) reported that the two strains of muskellunge recognized by the state of Michigan select different spawning sites. The northern muskellunge broadcasts eggs over a large area of shallow bays without currents while the Great Lakes strain spawns at the edges of river channels among logs and detritus. These comparisons suggest that different types of spawning habitat are utilized by muskellunge in different waters.

Considering the muskellunge's presumptive lack of behaviorial and morphophysiological adaptations for egg and larval survival, the importance of suitable spawning habitat is evident. The repeated spawning activities of muskellunge in Tomahawk Lake have been observed to result in agitation and mixing of flocculent organic substrates. Such intense and repeated activity likely causes previously deposited eggs to settle deeper into the soft substrate, further increasing egg mortality by suffocation (Richard Wendt, Wisconsin Department of Natural Resources, Woodruff, Wisconsin, USA, personal communication). The important question of what environmental features attract adults to spawning areas and release the spawning act remain unanswered. In an earlier study, Dombeck (1979) found that spawning areas in Moose and Black lakes were about 1.5 C warmer at spawning time than adjacent waters. L. D. Johnson stated that muskellunge seem to prefer spawning over warmer (because of dark coloration and radiant energy absorption) organic materials where the eggs are least likely to survive (Wisconsin Conservation Department, Federal Aid in Fish Restoration project F83R job progress reports, 1967-69, Madison, Wisconsin, USA). Our observations suggest that the earlier ice-out at muskellunge spawning sites is due to lotic influence of groundwater seepage or influent streams.

Harrison and Hadley (1978) hypothesized that, in the Niagara River, sympatric muskellunge and northern pike populations segregate during spawning, with pike selecting lentic waters while the muskellunge use the riverine habitat. Because six of the spawning areas that we studies were influenced by lotic water, it is possible that adults are responding to this factor as well as temperature. Clearly, however, water movement in at least some areas was insufficient to prevent DO stratification at the substrate-water interface.

Management implications

Present muskellunge management strategies focus on harvest regulations and stocking of fingerlings. In many areas, populations are maintained only through stocking, and introductions rarely produce self-sustaining populations (Hess and Heartwell 1978). Moreover, hatchery production of muskellunge is becoming a less viable management option owing to the difficulty and high cost of raising the fish to fall fingerling size (25 to 35 cm). In large part, this is because juvenile muskellunge will not accept artificial diets (Graff 1978). The present cost of 25-35 cm muskellunge is $7.50 each (Kalepp Fish Farms, Dorchester, Wisconsin, USA) not including stocking costs. Furthermore, survival of the stocked hatchery product to legal size is typically 10% or less (Johnson 1978). In consequence, the more easily reared and vigorous hybrid tiger musky (northern pike x muskellunge) has enjoyed increased popularity as the basis of artificial esocid sport fisheries. But, of course, this option also fails to provide self-sustaining populations.

Aside from the environmental and reproductive considerations discussed earlier, another limiting factor in the self-perpetuation of muskellunge populations may be low rates of fertilization. In an unpublished observational report, Edward Schneberger (Wisconsin Conservation Department, 1936, Madison, Wisconsin, USA) stated that nearly two-thirds of naturally spawned muskellunge eggs may not be fertilized. Speculative explanations given were (1) very short lived sperm, (2) eggs broadcast so widely that many are out of reach of sperm, (3) rapid sinking of eggs, and (4) blockage of micropile by bottom detritus. That high rates of egg fertility (up to 95%) can be achieved in hatcheries (Hess and Heartwell 1978) lends credence to Schneberger's speculations about causes of low natural fertilization rates.

Recently, the stocking of artificially fertilized muskellunge eggs on selected substrates in a northern Wisconsin lake was successful in producing a year class of muskellunge (David Hanson, Wisconsin Department of Natural Resources, Spooner, Wisconsin, USA, personal communication). This technique shows promise as an alternative to the costly stocking of hatchery-reared fingerlings, particularly in waters where natural spawning areas are subject to hypoxic conditions resulting in high early life mortality. Stocking artificially fertilized eggs provides a much higher fertilization rate, and their placement on selected favorable substrates should result in greater hatching rates than obtained from eggs deposited naturally.

Additionally, this study points out the need for identification and protection of muskellunge spawning habitat and suggests management strategies for enhancing natural reproduction through the direct improvement of spawning habitat by reducing BOD. Depending upon local conditions, some feasible management options might include water-level management to promote substrate aeration, removal of high BOD substrates, and placement of gravel, woody, or synthetic substrate materials in natural spawning sites. Management of adjacent terrestrial zones should discourage allochthonous leafy input, protect shorelines from erosion and development, and maintain high water quality of influent streams.

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A METHOD FOR MEASURING OXYGEN IN AQUATIC MICROZONES

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PART II. A METHOD FOR MEASURING OXYGEN IN AQUATIC MICROZONES

Abstract

A method to obtain accurate dissolved oxygen concentration (DO) measurements within a 16-mm microzone was developed using oxygen-permeable dialysis tubing with a 12-ml water sample and a modification of the micro-Winkler technique. Controlled experiments showed that DO within tubes reached 99% equilibrium with ambient water in less than 3 hours in lotic waters and in less than 5 hours in lentic waters with experimental error of 0.05 mg/liter. A kit to perform the DO measures can be assembled for about $150, and samples can be run in less than 10 minutes.

Introduction

Reduction of dissolved oxygen concentration (DO) in aquatic environments as a result of respiration and decomposition processes often has significant impacts on the ecology of aquatic biota. For example, oxygen depletion at the substrate-water interface of hypolimnetic waters is known to affect the distribution and activity of benthic organisms (reviews by Brundin 1951; Mortimer 1971; Brinkhurst 1974). Fremling and Evans (1963) and Peterka and Kent (1976) also described DO reductions associated with organic substrates in littoral waters. Low DO in such environments can adversely affect the early life history of fishes, often resulting in high mortality (review by

Doudoroff and Shumway 1970). Thus, the ability to accurately measure DO within narrow strata can be a useful tool for ecological investigations. At present, however, there are technological limitations to such measures. Conventional water collecting techniques obtain relatively large sample volumes and often tend to disturb situations of microstratification. Electronic probes have the advantage of precise location but require movement of water across a diffusion membrane and are least accurate at low DO levels. Peterka and Kent (1976) developed a pumping mechanism which collects water from microzones but may be awkward under many field conditions. Fremling and Evans (1963) developed a useful technique for determining DO near the substrate-water interface which employs an oxygen-permeable polyethylene bag as a water sampler. In brief, the bag is filled with tap water and placed in a desired location. After an appropriate diffusion period, during which DO within the bag reaches equilibrium with the ambient concentration, the bag is removed and DO is measured by the standard Winkler method. For measuring microzone DO, disadvantages of this technique are the large water sample volume (1-l) and requirement of a long diffusion period, from 30 to 48 hours, depending on temperature. Here, we describe and validate a modified Fremling and Evans technique involving a more convenient sampling medium, small sample volume, brief diffusion period, and DO determination by a micro-Winkler technique.

Materials and Methods

Oxygen-permeable standard cellulose dialysis tubing (Spectra/Por membrane tubing 16-mm diameter, molecular weight cutoff 12,000-14,000) was filled with distilled water and tied off with rubber bands at 100-mm intervals and cut to form tubular bags (16 x 100 mm) holding about 12 ml of water. Vertical suspension of the tubing before being tied eliminated the problem of trapping air bubbles in the bags.

To test the response time of the bags, we determined the time required for DO within the sample bag to reach equilibrium with ambient water. Additionally, because DO measures are routinely made at different temperatures and in both standing and flowing water environments, the influence of these variables was determined.

Experimental design

A deoxygenated environment was established by bubbling nitrogen gas through several air stones in a 50-l carboy filled with water. DO in the carboy was monitored continuously by using a Yellow Springs Instruments oxygen meter. In addition, oxygen determinations were made hourly on replicate samples by using the azide modification of the standard Winkler method (APHA AWWA WPCF 1975).

Dialysis tubing sample bags were placed in the carboy. At 1/2-hour intervals during the first 2 hours, and at 1-hour intervals thereafter, three bags (replicates) were removed for determination of DO. The experiment was terminated when the sample DO approximated the ambient DO.

To determine the influence of temperature, the experiment was run at 7 and 21 C. Additionally, to determine time to equilibrium in a flowing versus a stagnant water environment, two series of tests were run, one with continuous water circulation via nitrogen bubbling, the other without water circulation. Analysis of variance procedures were used to determine the experimental error of the technique and to make comparisons between treatments (temperature, flow).

Immediately upon removal of a bag from the carboy, the water sample was gently extracted by using a 10-ml graduated hypodermic syringe (Leur-Lok). DO subsequently was determined by using a modification of the microtechnique of Burke (1962).

Reagents

Reagents used in the Micro-Winkler procedure were standard Winkler solutions of manganous sulfate ($MnSO_4$), alkaline iodide azide (AIA), and ortho-phosphoric acid (H_2PO_4). These were held in small reagent bottles and capped with rubber septa. The reagents were dispensed by penetrating the septum with the hypodermic needle and drawing necessary volumes directly into the syringe containing the water sample. Starch indicator solution was dispensed from a dropper bottle, and 0.025 N phenyl arsine oxide (PAO) titrant was dispensed by using a Hach digital titrator and titration cartridge (Hach Company, Ames, Iowa).

DO measurement technique

The DO measurement technique was:

1. Remove sample bag from ambient water, gently penetrate the bag with a hypodermic syringe, and extract a 10 ml water sample.
2. Invert syringe and expel water to the 9.4 ml mark.
3. Draw 0.2 ml of $MnSO_4$, wipe needle tip, and rotate syringe gently to mix.
4. Draw 0.2 ml of AIA, wipe needle tip, and mix. Place syringe in test-tube rack and allow precipitate to settle. Mix again.
5. Draw 0.2 ml of H_2PO_4, wipe needle tip, and mix. Allow precipitate to dissolve.
6. Eject contents of syringe into a 25-ml flask.
7. Using the Hach digital titrator, dispense PAO until a pale yellow color is reached. Add one drop of starch indicator and titrate until blue color disappears.
8. Calculate DO as : DO (mg/liter) = 0.021 x ml PAO

Data analysis

Because the movement of oxygen between the inside of the bag and the surrounding environment is a diffusion reaction, the rate of oxygen movement is proportional to the difference (D) between the oxygen concentration of the environment and the oxygen concentration within the bag. This leads to an exponential relationship of the form

$$\ln(D) = \ln(D_o) - kt$$

where D is the difference in oxygen concentrations within and without the bag at time t, DO is the oxygen concentration at t = 0, and k is the rate constant. A linear regression of ln(D) on t was fitted to find the rate constants for the experimental data, pooled by treatment (temperature, flow). We then used the experimentally determined rate constants in the equation to find the length of time needed for the difference in oxygen concentration to be reduced to 95% ($D = 0.95 \cdot D_o$) and 99% ($D = 0.99 \cdot D_o$) of the original value.

