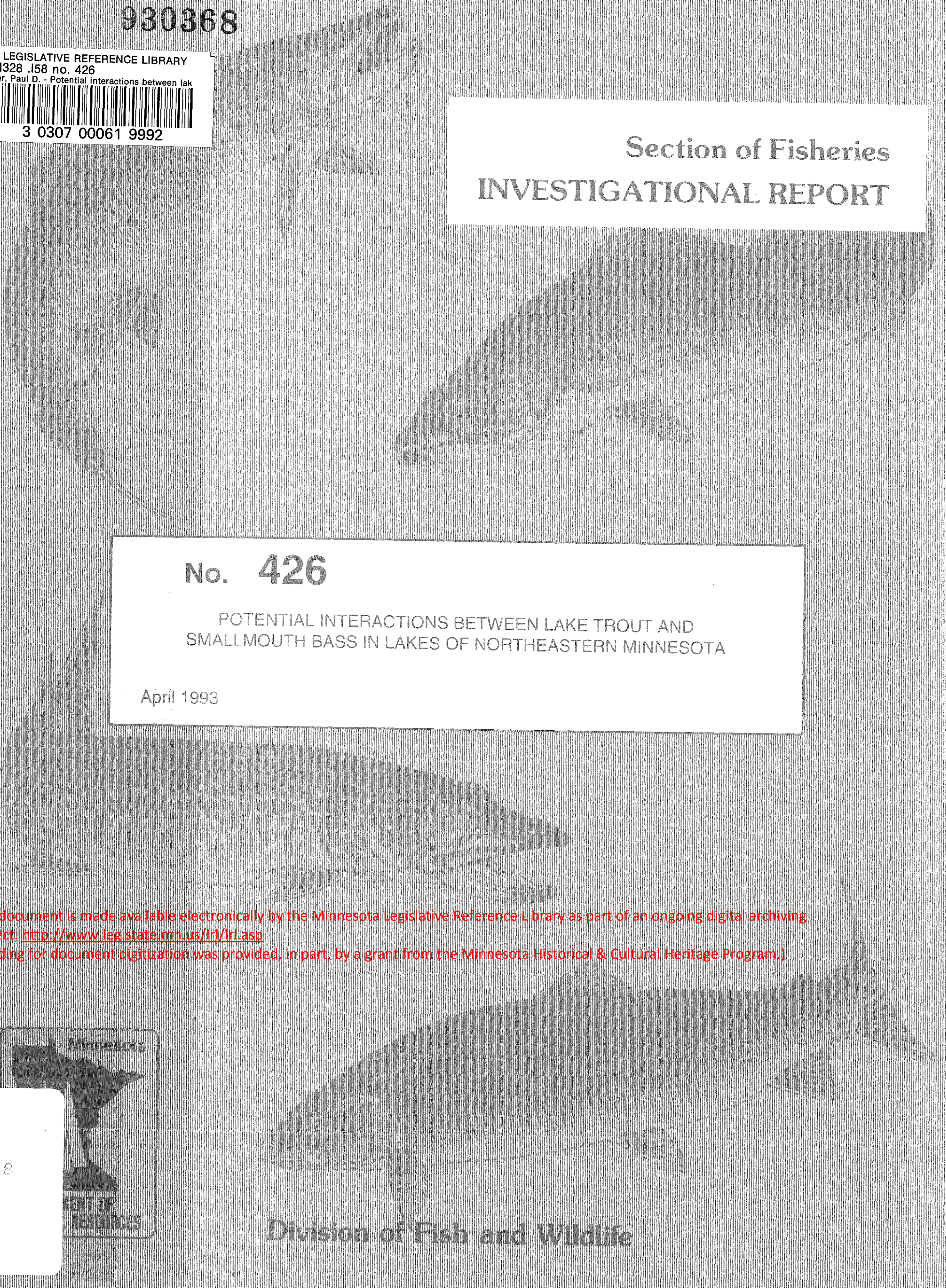

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POTENTIAL INTERACTIONS BETWEEN LAKE TROUT AND SMALLMOUTH BASS IN LAKES OF NORTHEASTERN MINNESOTA[1]

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Abstract.--This study examined existing sympatric and allopatric populations of lake trout *Salvelinus namaycush* and smallmouth bass *Micropterus dolomieui* to determine whether the two species interact in ways that affect their abundance, growth rate, or diet, or the harvest of lake trout. Four "SMB lakes" had no lake trout, four "LAT lakes" had no smallmouth bass, and four "sympatric lakes" had both species. Lake types tended to differ in their limnological and fish community characteristics.

Several apparent differences between allopatric and sympatric populations might be attributed to interspecific competition or to limnological and fish community characteristics. Catch rates of lake trout in gill nets and growth rates of juvenile lake trout tended to be higher in LAT lakes. Maximum size attained by lake trout was greatest in the sympatric lakes, coincident with the occurrence of cisco *Coregonus artedi* or rainbow smelt *Osmerus mordax*. Growth rates of smallmouth bass were highest in two SMB lakes, and higher in SMB lakes as a group than in sympatric lakes. Diets of lake trout and smallmouth bass in sympatry overlapped about as much as diets of each species overlapped between lakes. Winter angling yield of lake trout (kg per hectare) was significantly correlated with relative effort (angler-h per hectare) ($r^2 = 0.94$). The greater effort expended on the LAT lakes explained their higher lake trout yields, without invoking competition from smallmouth bass in the sympatric lakes.

Introduction

Smallmouth bass *Micropterus dolomieui* were introduced into lakes in northeastern Minnesota during the first half of this century by state fisheries personnel and unauthorized members of the public. They have become established in many lakes, including some having populations

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of lake trout *Salvelinus namaycush*. The concern has been raised that interspecific competition may occur in these relatively infertile lakes, causing smallmouth bass to negatively affect lake trout.

Currently available biological information from northeastern Minnesota pertaining to smallmouth bass is less extensive than it is for lake trout, and no information is available that directly pertains to interactions between the two species. While discussing species associations in Ontario lakes, Johnson et al. (1977) stated "...no hard evidence exists to demonstrate that smallmouth bass are detrimental to lake trout populations," and noted that smallmouth bass feed heavily on crayfish, which are not commonly eaten by lake trout. Because Minnesota's lake trout lakes tend to be smaller than Ontario's, competition with other predator species may be more intense in the Minnesota lakes (Schupp 1992; Payne et al. 1990).

Johnson and Hale (1977) investigated interactions between smallmouth bass and walleye *Stizostedion vitreum* in four lakes in northeastern Minnesota. They concluded that interspecific competition for food or habitat did not appear to be a factor in fluctuations of abundance of these species. Growth rates of these sympatric populations were density-dependent, suggesting that intraspecific, rather than interspecific, competition was the most important factor determining growth rates of each species. Summer diet compositions of the two species overlapped, but walleye fed primarily on fish, while smallmouth bass fed primarily on crayfish.

This study examines whether lake trout and smallmouth bass in lakes of northeastern Minnesota interact in ways that affect the abundance, growth rate, and diet of each species, and the harvest of lake trout.