Results and Discussion

Times (calculated from rate constants) required for DO in dialysis tubing to reach 95% and 99% equilibrium with deoxygenated lotic and lentic waters at 7 and 21 C are given in Table 1. Experimental results

Table 1. Calculated times required for dissolved oxygen concentration in dialysis tubing to reach equilibrium with deoxygenated environment at 7 and 21 C and lotic and lentic waters

		Time (hours)	
	Temperature C	95% Equilibrium	99% Equilibrium
Lotic Water	21	1.0	2.7
	7	1.0	2.7
Lentic Water	21	1.8	4.1
	7	1.9	4.5

closely fit the theoretical equation, r^2 ranging from 0.97 to 0.99 among the four treatments (Fig. 1). In lotic water, the calculated times were virtually identical (95% equilibrium in 1 hour, 99% of equilibrium in 2.7 hours). In lentic water, the calculated times at the two temperatures varied slightly (95% equilibrium at 7 C in 1.9 hours, 21 C in 1.8 hours, 99% equilibrium at 7 C in 4.5 hours, 21 C in 4.1 hours); however, for purposes of practical application these differences seem negligible. For general application, we recommend a slightly longer time (2 hours to attain 95% equilibrium and 5 hours to attain 99% equilibrium). Figure 1 shows the results of movement of DO through the membrane versus time for lotic and lentic waters at 7 and 21 C. Experimental error for DO measurement within a sample bag was 0.05 mg/liter.

This technique subsequently was used to measure microlayers both in laboratory and field situations quickly and inexpensively. Sample bags can be placed at any level in the water column and titrations can be run in less than 10 minutes with little practice. A kit containing the equipment and reagents can be assembled for approximately $150.00. Primary advantages of the technique include: use of small sample volume making it adaptable to laboratory situations for which a large number of replicate samples are needed; adaptability to a wide variety of laboratory and field situations well beyond measuring microstratification of DO; is simple and of low cost.

Note the time-to-equilibrium values given are specific to the particular dialysis tubing used, and by size and volume as well as shape. Therefore, time-to-equilibrium determinations must be made for any deviation of tubing and bag size.

Acknowledgments

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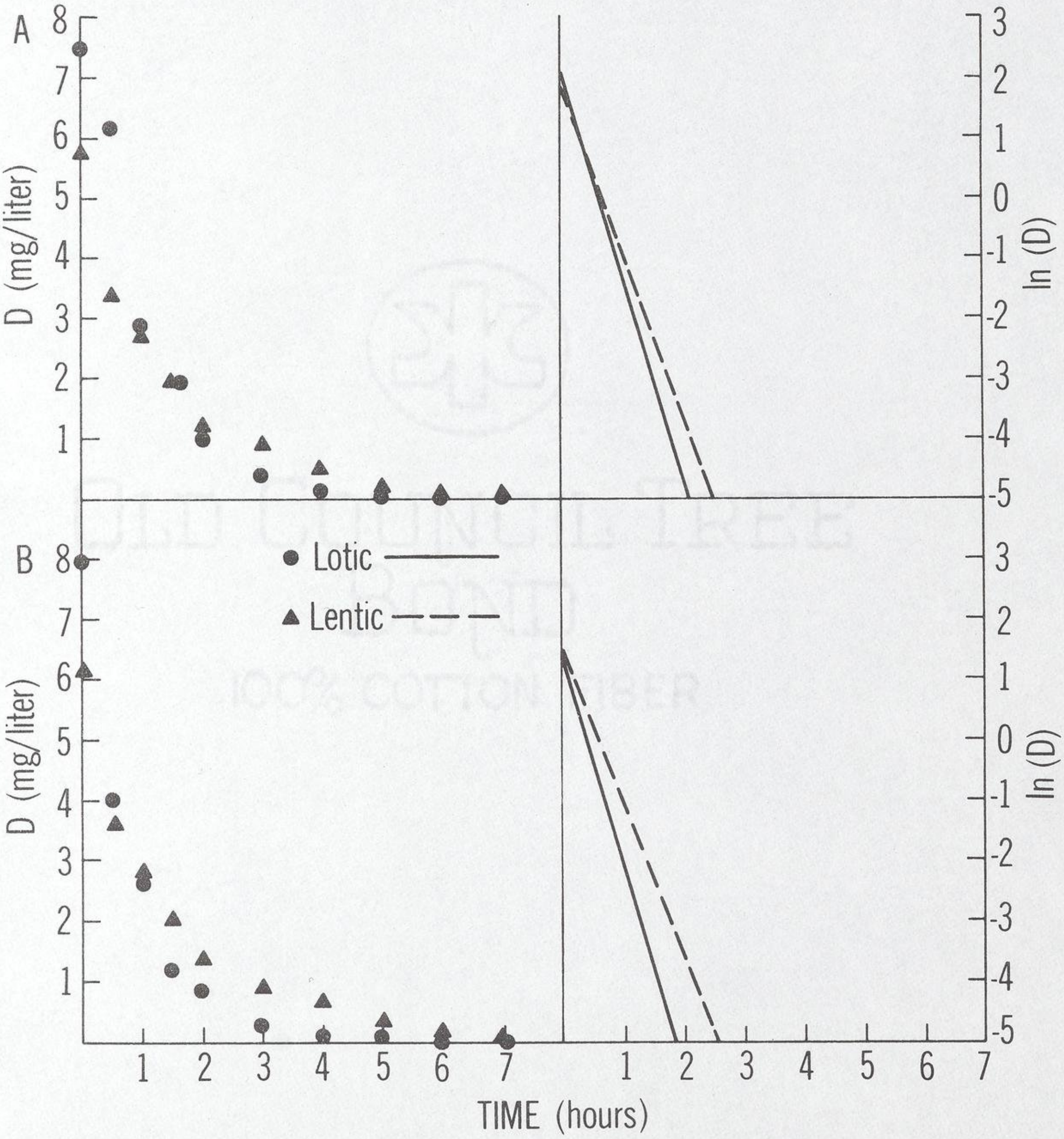
Figure 1--Difference (D) between DO of environment and DO within sample bags versus time at 21 C (A) and 7 C (B) in lotic and lentic environments. Each point represents three replicates for three runs


A
B
D (mg/liter)
ln (D)
Lotic
Lentic
TIME (hours)

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NATURAL MUSKELLUNGE REPRODUCTION IN MIDWESTERN LAKES

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PART III. NATURAL MUSKELLUNGE REPRODUCTION IN MIDWESTERN LAKES

Abstract

Throughout the native range of the muskellunge, self-sustaining lake populations of the species are declining. Because little is known of muskellunge reproductive requirements, this study had the objective of statistically identifying ecological variables that may influence natural reproduction in lakes and, further, to develop a procedure for estimating muskellunge reproductive potential in individual lakes by using readily accessible ecological data. The Natural Resources departments of Michigan, Minnesota, and Wisconsin provided file data on 117 selected lakes. Information on water chemistry, hydrology, watershed characteristics, fish communities, and cultural perturbations comprised 94 variables. In the various statistical operations, estimated muskellunge reproduction in each lake was treated as either (0) none (1) poor, (2) low, (3) moderate, or (4) high and self-sustaining. Analysis of variance and linear correlation procedures, followed by stepwise multiple linear regression analysis, were used to identify variables associated with the several levels of reproduction.

Nine variables accounted for 57% of the variability in reproduction. These included northern pike abundance, inflow water source, conductivity, spring water-level condition, discharge volume, shoreline development factor, cultural development of adjacent lands, and alkalinity. Conditions identified as most strongly promoting reproduction were limited northern pike abundance, rising springtime

water level, high alkalinity, and high shoreline development factor in drainage-lake systems. Complete data sets for these 5 variables were available for 89 muskellunge lakes. When organized by discriminant function analysis, 58% of the lakes were classified identically to manager-estimated reproductive level, and 91% were classified within ±1 reproductive level. Application of the discriminant function produced from the analysis may be useful for determining lake stocking and habitat improvement strategies directed toward creating or maintaining self-sustaining muskellunge populations.

Introduction

The muskellunge (*Esox masquinongy*) is a prized gamefish in northern states and Canada. In many midwestern lakes that formerly supported self-sustaining populations, natural reproduction of the species has greatly declined or ceased. Ecological reasons accounting for this decline include competition with the congeneric northern pike (*Esox lucius*) (Inskip and Magnuson 1983; Oehmcke et al. 1974) and reproductive failure due to loss or modification of habitat (Dombeck et al. 1984).

Muskellunge management strategies commonly involve harvest regulations and stocking of hatchery-reared fingerlings (Miller 1983). To date, little effort has been made to manage muskellunge habitats. In large part, this is attributable to a paucity of detailed ecological knowledge, especially relating to muskellunge habitat requirements and interspecific fish interactions.

One approach to gaining needed ecological information might be through long-term case studies. Such research, however, is costly, labor intensive, and often only of site-specific utility. Because of these disadvantages, management agencies tend to give such studies low priority. An alternative approach is to gain ecological insights through statistical analysis of an extensive data base, such as that readily available in management agency files. This approach requires no additional field work, is relatively inexpensive, can cover a broad geographical area, and with presently available computer technology, can analyze a large data base. Through various multivariate statistical techniques, this approach can be used to identify general ecological correlations and may have site-specific applications.

This study employed the latter approach to (1) identify ecological factors that influence natural muskellunge reproduction in midwestern lakes and (2) develop a quantitative procedure for evaluation of muskellunge potential in individual lakes by using readily accessible ecological data.