Methods

Several existing allopatric and sympatric populations of lake trout and smallmouth bass were compared. No attempts were made to manipulate fish populations over lakes or time. Study lakes that contained one or both species were chosen in Cook County, in northeastern Minnesota. Kemo, Mayhew, Trout, and Birch Lakes contain no smallmouth bass and are referred to as "LAT lakes" in this report. Caribou, Flour, Poplar, and Two Island Lakes have no lake trout and are referred to as "SMB lakes." Greenwood, Loon, Duncan, and West Bearskin Lakes contain both species and are referred to as "sympatric lakes."

Comparisons among the three lake types were basic to the design of this study. However, the lakes differed in ways other than the presence or absence of lake trout and smallmouth bass. Hume and Northcote (1985) cautioned that limnological differences among lakes may confound studies of competitive interactions between fish species. For this reason, variables related to lake morphometry, water quality, and fish communities were measured and used to predict or explain differences in relative abundance, growth rate, diet composition, and harvest among lakes and lake types.

Data were acquired from field sampling performed expressly for this study, a concurrent lake trout strain evaluation study (Siesennop 1992), concurrent fisheries assessments, and fisheries management files.

Limnological descriptions

Lake surface area, volume, shoreline length, mean depth, and maximum depth were obtained from bathymetric maps and planimetry. The shoreline development index (SDI), D_L (Cole 1979), was calculated. Water quality sampling was performed in August 1988 and 1989. Measurements included temperature and dissolved oxygen profiles, Secchi disc transparency, and surface measures of specific conductance, Ph, and total alkalinity. Some measures, and additional temperature and dissolved oxygen profiles, were obtained from files.

An ecological lake class (ELC) was assigned to each lake, in a classification developed for Minnesota lakes by Schupp (1992). The ELC is based on county (a surrogate for climate), surface area, percentage littoral area, maximum depth, Secchi disk transparency, total alkalinity, and shoreline development. By condensing this group of limnological variables into a single number, ELC offered a simpler way to compare allopatric and sympatric lake types to limnological lake types.

Ryder's morphoedaphic index (MEI), calculated as total dissolved solids (mg/L) divided by mean depth (m), has demonstrated some value in predicting fish yields (Ontario Ministry of Natural Resources (OMNR) 1982). It was obtained for all but two of the study lakes from fisheries management records.

Temperature and dissolved oxygen profiles were used to calculate the July lake trout thermal habitat volume (THV), a measure which correlated with lake trout harvest for the set of Ontario lakes examined by Payne et al. (1990). THV was defined by Payne et al. as the layer of lake water ranging from 12° C at the shallow boundary to 8° C (or a minimum of 6 mg/L dissolved oxygen) at the deep boundary. Based on comparisons of our July and August profiles within individual lakes, a modification of the criteria was arrived at to allow profiles from August to be used when July profiles were not available. The temperature limits were maintained, but dissolved oxygen limits were dropped 0.5 mg/L per week after July, through August. After determining the appropriate depth range THV was calculated from bathymetric maps, as was the ratio of THV to whole lake volume (THV/V).

Fish community descriptions

Fish community information was obtained in several ways. Stocking records since 1945 and fisheries assessment records were reviewed. Sampling for lake trout and smallmouth bass, and limited netting for forage fish (below), also provided information on other species.

The status (presence or absence) of lake trout and smallmouth bass was used throughout this study to categorize the fish communities for all analyses. Additional fish community variables were created: the status of coregonines and rainbow smelt *Osmerus mordax*, the number of major species, and the number of major predators in each lake. Following the criteria of Carl et al. (1990) for Ontario lakes containing lake trout, most forage species were not considered, except that rainbow smelt were included as major species in this study.

Relative abundance

Lake trout relative abundance was determined primarily from gill net sets. Minnesota's experimental nylon gill nets were set overnight. Each net measured 76 m long by 1.8 m deep, and comprised five separate mesh panels having bar measures of 19, 25, 32, 38, and 51 mm, in succession. Net orientation varied with respect to shoreline and depth. Gill nets were set in five lakes (Greenwood, Loon, Kemo, Trout, and Mayhew) in May 1989 expressly for this study, and four lakes (Greenwood, Loon, Kemo, and Trout) in July or August 1990 for both this study and periodic fisheries assessments. Some nets having only 13-mm mesh were set in Greenwood and Loon Lakes. Data from gill nets set for lake trout in four lakes (Birch, Mayhew, Duncan, and West Bearskin) in fall, 1988-1990, were provided by Siesennop (1992). The fisheries assessment netting in summer 1990 used historically standardized gill net locations. Locations for the balance of the gill netting were selected in an attempt to maximize the catch, and varied somewhat between years.

Trap nets set in fall, 1988-1990, by Siesennop (1992) furnished additional lake trout catch data. They were constructed with a mesh lead and two rectangular frames (1.8 m X 0.9 m), at the front of the net, with mesh funnels, supporting hoops and a mesh pot to the rear. Mesh sizes (bar measures) used were 6.4, 13, or 19 mm. Trap nets were set at standardized locations near shore, with the lead toward shore, and lifted after two nights.

Gill nets and trap nets provided catch data. Catch-per-unit-effort (CPUE) was calculated as mean number of each species and mean weight of lake trout per lift. The lake trout gill net CPUE data were compared to lake trout gill net CPUE data for the relevant ELC in northeastern Minnesota. Gill net and trap net CPUE data for lake trout were compared between LAT and sympatric lakes. For each sampling period and lake type, gill net catch data were pooled, and 13-mm and 19-mm trap net data were pooled together. Two-tailed Mann-Whitney tests were applied, with alpha set at 0.05. Using only the gill net catch data, three analyses of variance (ANOVA) were run for each sampling period (and the fall data pooled from the three years) to determine the proportion of the total variation in the lake trout catch explainable by 1) lake, 2) Minnesota's ecological lake class, and 3) the presence or absence of smallmouth bass.

Smallmouth bass relative abundance information was obtained for three sympatric lakes and four SMB lakes from electrofishing CPUE data. A boat-mounted boom shocker was used in spring 1988-1990. The equipment and procedure were refined in 1989 and again in 1990. Sampling stations were established near shore in 1988. A Coffelt VVP-2E or VVP-2C electrofishing unit was used for day or night electrofishing during the period 31 May through 29 June. Both AC and DC currents were used. In 1989 the Coffelt VVP-2E unit, pulsed DC, nighttime electrofishing, and a low-drag dip net were standardized. Electrofishing occurred in the seven lakes during the period 31 May through 23 June. In 1990 the same unit was set for a voltage of 1020, a pulse rate of 120/s, a pulse duration of 5 ms, and an amperage that ranged from 1.0 to 2.2, depending upon the lake water's conductivity. Electrofishing occurred in the seven lakes during the period 21 May through 21 June.

For each year and each lake, the weighted mean number of smallmouth bass per unit effort was calculated for each day or night and for all dates. Effort was defined as kilometers of shoreline shocked (1988 only), hours that the generator ran (time "on and off"), and hours that current was induced in the water (time "on"). CPUE data for smallmouth bass were compared between SMB and sympatric lakes by grouping electrofishing runs (defined as each combination of lake, date, and station) according to lake trout status and applying two-tailed Mann-Whitney tests, with alpha set at 0.05. This was done separately for 1989 and 1990 (1988 data were not tested). Additional information pertaining to the relative abundance of smallmouth bass was obtained from fisheries assessment files.

Growth

Samples and information for growth analysis were obtained while sampling the fish populations as described above. Total length and weight of each lake trout and smallmouth bass were measured at the time of sampling.