Methods

Collection of data and location of lakes

Ecological data were obtained from the respective Department of Natural Resources (DNR) survey files on 117 selected lakes within USDA-Forest Service Region 9, in Michigan, Minnesota, and Wisconsin. Lakes were selected on the basis of the availability and completeness of ecological information and their occurrence within the muskellunge's native range. All were surveyed between 1961 and 1981, but primarily after 1972. They occur within six major drainages: Upper Mississippi (20 lakes), Chippewa (42), St. Croix (5), and Wisconsin rivers (24), and lakes Michigan (15) and Superior (11) (Figure 1).

Muskellunge reproduction estimates

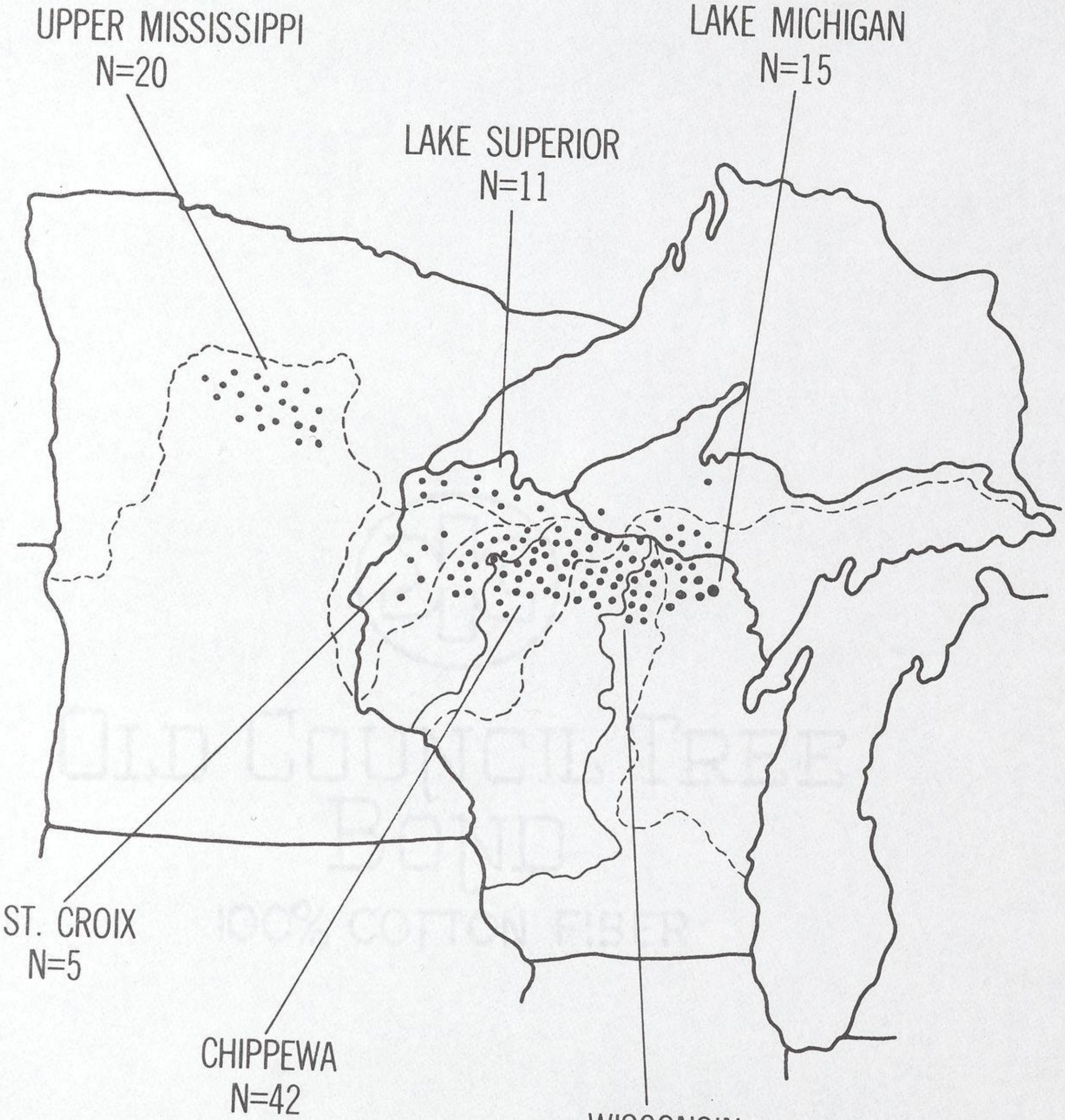
For each lake, estimates of the proportion of the muskellunge population recruited from natural reproduction were obtained from DNR fisheries biologists. Twenty-seven lakes support self-sustaining muskellunge populations, 67 are non-self-sustaining (i.e., populations maintained in part or wholly by stocking), and 23 were either former muskellunge lakes or non-muskellunge lakes randomly selected (excluding dystrophic lakes) from the same geographic range as, and of similar size to, the muskellunge lakes.

For statistical purposes, each lake was placed into one of five discrete groups, each group representing an estimated level of natural muskellunge reproduction: 0 (none), 1 (poor), 2 (low), 3 (moderate), and 4 (high or self-sustaining). The total number of lakes representing each reproductive category were: none-23, poor-24, low-17, moderate-19, and high or self-sustaining-34 (Table 1). In the subsequent statistical analyses, the discrete level of estimated natural reproduction was the dependent variable.

Ecological variables

Ecological data represented five general categories: fish communities, water quality, lake morphometry, natural watershed features,

Figure 1--Geographic distribution of study lakes showing drainage boundaries (----) and sample size. Each dot represents one lake


UPPER MISSISSIPPI
N=20
LAKE MICHIGAN
N=15
LAKE SUPERIOR
N=11
ST. CROIX
N=5
CHIPPEWA
N=42
WISCONSIN
N=24

and cultural development of watersheds, totaling 94 variables (Appendix I). Terminology and survey methods followed the procedures of Wisconsin Department of Natural Resources (1982). Where necessary, Michigan and Minnesota data were standardized to conform with Wisconsin's terminology and methods. Selected ecological features of study lakes are given in Table 1.

Data analysis

Analysis of variance (ANOVA) was used to test for significant relationships between level of muskellunge reproduction and each ecological variable. Because of the broad geographical distribution of the 117 lakes, there was concern that ecological distinctions exist between the six major drainage basins. Therefore, ANOVA was first used to remove significant interdrainage variance and then to determine those parameters most useful as predictors of muskellunge reproduction. For this analysis, $P < 0.1$ was used as the level of significance because the hazard in analyzing a data set compiled from several sources is, not that false relationships will be identified, but that existing relationships will be masked or weakened due to large variances.

After an array of nine predictive variables was developed, simple linear correlation analysis was employed to determine the direction of the relationship. Data for all nine variables were available for 68 lakes. The remaining lakes had missing data; therefore, sample sizes varied from parameter to parameter. Stepwise multiple linear regression, utilizing the maximum R^2 improvement technique (Helwig and Council 1979),

Table 1. Some ecological features of the 117 study lakes by drainage basin showing the number (*) of lakes in each category or the mean value and range () for the parameter

	Drainage					
Parameter	Lake Michigan	Lake Superior	Wisconsin River	Chippewa River	St.Croix River	Mississippi River
Total lakes	15	11	24	42	5	20
Muskellunge (*) reproduction						
High	5	6	1	9	0	13
Moderate	0	1	3	9	1	5
Low	0	2	9	6	0	0
Poor	1	0	6	15	2	0
None	9	2	5	3	2	2
Northern (*) pike abundance						
Abundant	0	1	1	3	2	15
Common	6	0	8	10	2	3
Rare	5	4	10	5	1	2
Absent	4	6	5	24	0	0

Lake (*) types						
Natural	12	8	14	17	4	7
Impoundment	3	3	10	23	1	13
Reservoir	0	0	0	2	0	0
Area (hectares)	324 (65-806)	150 (21-259)	331 (55-1373)	521 (38-6192)	465 (62-1044)	4675 (141-45135)
Alkalinity mg/l	65 (18-145)	37 (17-86)	40 (1-175)	44 (10-97)	41 (11-84)	150 (121-171)
Shoreline development factor	2 (1-3)	2 (2-5)	2 (1-4)	3 (1-13)	2 (1-5)	2 (1-4)
Cultural development index	0.01 (0.0-0.02)	0.01 (0.0-0.04)	0.03 (0.0-0.06)	0.02 (0.0-0.05)	0.02 (0.0-0.04)	0.001 (0.0-0.03)

was performed to order the variables in a fashion explaining the largest proportion of total variance in level of reproduction.

Because a strong relationship between muskellunge reproduction and northern pike emerged from these analyses, special attention was given to this relationship. Simple correlation analysis of muskellunge reproductive level versus northern pike abundance was first performed for each drainage basin. Resulting interbasin correlations suggested that confounding factors were involved; therefore, to determine factors influencing the muskellunge-pike association, lakes were identified as either: (1) self-sustaining muskellunge/abundant pike populations; (2) self-sustaining muskellunge/pike rare or absent; (3) non-self-sustaining muskellunge/abundant pike; (4) non-self-sustaining muskellunge/pike rare or absent. ANOVA procedures then were used to identify variables significantly related ($P < 0.1$) to the association (statistical interaction) of the two species in the four groups of lakes. The means of the variables identified by ANOVA were next examined to determine the nature of the association between the species.

Discriminant analysis was used to derive a predicted muskellunge reproductive level for individual lakes as based upon a limited array of ecological variables previously demonstrated as correlates of muskellunge reproductive success. Lakes lacking natural muskellunge reproduction presented a special problem because we could not always distinguish between those that had never supported natural muskellunge populations and those from which natural populations have been extirpated. We resolved this issue by deleting all lakes with a reproductive level of zero and, thus, employed only lakes with poor, low, moderate, or high reproduction. Ecological variables considered for use in the discriminant analysis included nine variables identified as being significantly ($P < 0.1$) related to level of reproduction by ANOVA. From this group, four variables were subjectively eliminated after consideration of their redundancy with other parameters, ease and accuracy of measurement, and completeness of the data set. Thus, the discriminant analysis employed five variables determined to best represent four of the five ecological data categories. These were: abundance of northern pike, spring water level, alkalinity, shoreline development factor (SDF), and lake hydrology (drainage or seepage lake). Rationale for selection of these variables is treated more fully in the Results section. Complete data sets for these five variables were available for 89 lakes.