Ages of lake trout collected in spring and summer were determined from pectoral fin rays. Ages of lake trout collected in fall were determined from fin rays or hatchery fin clips. Pectoral fin rays were mounted in epoxy, sectioned, and viewed under magnification to reveal annuli. For each sampling period that lake trout were collected, mean total length at capture, by age, was compared between LAT and sympatric lakes. Simple linear regressions of $\log_{10}$ weight (g) on $\log_{10}$ length (mm) were calculated for each lake and sampling date. Analysis of covariance (ANCOVA) was used to test for homogeneity of slopes among lakes.

Scales were taken from smallmouth bass at the time of electrofishing and trap netting. Annuli were read from magnified images of impressions of scales in acetate sheets. Mean total length at capture, by age, was calculated for each collection from 1989. Total lengths (1989 collection only) and scale radii were subjected to the linear growth model of Weisberg and Frie (1987). This procedure separated annual increments in total length and scale radius into components due to age (age effects) and calendar year (year, or environmental, effects). The model was also run on scale radius increment data pooled by lake type (SMB or sympatric). These procedures allowed smallmouth bass growth to be compared among lakes and between lake types.

Diet

Samples for diet analysis were obtained while sampling the fish populations as described above. Stomachs of dead and moribund lake trout collected with gill nets in May 1989 were removed at the lake, and the contents were preserved in alcohol. Stomach contents from lake trout gill-netted during summer and fall were examined at the lake. A method similar to that of Van Den Avyle and Roussel (1980) was used to remove stomach contents of some live smallmouth bass collected by electrofishing and angling in June 1988. A plexiglass tube was inserted in the gullet and a jet of water was directed into the tube to force the regurgitation of stomach contents. This procedure was abandoned because the stomachs retained food, and instead, a portion of the catch, based on quotas for length intervals, was killed to remove stomach contents, which were preserved in alcohol. The latter procedure was followed again in spring 1989. Preserved samples were taken to the laboratory for enumeration. Invertebrates were identified to order, and fish were identified to species, when possible.

The amount of each prey category was quantified in two or three ways, depending upon the particular collection (each combination of date, lake, and predator species). Percentage occurrence was calculated for each stomach collection as the percentage of all stomachs examined in the collection that contained the prey taxon. In addition, the total volume of all stomach contents and the percentage of that total composed of each prey taxon (percentage total volume) was determined for each collection of lake trout taken in May 1989 and smallmouth bass taken in June 1988 and 1989. Smallmouth bass collected in 1988 and 1989 were classified into three categories of total length, and percentage occurrence and percentage total volume of each prey taxon were calculated for each length category. Categories were 1) less than 152 mm, 2) 152 to 254 mm, and 3) greater than 254 mm. Lastly, the number and weight of several prey taxa in each stomach were measured for lake trout collected in May and smallmouth bass collected in June, 1989, from Greenwood and Loon Lakes. The number and weight of Amphipoda, Ephemeroptera, Odonata, and Diptera in the stomachs were each regressed on the fish's total length. This was done separately by lake and predator species, to determine the relation between the amount of prey and predator length. Total length was used as a covariate in (ANCOVA) to test for homogeneity of slopes between lake trout and smallmouth bass. When a nonsignificant interaction term in the model indicated that slopes of regression lines were not significantly different, intercepts were then tested for equality. Alpha was set at 0.05.

An index of diet similarity was calculated for collections made in 1989, both between lakes within species, and between species within lakes. The index calculated was similar to Schoener's index of niche overlap, which has been applied to percentage total volume in diet studies (Wallace 1981). For each paired comparison, the lesser of the two percentages of total volume for each prey taxon was summed over all prey taxa. This procedure yields the same result as Schoener's index (range 0.0 - 1.0) when the percentages of total volume in a collection sum to 100%. When this sum is less than 100%, as it usually is for this study's data, the procedure used here yields lower measures of overlap than does Schoener's index. This is because unrecorded percentages do not contribute to the modified overlap index, but would contribute to Schoener's index. Within-lake comparison of lake trout and smallmouth bass diets was possible only for Greenwood and Loon Lakes.

Lake trout harvest

For each of the eight study lakes containing lake trout, lake trout harvest estimates for one or more winter angling seasons were obtained from creel survey reports by Persons (1985, 1991, personal communication), and Siesennop (1992). Harvest data was available for six lakes from only a few summer angling creel surveys (Persons 1987). Several descriptors of lake trout harvest were calculated, including mean winter and annual harvest (number of fish, and weight in kg), yield, mean weight of individual fish (kg), and harvest per unit effort. Total effort (h) and relative effort were also calculated.

Angling yields were compared to potential yields predicted from MEI and THV. For MEI (metric units), an estimate of the potential yield of all fish = $1.4(\mathrm{MEI})^{0.45}$. This was multiplied by a proportion (partition factor), based on the number of major species present in each lake, to estimate potential yield of lake trout. For THV, a prediction of lake trout harvest was obtained from the simple linear regression equation of Payne et al. (1990): $\log_{10}\mathrm{harvest} = 2.15 + 0.714(\log_{10}\mathrm{THV})$. Yield predicted from THV was obtained by dividing the harvest estimate by lake surface area. The ratios of winter and annual angling yields to predicted yields were computed for each lake, and compared between LAT and sympatric lakes. Coefficients of determination (r^2) for simple linear regressions of angling yield on predicted yield were also determined using $\log_{10}$ transformations.

Pearson correlation coefficients (*r*) were computed and correlation matrices were constructed to reveal which "independent" variables correlated best with the harvest descriptors, following Payne et al. (1990). The first matrix used effort and abiotic limnological variables as independent variables: total effort, relative effort, lake area (hectares), mean and maximum depths (m), lake volume and THV ($m^3/10^6$), SDI, MEI, and ELC. A second matrix used fish community variables: number of major species, number of predators other than lake trout, and the presence or absence of smallmouth bass, coregonines, and rainbow smelt. A third matrix correlated the effort and abiotic limnological variables with the fish community variables. An additional matrix correlated effort variables with abiotic limnological variables. All continuous variables were $\log_{10}$ transformed prior to correlation. Discrete variables were not transformed. The categorical variable ELC was used as a treatment variable in ANOVA, rather than in correlation, to generate *r*.

Results

Limnological descriptions

Morphometric data showed some similarities among lakes within a lake type, and a few differences among the types (Table 1). The sympatric lakes had the greatest volume, and, as a group, the greatest maximum depth. The greatest surface area and mean depth were found among the sympatric lakes. Volumes and depths of SMB lakes were less than those of sympatric lakes. One of the SMB lakes had the least mean depth. Shoreline development tended to be greatest in the SMB lakes, and least in the LAT lakes. The LAT lakes had the least surface area and shoreline length.

Water quality sampling in August revealed fewer clear patterns (Tables 2 and 3). The SMB lakes tended to have shallower Secchi depth

Table 1. Morphometric characteristics of study lakes. Lakes are located in Cook County, northeastern Minnesota, and are grouped here by the presence of smallmouth bass and lake trout. "nd" indicates not determined.