The posterior probability (probability of a lake being placed within the given reproductive category) for each of the four reproductive categories (i) is given by the formula:

$$\text{Probability (that lake is in category i)} = \frac{\exp\left[-1/2(X-\overline{X}_i)'S^{-1}(X-\overline{X}_i)\right]}{\sum_{j=1}^{4} \exp\left[-1/2(X-\overline{X}_j)'S^{-1}(X-\overline{X}_j)\right]}$$

The symbols X, $\overline{X}_i$, and S represent the vector of measurements of the five ecological measurements for the lake, the vector of means for each variable for all lakes in each of the four reproductive categories, and the pooled variance-covariance matrix from the discriminant analysis respectively.

Results

Variables related to muskellunge reproduction

ANOVA identified nine significant relationships between ecological variables and muskellunge reproductive level after interdrainage variance was removed (Table 2). These included at least one variable from each of the five ecological data categories. Significant correlations (five positive and three negative) occurred between muskellunge reproductive level and eight of these variables, only conductivity yielding a non-significant correlation (Table 3).

Table 2. Anova results for ecological variables significantly related to level of muskellunge reproduction

Parameter	No. of Lakes	F
Northern pike abundance	117	13.5 ***
Seepage lake	117	6.0 ***
Rising spring water	117	3.3 ***
Drainage lake	117	3.0 **
Outlet volume	82	2.7 **
Conductivity	89	2.6 **
Shoreline development factor	112	2.4 **
Cultural development index	117	2.2 **
Alkalinity	117	1.9 *

Probability levels: ***= $P < 0.01$, **= $P < 0.05$, *= $P < 0.1$

Table 3. Correlation coefficients (r) among 9 ecological variables and level of muskellunge reproduction for the study lakes. Underscored values are significant at the 0.1 level

Parameter	Drnge. lake	Seepge lake	Rising spring water	Alkal.	Abund. of pike	Cult. devel. index	Cond.	Discharge volume	Shoreline devel. factor
Level of reproduction	<u>.33</u>	<u>-.29</u>	<u>.26</u>	<u>.33</u>	<u>-.21</u>	<u>-.18</u>	-.09[a]	<u>.36</u>	<u>.17</u>
Drainage lake		<u>-.74</u>	<u>.21</u>	<u>.32</u>	<u>.18</u>	-.01	<u>.33</u>	<u>.18</u>	.10
Seepage lake			<u>-.16</u>	<u>-.32</u>	-.11	.02	<u>-.46</u>	-.14	-.09
Rising spring water				<u>.24</u>	<u>.30</u>	.02	-.08	<u>.76</u>	<u>.28</u>
Alkalinity					<u>.50</u>	<u>-.30</u>	<u>.91</u>	<u>.45</u>	<u>-.17</u>
Northern pike abundance						-.04	<u>.19</u>	<u>.23</u>	-.11
Cultural Development index							.05	-.15	.05
Conductivity								-.12	-.15
Discharge volume									<u>.45</u>

[a]No data available for the upper Mississippi River drainage.

Additionally, there were significant intercorrelations among the nine parameters for about two-thirds of the possible paired comparisons.

Stepwise multiple linear regression indicated that the nine variables accounted for 57% of the variability of natural reproduction (Table 4). Northern pike abundance alone accounted for 42% of the variance. The best two-variable model included northern pike abundance and drainage lake system, which accounted for 50% of the variance.

Table 4. Results of stepwise multiple linear regression on nine ecological variables significantly related to level of natural muskellunge reproduction. Variables are ordered vertically according to placement in the regression. N = 68

Parameter	Cumulative R^2
Northern pike abundance	.417
Drainage lake	.501
Shoreline development factor	.527
Seepage lake	.531
Conductivity	.538
Rising spring water	.544
Outlet volume	.571
Alkalinity	.572
Cultural development index	.574

Association between muskellunge reproduction and northern pike abundance

Drainage-by-drainage correlation analyses of muskellunge reproductive level versus northern pike abundance produced significant negative relationships among lakes of the Chippewa River, St. Croix River, Lake Michigan, and Lake Superior drainages. A non-significant negative relationship occurred for the Wisconsin River drainage, and a virtually random association was indicated for the Mississippi River drainage (Table 5).

Table 5. Results of linear correlation analysis of level of muskellunge reproduction versus abundance of northern pike by drainage basin

Drainage	Number of lakes	r
Lake Superior	11	-.96 ***
St. Croix River	5	-.73 *
Chippewa River	41	-.64 ***
Lake Michigan	15	-.62 ***
Wisconsin River	25	-.13 n.s.
Mississippi River	20	.03 n.s.

ANOVA implicated 12 ecological variables as significant confounding factors in explaining the association (statistical interaction) of pike with muskellunge reproduction (Table 6). Of these, six have been previously implicated with the biology of the two species (Tables 2, 3): alkalinity, rising spring water, drainage lake, discharge volume, seepage lake, and cultural development index. Two sets of variables are clearly redundant because they are inverse characteristics; viz, rising spring water and stabilized water level, drainage lake and seepage lake.

Table 6. ANOVA results listing ecological variables significantly related to the association of muskellunge reproductive level versus northern pike abundance

Parameter	F
Alkalinity	24.8 ***
Rising spring water	10.5 ***
Drainage lake	10.0 ***
Outlet volume	7.6 ***
pH	7.5 ***
Maximum depth	4.9 ***
Area	3.6 **
Seepage lake	3.4 **
Impoundment	3.2 **
Cultural development index	2.5 *
% agriculture	2.4 *
Stabilized water level	2.3 *

Table 7 presents group means for these variables, partitioned according to the four muskellunge-pike association categories. Lakes with vigorous natural populations of both species are best characterized

Table 7. Groups means of ecological variables associated with the association of muskellunge reproductive level versus northern pike abundance. Standard errors given in parentheses; sample sizes given in brackets

	Muskellunge population			
	Self-sustaining		Non-self-sustaining	
	Pike Population			
Parameter	Abund. [12]	Rare-absent [22]	Abund. [8]	Rare-absent [18]
Area	6876 (3885)	512 (274)	1005 (316)	288 (60)
Maximum depth	22 (3)	13 (2)	16 (3)	13 (1)
Alkalinity	152 (4)	53 (9)	80 (21)	40 (5)
pH	8.3 (0)	7.4 (0.2)	7.3 (0.3)	7.2 (0.1)
Impoundment	0.75 (0.13)	0.36 (0.10)	0.50 (0)	0.22 (0.10)
Seepage lake	0	0.05 (0.05)	0	0.28 (0.11)
Drainage lake	1 (0)	0.91 (0.06)	1 (0)	0.44 (0.12)
Rising spring water	0.66 (0.14)	0.14 (0.07)	0.12 (0.12)	0
Stabilized water level	0.08 (0.08)	0.14 (0.07)	0.50 (0.19)	0.17 (0.09)
Discharge volume	7 (2)	1.8 (1.0)	0.5 (0.2)	0.1 (0.1)
% agri-culture	0	1.6 (0.6)	4.1 (1.7)	3.1 (1.4)
Cultural develop-ment index	0.003 (0.002)	0.011 (0.002)	0.015 (0.005)	0.014 (0.003)

as large impounded natural lakes, with high alkalinity, rising spring water, and limited cultural influences (agriculture and other development); all these lakes are located in the Upper Mississippi River drainage (Figure 1). On the other hand, lakes with poor populations of both species were characterized as being of small size, low alkalinity, and low discharge volume. This category included the largest number of seepage lakes and a relatively high cultural influence factor. Lakes in the remaining two categories were roughly similar, being comprised predominantly of unmodified drainage lakes of intermediate size and alkalinity levels, limited rising spring water, and moderate to high cultural influences. In such lakes, limited muskellunge reproduction associated with strong northern pike populations may be promoted by agricultural influences and stabilized water levels.

Discriminant analysis

A purpose of the discriminant analysis was to estimate potential muskellunge reproductive success in individual lakes as based on a simple array of readily measureable variables. From among the nine variables listed in Table 2, five were selected for the analysis: northern pike abundance, rising spring water level, alkalinity, SDF, and drainage lake system. The remaining variables identified in Table 2 were subjectively excluded because of considerations of redundance (conductivity, seepage lake), limitations of available data (discharge volume), and complexity of generating data (cultural development index). Predicted levels of muskellunge reproduction were calculated for the 89 individual lakes. Fifty-eight percent of the lakes were classified identically with manager estimates, and 91% were classified within ±1 manager estimated reproductive level.

In general, there was stronger agreement at the higher reproductive levels than at the lower (Table 8). No lake having poor or low muskellunge reproduction by manager estimates (N=41) was classified by the analysis as having high reproductive potential. Similarly, among lakes estimated by managers as having moderate to high muskellunge (N=48) only four lakes were predicted to be of poor or low reproduction.

Table 8. Agreement of 89 lakes classified by the five factor discriminant function analysis compared to original manager estimates of muskellunge natural reproductive level in individual lakes. Above: percentage agreement; below in parentheses: number of lakes

	Predicted level of natural reproduction				
Manager estimates	Poor	Low	Moderate	High	Total
Poor	58 (14)	21 (5)	21 (5)	0	100 (24)
Low	24 (4)	47 (8)	29 (5)	0	100 (17)
Moderate	6 (1)	6 (1)	69 (11)	18 (3)	100 (16)
High	6 (2)	0	34 (11)	59 (19)	100 (32)

Discussion

Muskellunge-northern pike associations

Demonstrated statistical correlations between muskellunge reproductive success and several ecological variables suggest that the historical decline of the species in many midwestern lakes may be attributable to a complex of geographically variable factors. Among these, the detrimental influence of the northern pike emerged as a critical element, particularly in the Chippewa River, St. Croix River, Lake Michigan, and Lake Superior drainage basins (Table 5) where the demise of self-sustaining populations has been most serious. On the other hand, there is little evidence here for negative influences of pike upon muskellunge reproduction in the Wisconsin River and Upper Mississippi River basins.