Lake	Surface area (km^2)	Shoreline length[a] (km)	Shoreline Development Index, D_L	Maximum depth (m)	Mean depth (m)	Volume ($m^3/10^6$)
Smallmouth bass present						
Caribou	2.95	15.6	4.40	8.2	nd	nd
Flour	1.35	12.9	3.13	22.9	8.4	11.2
Poplar	2.95	30.1	4.95	22.2	nd	nd
Two Island	2.96	17.9	2.94	8.2	2.6	7.8
Smallmouth bass and lake trout present						
Greenwood	8.18	35.2	3.47	30.8	9.9	82.0
Loon	4.15	22.8	3.16	61.6	20.6	88.7
Duncan	1.95	11.9	2.40	37.0	14.3	27.8
West Bearskin	2.00	12.1	2.41	23.8	10.2	20.3
Lake trout present						
Kemo	0.75	4.8	1.57	19.8	10.9	8.0
Mayhew	0.89	7.9	2.37	25.6	11.3	10.0
Trout	1.04	5.1	1.42	23.5	10.6	10.9
Birch	0.99	10.5	2.98	21.6	8.0	7.9

[a] Measurement includes islands.

Table 2. Water quality properties of study lakes in August 1988. Lakes are grouped by the presence of smallmouth bass and lake trout. "na" indicates not applicable.

Lake	Date	Secchi depth (m)	Surface Temp. (°C)				Thermocline depth (m)	Hypolimnion Temp. (°C)	
			Temp. (°C)	pH	Alk. (mg/L)	O^2 (mg/L)		Temp. (°C)	O^2 (ppm)
					Smallmouth bass present				
Caribou	11	1.8	22.2	7.92	30.5	8.4	8.0-9.0	15.0	0.0
Flour	8	5.6[a]	21.8	7.61	18.3	8.4	6.0-10.0	5.8-7.8	0.0-5.8
Poplar	19	1.8	21.5	7.20	9.4	7.7	5.5-7.0	7.0-10.0	0.3-3.8
Two Island	11	3.3	22.0	7.09	10.7	8.2	none	na	na
					Smallmouth bass and lake trout present				
Greenwood	9	6.7	20.5	7.07	6.0	8.0	9.0-13.0	8.2-9.2	5.2-7.3
Loon	8	5.5[b]	20.3	7.50	12.5	8.4	7.0-13.0	5.1-5.8	8.8-9.1
West Bearskin	9	5.2	21.0	7.65	17.3	8.5	7.0-11.0	7.8-8.8	2.8-6.5
					Lake trout present				
Kemo	10	4.3	21.0	7.57	10.7	8.4	6.0-9.0	6.0-8.8	0.1-7.2
Mayhew	8	5.5[c]	21.4	7.40	16.4	8.0	6.5-12.0	4.4-6.1	0.0-6.2
Trout	9	6.4	21.3	7.42	14.0	7.8	7.5-12.0	5.8-8.1	0.8-9.7

[a] August 15-18, 1956
[b] August 15-17, 1977
[c] July 6-10, 1953

Table 3. Water quality properties of study lakes in August 1989. Lakes are grouped by the presence of smallmouth bass and lake trout. "nd" indicates not determined. "na" indicates not applicable.

Lake	Secchi depth (m)	Surface Conduct. (μmhos/cm)					Thermocline depth (m)	Hypolimnion Temp. (°C)	
		Conduct. (μmhos/cm)	Temp. (°C)	pH	Alk. (mg/L)	O^2 (mg/L)		Temp. (°C)	O^2 (mg/l)
					Smallmouth bass present				
Caribou	2.13	56.2	19.5	7.27	22.9	6.8	7.5-8.8	13.6-17.3	0.1-0.3
Flour	5.64	47.2	20.5	7.53	18.9	7.6	4.5-8.5	6.6-9.3	0.1-3.7
Poplar	2.59	nd	20.4	7.05	7.7	7.5	4.5-7.5	7.2-9.7	0.2-5.0
Two Island	3.20	27.4	19.1	6.96	10.8	7.7	none	na	na
					Smallmouth bass and lake trout present				
Greenwood	5.79	21.7	18.9	6.86	6.0	8.2	8.5-10.5	8.5-10.2	5.0-6.4
Loon	4.42	34.4	20.0	7.26	13.5	8.9	5.5-9.5	6.0-8.0	8.7-9.7
West Bearskin	4.72	40.8	20.0	7.49	17.7	7.6	5.5-8.5	7.6-9.7	0.1-4.7
					Lake trout present				
Kemo	4.88	nd	18.7	7.21	10.6	8.6	5.5-9.5	5.3-7.3	0.2-4.5
Mayhew	6.40	nd	19.5	7.41	11.0	8.0	5.5-9.5	4.9-8.1	0.2-5.4
Trout	6.10	nd	19.4	7.23	13.3	7.9	6.5-9.5	6.3-9.3	0.1-6.6

readings, and warmer temperatures and less dissolved oxygen in the hypolimnion. Total alkalinities for Duncan and Birch Lakes (14.9 and 12.4 mg/L, respectively) were obtained from Siesennop (1992) and are similar to the other lakes.

Patterns were more evident with ELC (Table 4) than with comparisons of single water quality variables. The ecological lake classification system assigned five lake classes to the twelve study lakes. The four sympatric lakes were grouped together into Class 01. The four LAT lakes were classified as 03, 04, and 05 (two). Classes for the SMB lakes were 03 and 07 (two each). Thus, only ELC 03 was included in more than one of the three lake types based on the presence or absence of lake trout and smallmouth bass.

MEI values of the SMB lakes were higher than those of the sympatric lakes, with no overlap (Table 4). MEI values of the LAT lakes were intermediate and overlapped those of the other two lake types.

July lake trout thermal habitat volume showed both consistencies and discrepancies with respect to the three lake types (Table 4). No habitat meeting the criteria was present in three of the four SMB lakes, but Flour Lake had a THV within the range of those determined for the LAT lakes. The sympatric lakes tended to have the greatest THV. The ratio of THV to lake volume (THV/V) ranged from 0.10 to 0.17 for the LAT lakes, and from 0.06 to 0.28 for the sympatric lakes.

Fish community descriptions

Fisheries management records indicated that three of the four LAT lakes had been poisoned and restocked with preferred species. This reclamation occurred in Kemo Lake in 1964 and in Birch and Mayhew Lakes in 1969. Stocking records show that two or more game fish species have been stocked into each lake, except Duncan Lake, since 1945. Large numbers of walleye have been stocked into the SMB lakes during recent and past years. During the 1960s lake trout were stocked into one of the SMB lakes (Poplar Lake). The sympatric and LAT lakes have received primarily lake trout; of these, only Trout Lake has not received lake trout since 1984. Mayhew, Trout, and Birch Lakes have received several stockings of rainbow trout, though such stocking has not occurred in Mayhew Lake since 1981. The current primary management species is walleye in the SMB lakes and lake trout in the sympatric and LAT lakes (Table 4).

Results of gill netting and trap netting provided an indication of the major species in each lake (Table 5). The reclaimed lakes, and the LAT lakes as a group, tended to have the fewest major species and predator species (Tables 4 and 5). Numbers of major species and predator species were roughly similar between the sympatric lakes and the SMB lakes. The community tended to be phylogenetically most primitive in the LAT lakes, most advanced in the SMB lakes, and most diverse in the sympatric lakes. The status of small forage fish species was not well documented. The opossum shrimp *Mysis relicta* is known only from Trout Lake.

Relative abundance

The ranking of lake trout gill net CPUE among lakes, within a sampling period, generally paralleled the ranking historically observed for the corresponding ecological lake classes. The catch from one lake was out of place relative to the ELC catch in four of the five sampling periods. During the fall sampling, Birch Lake tended to rank higher than expected. Results of ANOVA, done separately for three treatment variables, showed that lake explained more of the variation in the gill net catch of lake trout than did ELC, which, in turn, often explained more variation than did smallmouth bass status (Table 6).

With respect to lake type, conflicting patterns of lake trout CPUE emerged for the two sampling gears. By both number and weight, lake trout CPUE from gill nets tended to be higher in lakes without smallmouth bass. Considering 13-mm and 19-mm trap nets, there was a tendency for lake trout CPUE from trap nets to be higher in sympatric lakes. Mann-Whitney tests revealed some significant differences (Table 7). The number caught per gill net lift during three of the five sampling periods was significantly

Table 4. Information that may describe or predict harvest, yield, CPUE, and fish communities of study lakes, including depth, volume, and proportion of lake volume (THV/V) meeting OMNR July lake trout thermal habitat volume criteria, morphoedaphic index (MEI), Minnesota's ecological lake class (ELC), and fish community descriptors. Lakes are located in Cook County, northeastern Minnesota.

	July lake trout thermal habitat							
Lake	Depth (m)	Volume ($m^3/10^6$)	THV/V	MEI	ELC	No. of major species	No. of major predator species	Primary management species
Caribou	none	0.00	0.00	21.12	07	6	3	walleye
Flour	7.6-9.8	1.22	0.11	5.77	03	7	3	walleye
Poplar	none	0.00	0.00	6.66	03	8	4	walleye
Two Island	none	0.00	0.00	20.57	07	5	3	walleye
Greenwood	10.7-29.9	19.83	0.24	3.30	01	8	3	lake trout
Loon	7.9-10.4	7.07	0.08	2.31	01	6	4	lake trout
Duncan	7.6-9.1	1.79	0.06	3.91	01	6	2	lake trout
W. Bearskin	8.8-18.0	5.78	0.28	5.71	01	6	2	lake trout
Kemo	7.3-10.1	1.18	0.15	6.74	05	3	2	lake trout
Mayhew	7.9-10.4	1.20	0.12	nd	04	4	1	lake trout
Trout	8.5-12.2	1.85	0.17	5.13	05	6	3	lake trout
Birch	8.5-11.0	0.83	0.10	nd	03	4	2	lake trout

Table 5. Occurrence of fish species considered to be of major importance in each study lake, by either their abundance or their role in the fish community. The entry is within parentheses for lakes where the species is of minor importance. "?" indicates possible occurrence. Additional forage species may be of major importance but are not considered here.

Lake: Species	Caribou	Flour	Poplar	Two Is.	Green-wood	Loon	West Bearskin	Duncan	Kemo	Mayhew	Trout	Birch
cisco		x			x	x		x			x	
lake whitefish			x		x							
rainbow trout											x	x
brook trout					x				(x)		x	
lake trout					x	x	x	x	x	x	x	x
splake					(x)				x			(x)
rainbow smelt							x	(x)			x	
white sucker	x	x	x	x	x	x	x	x	x	x		x
burbot			x									
northern pike	x	x	x	x		x	(x)					(x)
green sunfish	(?)	x	(?)	(?)	x		x	x		x		
smallmouth bass	x	x	x	x	x	x	x	x				
black crappie	x		x	(?)								
yellow perch	x	x	x	x	x		x	x		x	x	
walleye	x	x	x	x		x	(x)	(x)				
number of major species	6	7	8	5	8	6	6	6	3	4	6	3

Table 6. Results of one-way ANOVA on number and weight of lake trout in each gill net, using study lake, Minnesota's ecological lake class (ELC), or the presence or absence of smallmouth bass (SMB) as treatments. Fall data were pooled in the last three analyses.

				r^2	
Season	Year	Treatment	No. of levels	Number	Weight
Spring	89	Lake	5	0.608	0.516
		ELC	3	0.292	0.076
		SMB±	2	0.249	0.074
Summer	90	Lake	4	0.092	0.215
		ELC	2	0.068	0.161
		SMB±	2	0.068	0.161
Fall	88	Lake	3	0.487	0.552
		ELC	3	0.487	0.552
		SMB±	2	0.405	0.550
	89	Lake	4	0.510	0.213
		ELC	3	0.509	0.213
		SMB±	2	0.347	0.175
	90	Lake	4	0.322	0.247
		ELC	3	0.290	0.135
		SMB±	2	0.045	0.030
	88-90	Lake	4	0.382	0.150
		ELC	3	0.366	0.071
		SMB±	2	0.179	0.035

higher in the LAT lakes, and the weight per lift during one sampling period was significantly higher in the LAT lakes. The number caught per trap net lift during two of the three sampling periods was significantly higher in the sympatric lakes, and the weight per lift during the same two periods was significantly higher in the sympatric lakes.

Smallmouth bass CPUE varied greatly during electrofishing runs. During spring 1988 CPUE was highly variable among lakes of the same type. Statistical comparisons were not performed because of variations in gear and time of day sampling occurred. The lakes ranked about the same in electrofishing CPUE during spring 1989 and spring 1990. There was some tendency for CPUE to be higher in the sympatric lakes, but there was much variation among runs within a lake and a lake type. Smallmouth bass CPUE was not significantly different between the two lake types when data were pooled within lake type and compared using the Mann-Whitney test (Table 7).

More species and individuals of small forage fish, including fathead minnows *Pimephales promelas*, were found in Birch and Mayhew Lakes (LAT lakes) than in Duncan and West Bearskin Lakes (sympatric lakes), based on fall sampling with 6.4-mm trap nets (Siesennop 1992). Minnow species were not sampled effectively in the other eight lakes during this study, so their relative abundance there is not as well known. Assessment records provide slight evidence that minnow populations may have been higher in Trout and Caribou Lakes than in the remaining six lakes.

Growth

Gill net catches provided rough comparisons of lake trout growth rates, based on mean total length at capture for each age class. The growth rate of young lake trout sampled during May 1989 was greatest in Kemo Lake. Through about age six, lengths appeared to be greater in the LAT lakes than in the sympatric lakes. Lake trout sampled during summer 1990 appeared to be longer through age 8 in Kemo Lake than in the other three lakes. In fall gill net sampling, 1988-1990, lengths through four summers (age 3+) appeared to be greatest in Birch Lake, followed in order by Mayhew, West Bearskin, and Duncan Lakes. Thus, growth rates of young lake trout appeared to be higher in the LAT lakes than in the sympatric lakes. However, during all three sampling periods, the longest fish were taken from the sympatric lakes. Trends for growth of young lake trout caught in trap nets were similar, but maximum lengths were less than those from gill nets and not consistently associated with either lake type.

Regressions of $\log_{10}$ weight on $\log_{10}$ total length for gill-netted lake trout showed a clear trend relative to smallmouth bass status only for the four lakes sampled in fall. For collections from May 1989 and summer 1990, values of slopes for the two lake types overlapped (Table 8). Slopes and intercepts for fall-collected lake trout produced a consistent ranking of lakes in all three sampling years (Table 9). West Bearskin Lake had the steepest slope, followed in

Table 7. Results of Mann-Whitney tests for differences in CPUE between allopatric and sympatric populations. For smallmouth bass (SMB), data tested were CPUE from each electrofishing run. For lake trout (LAT), data tested were the number or weight in each gill net or trap net. Sample size is the number of runs or net lifts. Probabilities were computed from continuity-corrected normal approximations.