The pike is considered to have an ecological advantage over the muskellunge where the two species occur syntopically (Hess and Heartwell 1978). The invasion of muskellunge waters by pike has been associated with subsequent decline of the muskellunge (Inskip and Magnuson 1983) and has long been a concern in Wisconsin (Threinen and Oehmcke 1950). A notable example is one of Wisconsin's premier muskellunge lakes, Lac Courte Orielles, which produced a world record fish in 1949. The pike invasion in the mid-1930s was followed by the decline of muskellunge reproduction. Concurrent with pike invasion was the recreational development of shoreline adjacent to the muskellunge spawning area. Subsequently, highly eutrophic conditions developed, including decline of wild rice (*Zizania aquatica*) and other emergents, proliferation of dense submergent vegetation, and deposition of organic silts (Leon D. Johnson, Wisconsin Department of Natural Resources, personal communication). Stocking hatchery-reared fish became necessary to maintain Lac Courte Orielle's muskellunge fishery. This was verified by an experimental 5-year period in which none were stocked. Population studies showed a gap in muskellunge year classes corresponding to years of no stocking (Johnson 1981).

Several mechanisms have been implicated in the competitive interaction between muskellunge and northern pike. Earlier spawning of northern pike on common spawning grounds and subsequent predation on muskellunge larvae by pike is thought to greatly reduce muskellunge populations in Wisconsin lakes (Threinen and Oehmcke 1950). In a laboratory study, Caplin (1982) demonstrated the predation of young-of-the-year (YOY) muskellunge by YOY pike, whereas the converse did not occur. Caplin extrapolated that YOY pike can be important predators on YOY muskellunge in nature and may severely limit muskellunge recruitment. In addition, YOY pike gained efficiency as predators at a smaller size than muskellunge and had higher feeding efficiencies than did muskellunge of equal size (3.5-5.5 g). In another study, YOY pike exhibited less size selectivity for food, more aggressive feeding habits, and greater food conversion (Sorenson et al. 1966).

Morpho-edaphic influences The ecological mechanisms that favor the coexistence of the muskellunge and pike in some habitats, but not in others, are poorly understood. Considerations of ecological factors influencing lake fish communities implicate two major groups of factors, lake morphometry-hydrology and edaphic factors (Ryder et al. 1974). Several authors have implicated water body size as a determinant of fish community complexity (Barbour and Brown 1974; Emery 1978) when other ecological factors and geographical location are roughly similar. Literature on esocids suggests that a key factor in the coexistence of muskellunge and pike is habitat partitioning in sufficiently large and environmentally heterogeneous water bodies. At least in large river systems, such as the Niagara and St. Lawrence rivers, spatial segregation of the species occurs during reproduction, muskellunge selecting lotic spawning habitat and pike more lentic areas (Harrison and Hadly 1978; Donald M. Osterberg, State University College, Potsdam, NY, personal communication). It is notable that, in the upper Midwest, the native distribution of muskellunge includes, not only the northern lakes region of Wisconsin, Michigan, and Minnesota, but also extends southward in the large rivers draining these basins; namely, the Wisconsin, Chippewa, St. Croix, and Mississippi. In these large-river environments, the two species coexisted until recent times when cultural perturbations have seemingly shifted the ecological balance in favor of the pike. Within the study area, vigorous syntopic populations occur chiefly in lakes of the upper Mississippi basin. Leech Lake, Minnesota, serves as an example of a large lake affording spatial isolation of the two species during their early life histories. Whereas pike spawn in marshy near-shore areas, muskellunge spawn offshore in shallow bays in water 1 to 2-m deep over dense mats of stonewort (Chara) (Strand 1983).

It is of interest to pose the question of minimum water body size needed to support natural populations of the two species. In general, pike seem to be better adapted to smaller lotic and lentic systems, particularly those associated with marsh habitat (Trautman 1981). Tonn and Magnuson (1982) reported that small (mean, ca. 11 ha) winterkill-prone seepage lakes of northern Wisconsin support neither species, but rather are characterized by an Umbra-cyprinid community. In larger lakes (mean, ca. 31 ha) however, a pike-centrarchid assemblage exists. These lakes have either high, winter dissolved-oxygen levels or access to high winter oxygen refuges through inlet or outlet streams. None of their study lakes ranging in size to 90 ha contained muskellunge.

Although our data set was biased toward larger lakes, several observations may be made about esocid populations in the smaller lakes. Only three lakes in our study contained neither species. These were among the smallest lakes included in the data set, averaging 137 ha in area, and were either seepage or spring lakes. Marginal populations of both species or muskellunge alone occurred in 22 lakes as small as 38 ha and averaging approximately 220 ha; over two-thirds were drainage lakes. Marginal pike populations alone were present in five lakes of larger average size (mean, 521 ha), two being seepage lakes, two drainage lakes, and one a spring-fed lake. Lakes supporting both species, but with populations of one or the other tending to predominate, were even larger (means, 512-1005 ha), and nearly all were drainage lakes (Table 7). In summary, our data suggest that coexistence of the species is favored in drainage lakes of large area. Populations of both species are typically marginal in seepage lakes of small size. The status of populations in lakes of intermediate size may depend on local microhabitat factors such as edaphic conditions and cultural influences.

Consideration of the original distributional range of the muskellunge implies that it evolved in and is primarily adapted to oligotrophic waters characteristic to the Laurentian Shield. On the other hand, the broad circumpolar distribution of the pike, encompassing both oligotrophic and cooler eutrophic waters, implies generally greater environmental tolerance on the part of the pike. As discussed by Dombeck et al. (1984), early life and reproductive adaptations further support this view on ecological distinctions between the species. For example, the muskellunge broadcasts its demersal non-adhesive eggs over the bottom, and newly hatched young remain quiescent at the bottom, becoming active only after yolk-sac consumption. These features have been interpreted as being adaptations for well-oxygenated environments (Balon 1975). In contrast, the pike's adaptations include deposition of highly adhesive eggs onto aquatic vegetation above the bottom. Immediately after hatching, larvae are temporarily active before attaching to vegetation by means of a cephalic cement gland, behavior that would tend to promote survival under conditions of oxygen depletion. Historical evidence indicates, that with increasing cultural eutrophication, northern pike have tended to displace the muskellunge (Becker 1983). There is evidence that neither species is adapted to dystrophic waters or with edaphic factors associated with such waters. Neither occur in small bog lakes (Tonn and Magnuson 1982), and in the present study, three nonesocid lakes were characterized by low alkalinity (mean, 26 mg/liter), pH (mean, 6.8), and conductivity (mean, 48 umhos/cm). In contrast, the most abundant coexisting populations of the two species occurred chiefly in the Upper Mississippi drainage lakes of Minnesota. These are hard-water (mean alkalinity, 152 mg/liter) eutrophic lakes (mean pH, 8.3), owing to the basin's limestone bedrock features (Eddy and Underhill 1974). In contrast to eutrophic soft-water lakes, which tend to accumulate fine organic sediments, these lakes are notable for extensive marl deposits and limited organic sediments, a factor that may favor the survival of early life stages of both species.

Various authors have associated declines in northern pike populations with cultural eutrophication along with other cultural habitat perturbations (Trautman 1981; Forney 1977). Although there is little previous evidence implicating eutrophication with the decline of muskellunge populations, the biology of the species suggests that it may be particularly sensitive to environmental changes commonly associated with eutrophication. From the present data, several observations may be made in this regard. Highest levels of muskellunge reproduction were correlated with little or no agricultural or other human developments within the direct drainage area (Table 7). On the other hand, lakes lacking muskellunge or supporting only limited natural populations were characterized by high cultural development factors.

Water-level influences In addition to morpho-edaphic factors, there is evidence that water-level modification can influence the well-being of these species and their ecological associations. Trautman

(1981) suggested that wetland drainage has contributed to the demise of Ohio populations of both species. Donald M. Osterberg, (personal communication) believes that construction of dams on the St. Lawrence River and subsequent creation of lentic habitats has favored pike and contributed to a historical decline of muskellunge. Similarly, the decline of muskellunge in large midwestern rivers may be partly attributable to dam construction. In Osterberg's view, the ecological effect of more uniform lentic conditions may have been the breakdown of the early life history spatial separation of the two species.

The literature implicates seasonal spring flooding of terrestrial and wetland habitats with reproductive success of northern pike (Carbine 1941; Johnson 1957). Similarly, Dombeck (1979) and Dombeck et al. (1984) have identified muskellunge spawning in flooded near-shore areas in several Wisconsin and Michigan lakes. This suggests that, in lakes, spatial isolation of early life history stages of the two species is associated with slightly different spawning habitat created by rising waters. Results of this study identified rising spring water as a common feature in lakes maintaining naturally reproducing muskellunge (Tables 2,3) as well as in lakes maintaining strong pike populations (Tables 6, 7).

To the possible detriment of both species however, among many esocid lakes in the upper Midwest, there has been recent manipulation of water levels. Natural lakes have been impounded with low-head spillway dams for general recreational purposes, and for flow augmentation, larger dams have been constructed. The effect of the low-head dams has been to increase lake area and to stabilize seasonal water level fluctuation by dampening spring flooding. Conversely, in flow-augmentation impoundments, a seasonal water-level pattern is maintained that is similar to natural water-level fluctuation but seasonally more extreme; i.e., water levels are lowered during low flow periods (late summer-winter) and filled during peak flow (spring). From evidence presented here, it may be inferred that such water-level manipulation can affect muskellunge reproductive success and associations of esocid populations. In general, both species seem to benefit from rising springtime water level (tables 2, 3, 4, 6, 7). Stabilized water levels, however, seem to be detrimental to muskellunge reproduction ($r=-0.22$, $P=0.03$, $N=97$) and of little influence upon pike ($r=0.06$, $P=0.56$, $N=114$). To explain this, it may be speculated that under stable water-level conditions, spatial isolation between the species is reduced, and northern pike YOY enjoy an ecological advantage as hypothesized earlier.

Management implications

The discriminant function developed here provides a technique for estimating the potential of individual lakes to support natural muskellunge reproduction. It is based upon five ecological variables that have been shown to be significant correlates of reproductive success and that also are available in many ecological survey reports or that may be generated with relatively little effort. Superficially, the strength and utility of the model might be questioned because of the relatively low agreement between manager-estimated and predicted reproductive levels (Table 8). It is important, however, to realize that the strength of the posterior probability within each reproductive level provides valuable information for the manager.