Gear	Year	Time or season	Study species present	No. of runs	No. of runs sample size	Rank sum	Average rank	*U* stat.	2-tailed approx. *P*
Number of smallmouth bass									
Electrofishing	1989	on	SMB	4	17	229	13.5	76	0.670
			SMB,LAT	3	10	149	14.9	94	
		on & off	SMB	4	17	224	13.2	71	0.498
			SMB,LAT	3	10	154	15.4	99	
	1990	on	SMB	4	21	312	14.9	81	0.321
			SMB,LAT	3	10	184	18.4	129	
		on & off	SMB	4	20	269	13.5	59	0.075
			SMB,LAT	3	10	196	19.6	141	
Number of lake trout									
Gill nets	1988	fall	SMB,LAT	1	2	3	1.5	0	0.105
			LAT	2	4	18	4.5	8	
	1989	spring	SMB,LAT	2	21	305	14.5	74	0.028
			LAT	3	13	290	22.3	199	
		fall	SMB,LAT	2	14	124	8.9	19	0.013
			LAT	2	8	129	16.1	93	
	1990	summer	SMB,LAT	2	24	413.5	17.2	113.5	0.031
			LAT	2	16	406.5	25.4	270.5	
		fall	SMB,LAT	2	16	234	14.6	98	0.809
			LAT	2	13	201	15.5	110	
Trap nets	1988	fall	SMB,LAT	2	159	29,190	183.6	16,470	0.000
			LAT	2	160	21,850	136.6	8,971	
	1989	fall	SMB,LAT	2	188	33,510	178.2	15,740	0.338
			LAT	2	158	26,520	167.9	13,960	
	1990	fall	SMB,LAT	2	158	26,980	170.7	14,410	0.007
			LAT	2	155	22,170	143.0	10,080	
Weight of lake trout									
Gill nets	1988	fall	SMB,LAT	1	2	11	5.5	8	0.105
			LAT	2	4	10	2.5	0	
	1989	spring	SMB,LAT	2	21	325	15.5	94	0.137
			LAT	3	13	270	20.8	179	
		fall	SMB,LAT	2	14	137.5	9.8	32.5	0.116
			LAT	2	8	115.5	14.4	79.5	
	1990	summer	SMB,LAT	2	24	387	16.1	87	0.004
			LAT	2	16	433	27.1	297	
		fall	SMB,LAT	2	16	219	13.7	83	0.369
			LAT	2	13	216	16.6	125	
Trap nets	1988	fall	SMB,LAT	2	159	28,220	177.5	15,500	0.001
			LAT	2	160	22,820	142.6	9,938	
	1989	fall	SMB,LAT	2	188	32,580	173.3	14,810	0.966
			LAT	2	158	27,450	173.8	14,890	
	1990	fall	SMB,LAT	2	158	26,420	167.2	13,860	0.044
			LAT	2	155	22,720	146.6	10,630	

Table 8. Regressions of $\log_{10}$ weight on $\log_{10}$ length, and tests for homogeneity of slopes among lakes (ANCOVA), for lake trout taken with experimental gill nets during May 1989 and summer 1990.

Lake	Smallmouth bass[a]	N	r^2	Slope	Slope rank	Intercept
			May 1989			
Kemo	A	32	0.930	2.986	1	-5.017
Mayhew	A	21	0.995	3.162	2	-5.521
Trout	A	15	0.990	3.417	5	-6.114
Greenwood	P	32	0.989	3.402	4	-6.151
Loon	P	18	0.989	3.240	3	-5.718
			$P = 0.008$[b]			
			Summer 1990			
Kemo	A	45	0.988	3.248	1	-5.731
Trout	A	18	0.961	3.684	3	-6.846
Greenwood	P	37	0.962	3.289	2	-5.897
Loon	P	25	0.979	4.034	4	-7.782
			$P < 0.001$[b]			

[a] A = absent; P = present.
[b] Test that slopes are homogeneous.

Table 9. Regressions of $\log_{10}$ weight on $\log_{10}$ length, and tests for homogeneity of slopes among lakes (ANCOVA), for lake trout taken with experimental gill nets and trap nets during fall, 1988-1990.

Lake	Smallmouth bass[a]	N	r^2	Slope	Slope rank	Intercept
			Fall 1988			
Birch	A	67	0.988	3.062	1	-5.164
Mayhew	A	70	0.993	3.161	2	-5.470
Duncan	P	54	0.985	3.166	3	-5.610
W. Bearskin	P	102	0.994	3.336	4	-5.977
			$P < 0.001$[b]			
			Fall 1989			
Birch	A	81	0.965	2.826	1	-4.524
Mayhew	A	94	0.970	3.210	2	-5.577
Duncan	P	67	0.987	3.258	3	-5.803
W. Bearskin	P	81	0.989	3.326	4	-5.919
			$P < 0.001$[b]			
			Fall 1990			
Birch	A	55	0.971	3.042	1	-5.095
Mayhew	A	76	0.962	3.255	2	-5.710
Duncan	P	81	0.969	3.269	3	-5.829
W. Bearskin	P	71	0.990	3.292	4	-5.825
			$P < 0.028$[b]			

[a] A = absent; P = present.
[b] Test that slopes are homogeneous.

descending order by Duncan, Mayhew, and Birch Lakes. Thus, lake trout in the two sympatric lakes were thinner at any given length (up to 789 mm), but appeared to gain weight more rapidly with increasing length than did lake trout in the two LAT lakes.

Smallmouth bass growth data from spring electrofishing showed differences among lakes that also suggested differences among lake types. Mean total length at capture in 1989, by age, was greatest in Caribou and Poplar Lakes (SMB lakes) and least in Loon and West Bearskin Lakes (sympatric lakes). Lengths were intermediate in the remaining three lakes, though, after the first year, lengths in Greenwood Lake exceeded those of Flour and Two Island Lakes. Linear model estimates of age and year components of annual increments in total length (Table 10) show that age effects were highest for Caribou and Poplar Lakes and lowest for Loon and West Bearskin Lakes, where age classes can be compared. The relation of age effects among the remaining three lakes was not as consistent as for mean total length at capture. Applying the linear growth model to annual-radius-increment data from scales taken during 1988-1990, pooled by lake type, revealed that lake types shared similar calendar year effects but differed in their age effects. Smallmouth bass in both lake types experienced the least favorable growth conditions during 1985. Age coefficients generally increased to age 6 in SMB lakes, but decreased after age 2 in sympatric lakes. Considering both length at capture and linear growth model results, smallmouth bass appear to grow slower in the sympatric lakes.

Diet

Common prey of lake trout included insects, zooplankton, amphipods, crayfish, and several fish species, including rainbow smelt, sculpin *Cottus spp.*, darters *Etheostoma spp.*, and green sunfish *Lepomis cyanellus*. Prey consumed in apparently lesser amounts included leeches, common shiner *Notropis cornutus*, fathead minnow, smallmouth bass, cisco *Coregonus artedi*, brook stickleback *Culaea inconstans*, and yellow perch *Perca flavescens*.

Table 10. Linear model estimates of age effects and year effects, in mm, on annual length increments of smallmouth bass collected from eight northeastern Minnesota lakes in 1989. Lakes are grouped by the presence or absence of lake trout.

	Lake trout absent				Lake trout present			
Lake[a]:	CB	FL	PO	TI	GR	LN	WB	DC
Gear[b]:	E	E	E	E	E	E	E	TN
Age				Age Effects				
1	78.3	72.7	78.6	79.1	73.5	62.6	53.3	93.7
2	87.3	62.5	89.8	49.7	69.5	45.8	48.0	51.5
3	85.3	57.3	----	50.1	57.6	32.4	42.2	51.4
4	71.5	54.1	----	50.2	46.8	16.9	----	27.9
5	69.1	37.4	----	50.8	53.5	41.9	----	46.4
6	----	55.8	----	38.0	56.8	28.4	----	37.0
7	----	73.0	----	38.0	56.8	24.3	----	13.2
8	----	----	----	----	----	12.6	----	----
9	----	----	----	----	----	27.9	----	----
10	----	----	----	----	----	-2.7	----	----
Year				Year Effects				
1979	----	----	----	----	----	4.7	----	----
1980	----	----	----	----	----	-0.6	----	----
1981	----	----	----	----	----	-2.9	----	----
1982	----	-19.7	----	----	----	-4.2	----	----
1983	----	-17.8	----	-5.2	-5.1	-2.2	----	-4.6
1984	-5.5	-14.1	----	-11.7	-10.2	-3.6	----	-6.6
1985	-16.3	-21.9	----	-19.3	-21.9	-7.9	----	-12.1
1986	-9.3	-12.7	----	-14.8	-18.1	-6.8	1.9	-10.6
1987	-5.4	-5.1	-7.8	-6.1	-6.3	-4.0	5.8	-6.2
1988	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

[a] CB = Caribou; FL = Flour; PO = Poplar; TI = Two Island; GR = Greenwood; LN = Loon; WB = West Bearskin; DC = Duncan.

[b] E = electrofishing, 31 May - 23 June; TN = trap netting, 10-13 October.

A comparison of lake trout diets among lakes showed some similarities, such as the importance of Ephemeroptera and Diptera in May 1989, as well as differences. Diet differences sometimes reflected different prey communities, such as the presence of rainbow smelt in Trout Lake but not in the other lakes sampled during May 1989. Exceptions occurred, however, in that cisco were identified only in stomachs from Duncan Lake, though they also occur in Greenwood, Loon, and Trout Lakes. Unidentified fish cannot account for all of these discrepancies. There are no clear differences in lake trout stomach contents between LAT and sympatric lakes.

Common prey of smallmouth bass in most lakes included insects, especially Ephemeroptera, Odonata, and Diptera, along with crayfish, leeches, amphipods, and fish, which were not always identified but included sculpin, yellow perch, and smallmouth bass. Crayfish tended to rank higher among prey taxa by volume than by number, whereas the opposite was true for Diptera. Crayfish were not identified in stomachs from Two Island or Greenwood Lakes. It is not known whether they occur in these lakes, so the degree to which gut contents reflect prey community differences among lakes is not as clear as for lake trout. Differences in smallmouth bass diets between SMB and sympatric lakes are not clearly evident.

Some dietary trends were apparent among size classes of smallmouth bass. Percentage occurrence of prey in bass less than 152 mm in total length was highest for smaller insects, such as Ephemeroptera and Diptera. Bass 152 mm to 254 mm long consumed the greatest variety of prey. Bass longer than 254 mm consumed crayfish more frequently than smaller bass. Crayfish appeared to contribute a higher percentage of stomach content volume to the largest bass than to the smaller bass categories.

Data from Greenwood and Loon Lakes were used to determine the relation between consumption and predator length. Regressing the quantity of selected prey taxa on lake trout length produced a significantly positive slope in two out of ten cases (Table 11). These occurred for the number and weight of Ephemeroptera consumed by lake trout in Greenwood Lake. Similar regressions on smallmouth bass length produced one significant slope, which was negative, for the number of Diptera consumed by smallmouth bass in Greenwood Lake. Slopes of regression lines were compared between predator species with ANCOVA. Significant differences occurred in the same two cases for Ephemeroptera in Greenwood Lake, indicating that the increase

Table 11. Results of regression of prey weight (g) and number on predator length (mm), and analysis of covariance (ANCOVA) using predator species as treatment and predator length as covariate in predicting prey consumption. Lake trout (LAT) were gill netted in May, and smallmouth bass (SMB) were taken by electrofishing and angling in June, 1989. "na" indicates not applicable.

Prey		Predator		Regression			ANCOVA Interact.	Species	Length
Taxon	Measure	sp.	N	r^2	Slope	P^a	P^b	P^c	P^d
				Loon Lake					
Ephemeroptera	weight	LAT	14	0.063	0.001	0.387	0.667	0.435	0.315
		SMB	7	0.110	0.001	0.468			
	number	LAT	14	0.277	0.030	0.053	0.218	0.511	0.047
		SMB	7	0.221	0.008	0.287			
				Greenwood Lake					
Ephemeroptera	weight	LAT	27	0.331	0.082	0.002	0.038^L	na	na
		SMB	5	0.035	0.008	0.764			
	number	LAT	27	0.311	1.668	0.003	0.033^L	na	na
		SMB	5	0.226	0.079	0.418			
Amphipoda	weight	LAT	21	0.001	-0.000	0.912	0.955	0.477	0.909
		SMB	6	0.043	0.000	0.694			
	number	LAT	21	0.001	-0.006	0.917	0.779	0.639	0.854
		SMB	6	0.155	-0.072	0.440			
				Greenwood Lake					
Diptera	weight	LAT	18	0.069	-0.002	0.292	0.404	0.060	0.250
		SMB	10	0.245	-0.000	0.146			
	number	LAT	18	0.024	-0.082	0.538	0.994	0.058	0.269
		SMB	10	0.408	-0.042	0.047			
Odonata	weight	LAT	5	0.060	-0.001	0.691	0.419	0.126	0.994
		SMB	7	0.133	0.001	0.421			
	number	LAT	5	0.242	-0.008	0.400	0.863	0.021^L	0.099
		SMB	7	0.357	-0.007	0.157			

[a] Probability (two-tailed) that slope = 0.

[b] Probability of no interaction between predator species and predator length. (Probability that slopes of regressions for predator species are equal.)

[c] Probability that mean value of measure does not differ between predator species. (Probability that regressions for predator species have equal intercepts, given equal slopes.)

[d] Probability that predator length has no effect on value of measure.

[L] Value for lake trout is significantly greater than value for smallmouth bass.

in number and weight of Ephemeroptera consumed per unit increase in predator length was greater for lake trout than for smallmouth bass. Intercepts were compared for those cases where slopes were not significantly different, yielding one significant result. In Greenwood Lake, lake trout consumed more odonates than did smallmouth bass of similar length. Weights consumed by each species were not different, however, as a result of lake trout eating primarily nymphs (in May), and smallmouth bass eating more adults (in June). Cases with nearly significant results ($0.05 < P < 0.1$) showed the same trend of greater consumption by lake trout.