In Table 9, several examples of application are illustrated. Lake Chippewa (Sawyer Co., WI) is a large (6,192 ha) soft-water flow augmentation impoundment, the water level of which is lowered more than 3 m each winter and raised in early spring. It has traditionally

Table 9. Example of management application of the posterior probabilities generated by the discriminant analysis model. Original manager estimated muskellunge reproductive levels are underscored

Reproductive level	Lake: Chippewa	Connors	Ghost	Butternut
	Posterior probabilities			
Poor (1)	0	71	8	29
Low (2)	1	18	19	25
Moderate (3)	13	8	50	33
High (4)	88	3	22	14

Management options: Lake Chippewa; monitor muskellunge reproduction, identify, protect, and enhance spawning and nursery areas, and prevent increase in pike numbers. Connors Lake; stocking, manage water level, and control pike. Ghost Lake; water level management and spawning habitat improvement. Butternut Lake; promote water quality, improve spawning habitat, and control pike.

had a good naturally reproducing muskellunge fishery, with pike rare or absent until the past few years when a substantial increase in the pike population has been observed. There is good agreement between manager-estimated and predicted level of muskellunge reproduction (Table 9). The generated posterior probabilities indicate that Lake Chippewa probably has suitable elements for good muskellunge reproduction. Management options might be to monitor the population's reproduction, identify, protect, and enhance the spawning and nursery areas and take steps to prevent the increase in pike numbers. Although Lake Chippewa has received token stockings of hatchery-reared muskellunge (possibly for social or political reasons), it is likely that natural reproduction is sufficient to maintain the fishery.

The second example, Connors Lake (Sawyer Co., WI) is a 174-ha soft-water lake whose water level is stabilized by a rock dam. Muskellunge were native to Connors Lake, pike are presently common, and there is only limited muskellunge spawning habitat. Both the model and manager estimate agree that this lake has poor potential for successful muskellunge reproduction. Present management includes the stocking of hatchery reared fingerling muskellunge. Other management options might include pike population control or water level management. It may be, however, that there are limits to what can be done. Lacking the ability to control these factors, the most feasible management solution might be to continue stocking hatchery-reared muskellunge of size at which they are no longer vulnerable to esocid predation.

These two examples illustrate how stocking determinations can be made relative to benefit/cost considerations. It would appear that fish stocking would be more beneficial in Connors Lake.

Ghost Lake (Sawyer County, WI), is a 151-ha soft-water stabilized impoundment with a natural muskellunge population but lacking northern pike. Natural muskellunge reproduction does occur; however, hatchery-reared fingerlings are stocked to maintain the desired population level. In Table 9, note that both the manager-estimated and predicted reproductive levels are in agreement that natural muskellunge reproduction is moderate. Management efforts to restore Ghost Lake's muskellunge fishery to the self-sustaining status might include water-level management or other reproductive habitat enhancement measures. Our last example, Butternut Lake (Price County, WI), is a 467-ha soft-water natural lake with northern pike common. Muskellunge were native to Butternut Lake, but, the population is presently maintained by fingerling stocking. Although the manager-estimated low muskellunge reproduction, results of the discriminant function model were ambiguous. Note that no reproductive level has a posterior probability over 40%. We have empirically determined that lakes with an individual probability above 60%, which corresponds to high agreement with the manager estimate, the model is strongest. Conversely, for lakes with all probabilities below 40%, the discriminant model has little utility. In such cases, we recommend that the input data be examined for accuracy or that other factors not addressed by the model be considered. Relative to Butternut Lake, eutrophication from sewage may be the proximate factor limiting muskellunge reproductive potential. The model will likely not be useful where cultural eutrophication is overwhelming.

We do not propose this model as the sole basis for muskellunge management decisions in midwestern lakes, but rather, as another tool to be used in combination with other decision variables. The greatest utility of the model perhaps is to assist in determining stocking or habitat improvement priorities. We also recommend caution in applying it beyond the geographic range for which it was developed.

Discriminant analysis of this sort would seem to have general utility to lake management objectives and strategies. Although other forms of multivariate analyses might also be applied (e.g., factor analysis), discriminant analysis is particularly useful when only qualitative or semi-quantitative data is available (Kachigan 1982), as is often the case for management data bases. Additionally, categorizing lakes provides insights regarding ecological relationships over a broad geographical range and provides information concerning specific variables.

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OLD COUNCIL TREE BOND 100% COTTON FIBER

Appendix I

Ecological variables obtained from state agency files included in data analysis.

Fish Community data with species and abundance indicated as:

0 (absent), 1 (rare), 2 (common), or 3 (abundant).

Northern pike (Esox lucius)

Mud pickerel (E. americanus americanus)

Walleye (Stizostedion vitreum

Yellow perch (Perca flavescens)

Log perch (Percina caprodes)

Johnny darter (Etheostoma nigrum)

Iowa darter (E. exile)

Largemouth bass (Micropterus salmoides)

Smallmouth bass (M. dolomieui)

Rock bass (Ambloplites rupestris)

Black crappie (Pomoxis nigromaculatus)

White crappie (P. annularis)

Bluegill (Lepomis macrochirus)

Pumpkinseed (L. gibbosus)

Warmouth (L. gulosus)

Green sunfish (L. cyanellus)

Yellow bass (Morone mississippiensis)

Channel catfish (Ictalurus punctatus)

Black bullhead (I. melas)

Brown bullhead (*I. nebulosus*)

Yellow bullhead (*I. natalis*)

Lake trout (*Salvelinus namaycush*)

Brook trout (*S. fontinalis*)

Brown trout (*Salmo trutta*)

Rainbow trout (*S. gairdneri*)

Cisco (*Coregonus artedi*)

Whitefish (*C. clupeaformis*)

White sucker (*Catostomus commersoni*)

Redhorse (*Moxostoma* spp.)

Lake chubsucker (*Erimyzon sucetta*)

Longnose gar (*Lepisosteus osseus*)

Shortnose gar (*L. platostomus*)

Bowfin (*Amia calva*)

Burbot (*Lota lota*)

Sturgeon (*Acipenser fulvescens*)

Carp (*Cyprinus carpio*)

Bluntnose minnow (*Pimephales notatus*)

Emerald shiner (*Notropis atherinoides*)

Common shiner (*N. cornutus*)

Golden shiner (*Notemigonus crysoleucas*)

Redbelly dace (*Chrosomus eos*)

Creek chub (*Semotilus atromaculatus*)

Trout-perch (*Percopsis omiscomaycus*)

Lake morphometry

Area (hectares)

Length (km)

Width (km)

Shoreline length (km)

Maximum depth (m)

Mean depth (m)

% < 1-m in depth

% > 7-m in depth

Area (hectares) > 1-m in depth

Shoreline development factor

Water quality

pH

Alkalinity (mg/liter)

Secchi depth (m)

Conductance (umhos/cm)

Color (clear, light brown, medium brown, dark brown, turbid)

Watershed features

Lake type: natural lake, impounded natural lake, reservoir

Water level fluctuation: natural, rising spring water (> 0.5m), none (stabilized by a control structure)

Water source: drainage lake, seepage lake, spring lake

Discharge volume (m^3/second)

Area direct drainage (km^2)

Watershed area (km^2)

% agriculture (of direct drainage area)

% wildlands

Number of inlets

Area adjacent wetland (hectares)

% marsh

% wooded wetland

Area marsh (hectares)

Area wooded wetland (hectares)

Area marsh (hectares)/lake area (hectares)

Area wooded wetland (hectares)/lake area (hectares)

Littoral bottom types (%): sand, gravel, bedrock, clay, boulder, silt, marl, rubble, detritus

Cultural development of watersheds

Number of commercial facilities (boat rentals, resorts, campgrounds)

Number of dwellings

Commercial facilities/lake area (hectares)

Dwellings/lake area (hectares)

$$\text{Cultural development index} = \frac{\text{commercial facilities + dwellings}}{\text{lake area}}$$

Appendix II

The following program can be used to calculate the probability for natural muskellunge reproduction for a given lake by using the discriminant function model derived from this study. It is designed for use by resource managers on most personal computers and is written in a simple style with all input data prompted and output displayed on the screen.

Information needed to perform the calculation includes data from the lake to be classified as follows: rising spring water level and drainage lake as no = 0, yes = 1; alkalinity and SDF, actual values; and northern pike abundance as absent = 0, rare = 1, commmon = 2, and abundant = 3. The results are the percentage probability for a lake having a muskellunge reproductive level (1=poor, 2=low, 3=moderate, 4=high) calculated as follows:

Probability (%) that the lake is in reproductive category (i)

$$= \frac{\exp\left[-1/2(X-\overline{X}_i)'S^{-1}(X-\overline{X}_i)\right]}{\sum_{j=1}^{4} \exp\left[-1/2(X-\overline{X}_j)'S^{-1}(X-\overline{X}_j)\right]}$$

where X is the value for each of the five ecological parameters for the given lake, $\overline{X}_i$ is the mean value for each of the parameters at the ith reproductive level, and S^{-1} is the inverse of the pooled variance-covariance matrix for the five parameters. Both $\overline{X}_i$ and S^{-1} are included in the following program as constants derived from this study. Comment statements are preceded by "!".

```
100 !                          BASIC PROGRAM
110 !         FOR ESTIMATING MUSKELLUNGE REPRODUCTIVE POTENTIAL
120 !                          IN MIDWESTERN LAKES
130 !
140 ! BASED ON PAPER BY:  DOMBECK, MENZEL, & HINZ
150 ! PROGRAMMED BY:  MARTIN J. HANSON, P.E., 1984
160 !
170 ! ************ INITIALIZE VARIBLES AND READ CONSTANTS ***********
180 !
190 DISPLAY ERASE ALL                      ! CLEAR SCREEN
200 !
210 GO SUB 1280                             ! WRITE SCREEN TEMPLATE
220 !
230 INTEGER I,J,K                          ! DEFINE VARIABLES
240 REAL X(4),RLM(3,4),DELTA(3,4),IPVCM(4,4),DOT1(3,4),PP(3),DOT2(4),D
250 !
260 !
270 !
280 DATA 0.13, 0.48, 0.79, 0.80, 0.47
290 DATA 0.29, 0.43, 0.76, 0.50, 0.55   ! REPRODUCTIVE LEVEL
300 DATA 0.13, 0.54, 1.00, 0.30, 0.60   ! MEANS MATRIX (RLM)
310 DATA 0.31, 0.85, 0.94, 0.55, 0.65
320 !
330 !
340 !
350 DATA  8.21, -0.26, -0.97, -2.74, -2.79
360 DATA -0.26, 10.23, -0.68, -4.79,  2.66      ! INVERSE OF POOLED
370 DATA -0.97, -0.68, 10.25, -0.60, -0.83      ! VARIANCE-COVARIANCE MATRIX
380 DATA -2.74, -4.79, -0.60,  6.82,  0.14      ! (IPVCM)
390 DATA -2.79,  2.66, -0.83,  0.14,  9.68
400 !
410 !
420 !
430 FOR I = 0 TO 3
440 FOR J= 0 TO 4
450 READ RLM (I,J)                          ! LOAD REPRODUCTIVE LEVEL MEANS
```

```
460 NEXT J
470 NEXT I
480 !
490 !
500 !
510 FOR I = 0 TO 4
520 FOR J = 0 TO 4
530 READ IPVCM (I,J)                              ! LOAD INVERSE OF POOLED
540 NEXT J                                        ! VARIANCE-COVARINACE
550 NEXT I
560 !
570 ! ********************  DATA INPUT SECTION  *********************
580 !
590 INPUT AT (7,31)SIZE (-40)" ":A$         ! LAKE NAME
600 !
610 INPUT AT (9,61)SIZE(-5)" ":X(0)         ! RISING SPRING WATER LEVEL (N=0, Y=1)
620 !
630 INPUT AT (10,61)SIZE(-5)" ":X(1)        ! ALKALINITY (METHYL ORANGE)
640 X(1)=X(1)/100
650 !
660 INPUT AT (11,61)SIZE(-5)" ":X(2)        ! DRAINAGE LAKE (N=0, Y=1)
670 !
680 INPUT AT (13,61)SIZE(-5)" ":X(3)        ! NORTHERN PIKE ABUNDANCE
690 X(3)=X(3)/2                             ! ABSENT=0, RARE=1, COMMON=2
700                                         ! ABUNDANT=3
710 !
720 INPUT AT (14,61)SIZE(-5)" ":X(4)        ! SHORELINE DEVELOPMENT_FACTOR
730 X(4)=X(4)/4
740 !
750 ! ***************  COMPUTE REPRODUCTIVE LEVELS  ******************
760 !
770 FOR I = 0 TO 3
780 FOR J = 0 TO 4
790 DELTA (I,J) = X(J) - RLM (I,J)          ! COMPUTE DELTA MATRIX
800 NEXT J
810 NEXT I
820 !
```

```
830 !
840 !
850 FOR I = 0 TO 3
860 FOR J = 0 TO 4
870 DOT1(I,J)=0                             ! COMPUTE DOT1 MATRIX
880 FOR K = 0 TO 4
890 DOT1(I,J) = DOT1(I,J) + DELTA(I,K) * IPVCM(J,K)
900 NEXT K
910 NEXT J
920 NEXT I
930 !
940 !
950 !
960 FOR I = 0 TO 3
970 DOT2(I)=0                               ! COMPUTE DOT2 MATRIX
980 FOR J = 0 TO 4
990 DOT2(I) = DOT2(I) + DELTA (I,J) * DOT1(I,J)
1000 NEXT J
1010 NEXT I
1020 !
1030 !
1040 !
1050 D = 0
1060 FOR I = 0 TO 3
1070 PP(I) = EXP(-0.5 * DOT2(I))            ! COMPUTE PP MATRIX
1080 !
1090 D = D + PP(I)                          ! COMPUTE CONSTANT D
1100 NEXT I
1110 !
1120 !********************  OUTPUT SECTION  ********************
1130 !
1140 FOR I = 1 TO 4
1150 IMAGE ##.#
1160 DISPLAY AT(22,17*I-4)USING 1150:(PP(I-1)/D)*100
1170 NEXT I
1180 !
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1190 !
1200 !
1210 DISPLAY AT (24,44)"Y"
1220 INPUT AT (24,1)SIZE(-1)"Do you wish to make another analysis? (Y/N)":C$
1230 IF C$ = "Y" THEN 570
1240 STOP
1250 !
1260 ! ****************  DISPLAY CONTROL SUBROUTINE  ****************
1270 !
1280 A$ = "****************************************"
1290 B$="**********"
1300 DISPLAY AT (1,69)"Version 1.0"
1310 DISPLAY AT (2,1)A$;A$
1320 DISPLAY AT (3,1)B$
1330 DISPLAY AT (3,20)"PREDICTED NATURAL MUSKELLENGE REPRODUCTION"
1340 DISPLAY AT (3,71)B$
1350 DISPLAY AT (4,1)A$;A$
1360 DISPLAY AT (7,21)"LAKE NAME:"
1370 DISPLAY AT (9,10)"Rising Spring Water Level (No=0, Yes=1) . . . . . . "
1380 DISPLAY AT (10,10)"Alkalinity (Methyl Orange). . . . . . . . . . . . . "
1390 DISPLAY AT (11,10)"Drainage Lake (No=0, Yes=1) . . . . . . . . . . . . "
1400 DISPLAY AT (12,10)"Abundance of Northern Pike (Absent=0, Rare=1,"
1410 DISPLAY AT (13,10)"Common=2, and Abundant=3) . . . . . . . . . . . . . "
1420 DISPLAY AT (14,10)"Shoreline Development Factor  . . . . . . . . . . . "
1430 DISPLAY AT (16,15)"PROBABILITY OF NATURAL MUSKELLENGE REPRODUCTION (%)"
1440 DISPLAY AT (17,29)"Posterior Probability"
1450 FOR I = 1 TO 4
1460 DISPLAY AT (19,I*17-5)"LEVEL";I
1470 DISPLAY AT (21,I*17-5)"_______"
1480 NEXT I
1490 DISPLAY AT (20,12)"(poor)"
1500 DISPLAY AT (20,30)"(low)"
1510 DISPLAY AT (20,45)"(moderate)"
1520 DISPLAY AT (20,63)"(high)"
1530 RETURN
1540 END
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GENERAL SUMMARY

Results of laboratory studies showed high muskellunge egg mortality associated with high biological oxygen demand (BOD) substrates where hypoxic conditions developed at the substrate-water interface. Measured dissolved oxygen concentration (DO) at the substrate-water interface in muskellunge spawning sites in eight midwestern lakes showed that four lakes had high DO (mean, 6.0-8.4 mg/liter) and little microstratification, and support self-sustaining muskellunge populations. The other four lakes showed extreme DO microstratification and virtual anoxia (mean, 0.4-2.4 mg/liter) at the substrate-water interface. Populations of these four lakes are almost solely supported by stocking.

Qualitative and quantitative observations of spawning areas in the eight lakes showed that suitable spawning area characteristics include low BOD substrates, dense stonewort Chara sp. beds, or reservoirs where water level is lowered annually, resulting in substrate aeration. Reproductive failure is associated with spawning areas characterized by deep accumulations of organic matter and dense macrophyte growth. Improvements of spawning habitat to prevent or alleviate DO depletion are among the options available to manage this species.

A method to obtain DO measures within 8 mm of the bottom was developed using oxygen-permeable dialysis to obtain a sample, followed by a modification of the micro-Winkler technique. In controlled experiments, results showed that DO within dialysis tubing reach 99% equilibrium (via diffusion) with environmental DO within 3 hours in flowing water and 5 hours in stagnant water. The technique has an experimental error of 0.05 mg/liter and can be adapted for a wide variety of water quality measurements.

Statistical analysis of ecological information on 117 selected lakes showed that nine variables accounted for 57% of the variability in natural muskellunge reproduction. These included northern pike abundance, inflow water source, conductivity, spring water level condition, discharge volume, shoreline development factor, cultural development of adjacent lands, and alkalinity. Conditions identified as most strongly promoting reproduction were limited northern pike abundance, rising springtime water level, high alkalinity, and high shoreline development factor in drainage lake systems. When organized by discriminant function analysis, 58% of the lakes were classified identically to manager-estimated reproductive level, and 91% were classified within ±1 reproductive level. Application of the discriminant function produced from this analysis may be useful for determining lake stocking and habitat improvement strategies directed toward creating or maintaining self-sustaining muskellunge populations.

Muskellunge Habitat Management

Loss or alteration of habitat, especially reproductive habitat, is considered to be a major cause responsible for the decline of native muskellunge populations. In 1969, Wisconsin identified five major approaches to muskellunge management, listing habitat preservation and protection as most important (Oehmcke 1969). A 1981 survey of muskellunge management in North America found that only two states reported habitat protection/improvement as a principal component of their programs (Miller 1983). Current muskellunge management strategies commonly include stocking hatchery reared fingerling and harvest regulations. The scarcity of muskellunge habitat management programs is likely due to paucity of knowledge rather than lack of interest. The objective here is to provide the resource manager with state of the art information and a basis for implementing muskellunge habitat management measures in a brief, non-technical format.

The following guidelines with subsequent rationale are recommended for application to existing and potential muskellunge waters. They should be used until further experience reveals more efficient methods of improving/preserving muskellunge habitat. Lakes are complicated ecosystems, each with its own unique characteristics. Habitat improvement measures, therefore, must be applied on a case-by-case basis following careful evaluation by a professional fisheries biologist. No measure or combination of measures should be applied indiscriminately to a lake.

Initial consideration should include the identification of factors limiting the muskellunge on a lake-by-lake basis. Additionally, the different life stages of muskellunge have different requirements and preferences. It is useful to consider limiting factors as they relate to each of these four life stages: spawning/egg-larvae, fry, juvenile, and adult (Inskip 1982).

Since the emphasis here is reproductive habitat, these guidelines are directed primarily toward enhancing natural reproduction with the assumed management objective of restoring a lake's muskellunge fishery to the self-sustaining status (not requiring stocking). In many lakes, limiting factors beyond successful natural reproduction undoubtedly exist, such as overharvest, competition with northern pike, or predation of young muskellunge by northern pike or stunted panfish populations. An evaluation of the entire lake ecosystem is necessary if the efforts of reproductive habitat improvements are to be realized by the angler. Therefore, species management suggestions have been included to be carried out by, or cooperatively with, the appropriate state agency.

Muskellunge Habitat Management Guidelines

1. Control northern pike populations.
2. Maintain balanced fish populations, particularly panfish utilizing muskellunge early life habitat.
3. Consider acquisition of lands adjacent to and influencing spawning areas.
4. Identify location of spawning areas and document in survey files.
5. Manage watershed to maintain high water quality and minimize eutrophication.
6. Monitor dissolved oxygen concentration at the bottom-water interface in spawning areas.

7. Rehabilitate spawning substrates where bottom DO falls below 3.2 mg/liter.
8. Design dams to facilitate water level management on reservoirs.
9. Place spawning substrates to improve early life habitat.
10. Develop new spawning marshes.
11. Manage riparian zone vegetation for coniferous species and allow timber adjacent to shoreline to over-mature.

Rationale

Control northern pike populations The closely related northern pike is a major competitor with the muskellunge in most lakes when they occur together (Hess and Heartwell 1978). Pike and muskellunge typically use common spawning grounds; however, the pike spawns earlier than muskellunge and pike fry prey heavily on muskellunge larvae and fry (Caplin 1982). Pike are better adapted to reproduce in more eutrophic spawning areas than are muskellunge (Dombeck et al. 1984), therefore as spawning habitat deteriorates the balance is tipped against muskellunge reproduction in favor of pike. The pike has invaded and become the dominant large predator species in many formerly exclusive muskellunge waters (Threinen and Oehmcke 1950). Management options to reduce pike might include liberalized regulations, population manipulation, and controlled water-level drawdown during and prior to spawning to reduce pike reproduction.

Maintain balanced fish populations   In addition to pike, many other fishes prey on very young, nearly immobile muskellunge (Scott and Crossman 1973). Overabundant panfish populations should be reduced using conventional population manipulation techniques if muskellunge spawning habitat improvement measures are under consideration.

Land acquisition   Consider acquisition of lands adjacent to and influencing muskellunge spawning habitat. Wisconsin has identified five major approaches to muskellunge management in order of their importance: (1) habitat preservation and protection; (2) angling regulation; (3) stocking hatchery-reared fish; (4) population control; and (5) classification of waters (Oehmcke 1969). Modification of shoreline on innumerable waters has resulted in degradation or destruction of muskellunge spawning habitat. It is imperative that remaining high-quality spawning habitat be identified and preserved.

Identify spawning areas   Identify locations of spawning areas and document in survey files. Muskellunge typically spawn in April-May when water temperatures reach 54-60 F in bays or along shorelines in water less that three feet deep. Many spawning areas thaw a few days earlier than the remainder of the lake and have slightly warmer water temperatures. Known spawning areas are located near influent streams or areas of ground water seepage which likely influences the earlier thaw. The bottom materials at spawning areas are variable, but mucky areas with debris, woody material, or aquatic plants are often utilized. For a more detailed description of muskellunge spawning habitat in midwestern lakes, refer to Dombeck et al. (1984).

Manage watershed   Manage watershed to maintain high water quality and minimize eutrophication. Organic loading from natural and human sources should not exceed levels that will result in depression of dissolved oxygen concentration (DO) in spawning areas at the substrate-water interface. Results of laboratory and field studies have shown that the biological oxygen demand exerted by organic bottom materials is associated with low DO at the substrate-water interface (Dombeck et al. 1984). Deposition of sediment on spawning substrates also degrades the habitat for egg development. Management practices such as road building and logging operations should not increase sediment and nutrient input from surface runoff. Sediment traps should be utilized in influent streams where necessary to reduce sediment loading resulting from construction (bridge or road building) activities. Manage area of direct drainage to protect shorelines from erosion and modification.

Monitor dissolved oxygen   Monitor DO concentration at the substrate-water interface in muskellunge spawning areas. Low DO at the substrate-water interface results in high muskellunge egg mortality. Similarly, low DO was measured near bottom in spawning areas in four lakes having little or no natural reproduction, while no DO depletion was observed in spawning areas studied in four self-sustaining muskellunge lakes (Dombeck et al. 1984). Should daily low DO concentrations drop below the critical level (3.2 mg/liter) (Siefert et al. 1973), management efforts to rehabilitate spawning habitat should be considered.

Spawning substrate rehabilitation Where DO falls below the critical level for muskellunge egg and larvae survival (3.2 mg/liter) at dawn (the time of daily low DO) during the time of egg and larvae development (April-June), efforts should be directed at determining the cause(s) of DO depletion. This typically includes high biochemical oxygen demand (BOD) caused by decomposition of organic-rich substrates and/or nighttime respiration of dense aquatic plants. Depending upon logistics, some rehabilitative measures might include water level fluctuation, dredging, and lake bottom sealing. Dredging and sealing high BOD bottoms with artificial fabric have been utilized in lake rehabilitation (Dunst et al. 1974; Nichols 1974) and may be management options, depending upon local conditions. Water level management (drawdown) to aerate high BOD substrates results in desiccation and consolidation of organic material. The subsequent chemical oxidation greatly reduces BOD and causes physical shrinkage of substrates, resulting in a more suitable environment for egg and larvae development for other species as well as muskellunge. Oxidation of substrates also "locks up nutrients" and slows the natural eutrophication rate (Dunst et al. 1974). Additionally, overwinter drawdown causes aquatic plants to freeze out and can be used to control aquatic vegetation problems (Beard 1973; Nichols 1974).

The presence or construction of a dam may not always be necessary for fluctuation of lake level. The management of outlet riparian zone for aspen to be utilized by beaver as a food source can enhance beaver activity and may be an alternative on lakes with a warmwater outlet. Beaver activity is most often detrimental to trout streams (coldwater), therefore care should be taken not to encourage beaver on coldwater streams. Water level fluctuation caused by a beaver dam is beneficial to lake spawning substrates. The flooding of terrestrial areas during spring and early summer also provides highly desirable muskellunge spawning habitat.

Dam design Design dams to facilitate water level management on reservoirs or flowages. The ability to manage water level at low cost, over the long term, is a valuable management tool. In addition to items related to guideline 7, occasional drawdown greatly increases the life of reservoirs and facilitates shoreline vegetation management and erosion control.

Place spawning substrates Placement of spawning substrates can improve habitat for early life survival and should be considered, particularly in combination with bottom sealing. Sand or gravel may be placed over fabric used in bottom sealing (Dunst et al. 1974). The selective placement of artificial turf as a spawning substrate may also be an option since it can function in bottom sealing, where logistics for dredging are unfavorable, and provide a substrate conducive to muskellunge early life survival.

Judicious placement of woody materials should be considered in conjunction with substrate rehabilitation measures, particularly as a method of encouraging and concentrating natural egg deposition in suitable areas. Nevin (1901) reported muskellunge spawning in areas of greatest log, stump, and brush density in Wisconsin flowages.

Spawning in similar areas was observed by Dombeck (1979). Results of placing substrates to enhance muskellunge reproduction have not been documented and careful evaluation of such projects should be conducted.

Develop spawning marshes Development of spawning marshes may be an option, depending upon local conditions. The management of spawning marshes to improve northern pike reproduction is a common practice (Williams and Jacob 1971) and should be considered for muskellunge as well. Field inventories should search for potential areas for development such as marshes with influent streams where a water control structure might be logistically feasible to facilitate water level management for a spawning/nursery area or cut-off bays which might be modified. The placement of culverts and bridges on small streams near lakes might also be modified to facilitate management of spawning/nursery areas. The following is a general description of pike spawning marsh management from Williams and Jacob (1971). "A managed marsh is typically a flood plain with a dike and water level control structure at its outlet end. The control structure ordinarily serves as a barrier to the upstream movement of panfish and minnows. Ideally, the area to be inundated has a good stand of grass or fragile non-woody annual plants, is capable of being completely drained, and has a watershed just large enough to keep the marsh filled with a minimum of overflow. Such an area provides ideal spawning substrate, in the event that broodstock are introduced. The grass infusion nourishes an abundance of food for the young pike, there is good protection from predation by other fish, and there is minimum competition by panfish and minnows." Although spawning marshes have been successful in pike management, managed marshes for muskellunge reproduction have not been evaluated, therefore, careful evaluation of such projects should also be carried out.

Manage riparian zones   Manage forested riparian zones adjacent to muskellunge spawning areas for coniferous species and allow timber adjacent to the shoreline to over-mature and die naturally. The input of deciduous leaves into spawning sites, especially those with already high BOD substrates, adds to the organic loading of sediments. Additionally, deciduous leaves which blanket the substrate exert high BOD as water temperatures rise in spring, resulting in reduction of bottom DO (Dombeck et al. 1984). In contrast, conifer needles are less often blown into the water and have a much slower rate of decomposition (lower BOD). Organic loading should not exceed levels that cause depression of spawning area DO at the substrate-water interface.

The input of woody cover from trees falling into a lake is an important natural source of cover, providing much needed habitat for many fish species. A recent study of muskellunge populations in two Kentucky streams showed that muskellunge were more likely to occur where a fallen tree was located, particularly if brush and debris had accumulated within the tree limbs (Kornman 1983). Kornman concluded that the presence of instream debris, especially in the form of fallen trees, is very important muskellunge habitat. Additionally, a recently completed telemetry study has shown young-of-the-year muskellunge preferred habitat includes bullrush Scirpus beds (Hanson 1984) and submerged tree tops (D. A. Hanson, Wisconsin Department of Natural

Resources, Spooner, Wisconsin, USA, personal communication). In contrast to deciduous leaves, wood exerts low BOD and the input of fallen trees into lakes over the long term adds diversity to the aquatic ecosystem. Due to its growth form and resistance to decay, cedar is a desirable species adjacent to the shoreline, and management for cedar should be a long-term objective. Other desirable species include white pine and hemlock. Where site index limits management of previously mentioned species, a long-term objective might be uneven-age management of northern hardwoods to increase the white pine and hemlock component.

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