Diet overlap within species between lakes was quite variable. Similarity of lake trout diets between lakes ranged from 0.05 to 0.59 (Table 12). There was no clear pattern of similarity values with respect to the presence or absence of smallmouth bass. Similarity of smallmouth bass diets between lakes ranged from 0.13 to 0.62. The lowest and highest values occurred between SMB lakes. These results suggest that diets of each species were neither more nor less similar among lakes when the other species was present.

Lake trout and smallmouth bass diets overlapped within lakes about as much as diets of each species overlapped between lakes. Similarity of lake trout and smallmouth bass diets in Greenwood Lake was 0.38 (Table 12). This value is higher than midway in the range of similarities of lake trout diets between Greenwood Lake and other lakes (0.06 to 0.59), and about midway in the range of similarities of smallmouth bass diets between Greenwood Lake and other lakes (0.19 to 0.62). Similarity of lake trout and smallmouth bass diets in Loon Lake was 0.27. This value is higher than midway in the range of similarities of lake trout diets between Loon Lake and other lakes (0.09 to 0.35), and about midway in the range of similarities of smallmouth bass diets between Loon Lake and other lakes (0.13 to 0.43).

Table 12. Diet similarity within species among lakes, and between species within lakes. Lake trout were taken with gill nets in May, and smallmouth bass were taken by angling and nighttime electrofishing in June, 1989. Similarity is computed by summing over all prey items the lesser of the two proportions of total volume for each prey item.

Lake trout diet similarity among lakes

Lake:	Greenwood	Loon	Kemo	Mayhew	Trout
Greenwood	1.00				
Loon	0.09	1.00			
Kemo	0.16	0.35	1.00		
Mayhew	0.59	0.16	0.19	1.00	
Trout	0.06	0.10	0.09	0.05	1.00

Smallmouth bass diet similarity among lakes

Lake:	Caribou	Flour	Poplar	Two Island	Green-wood	Loon	West Bear-skin
Caribou	1.00						
Flour	0.58	1.00					
Poplar	0.47	0.46	1.00				
Two Island	0.13	0.29	0.38	1.00			
Greenwood	0.37	0.41	0.62	0.33	1.00		
Loon	0.13	0.30	0.39	0.43	0.19	1.00	
W. Bearskin	0.35	0.47	0.30	0.28	0.25	0.25	1.00

Diet similarity between lake trout and smallmouth bass

Lake:	Greenwood	Loon
	0.38	0.27

Lake trout harvest

Lake trout yields predicted from THV were slightly higher than those predicted from MEI (Table 13). Yields predicted from either MEI or THV were roughly similar between LAT lakes and sympatric lakes.

Creel surveys furnished estimates of winter angling yields of lake trout for all study lakes having lake trout, and rougher estimates of annual angling yields of lake trout from all but two of these lakes. Winter yields, in kg/hectare, ranged from 1.63 to 3.84 for the LAT lakes, and from 0.09 to 0.67 for the sympatric lakes, amounting to an order of magnitude difference (Table 13). Ratios of angler yields to predicted yields were higher in the LAT lakes, being greater than one in the LAT lakes, and, with one exception considered to be a high estimate, less than one in the sympatric lakes. It must be noted that relative effort (angler-h per hectare) in the LAT lakes was an order of magnitude higher than it was in the sympatric lakes. Neither yield predictor explained a significant amount of the variation in winter angling yield of lake trout ($P < 0.05$). For MEI, $r^2 = 0.282$, $N = 6$, and for THV, $r^2 = 0.163$, $N = 8$.

Matrices of Pearson correlation coefficients helped to rank the association of winter harvest descriptors with effort and abiotic limnological variables. Effort generally gave the highest correlations with harvest and yield, and these were significantly positive (Table 14). Harvest descriptors were significantly negatively correlated with lake area, maximum depth, SDI, lake volume, and THV. The *r* values associated with ELC were relatively high. ELC could explain a significant amount of the variation in two of the seven harvest descriptors (harvest per unit effort and yield, both by number).

Winter lake trout harvest descriptors correlated significantly with only two of the six fish community variables (Table 15). The number of major species correlated negatively with yield, by number, and harvest and yield were lower where smallmouth bass were present.

Some significant correlations occurred between the abiotic variables and the fish community variables (Table 16). Smallmouth bass were associated with lowered winter angling effort

Table 13. Comparison of mean angling yield to yield predicted from MEI and July lake trout thermal habitat volume (THV), for lakes with and without smallmouth bass. Yields are in $kg \cdot ha^{-1} \cdot y^{-1}$. Proportion of MEI-predicted total fish yield (partition factor) is based on number of major species. Mean relative effort ($h\ h \cdot ha^{-1}$) is also shown for winter angling. "nd" indicates no data.

	Lakes with smallmouth bass				Lakes without smallmouth bass			
Estimator	Greenwood	Loon	W. Bearskin	Duncan	Kemo	Mayhew	Trout	Birch
			Predicted yield					
partition factor	0.32	0.42	0.42	0.42	0.58	0.54	0.42	0.58
partitioned MEI	0.76	1.46	1.19	1.08	1.90	nd	1.22	nd
THV	1.46	1.82	2.48	1.10	2.14	1.81	2.11	1.22
			Angler yield					
relative effort	0.63	1.61	7.91	2.81	22.13	17.29	24.15	22.67
winter creel	0.09	0.10	0.67	0.16	2.23	1.81	3.84	1.63
annual creel	nd	0.13	1.45[a]	0.16	nd	2.37[b]	5.80	1.63[b]
			Ratio of angler yield to predicted yield					
winter:MEI	0.12	0.07	0.56	0.15	1.18	nd	3.16	nd
annual:MEI	nd	0.09	1.22[a]	0.15	nd	nd	4.76	nd
winter:THV	0.06	0.06	0.27	0.15	1.04	1.00	1.82	1.34
annual:THV	nd	0.07	0.58[a]	0.15	nd	1.31[b]	2.75	1.34[b]

[a] Considered to be a high estimate.
[b] Considered to be a low estimate.

and higher measures of lake area, volume, and THV, consistent with their occurrence in the larger and less intensely fished sympatric lakes. The number of major species also correlated positively with lake area, though fewer species would be expected in the three smallest (reclaimed) study lakes.

An additional matrix was constructed to clarify the correlation of winter angling effort with the abiotic limnological variables (Table 17). Effort was significantly negatively correlated with lake area, volume, THV, and maximum depth. MEI was positively correlated with effort. These results clearly reflect the decreased effort observed on the sympatric lakes.

Table 14. Pearson correlation coefficients (*r*) for lake trout winter angling catch descriptors versus angling effort and abiotic variables. For ELC, *r* is taken from ANOVA and has no sign. All measures except ELC were $\log_{10}$ transformed means from creel surveys. Sample size is eight lakes (six for MEI). Smallmouth bass are found in four lakes. Asterisk (*) indicates $p < 0.05$.

	Total harvest		Harvest per unit effort		Yield per winter		Mean weight
	(no)	(kg)	(no/h)	(kg/h)	(no/ha)	(kg/ha)	(kg)
Total effort (h)	0.91*	0.92*	0.32	0.35	0.92*	0.96*	-0.05
Relative effort (h/ha)	0.86*	0.79*	0.32	0.15	0.97*	0.97*	-0.31
Lake area (ha)	-0.74*	-0.60	-0.29	0.04	-0.93*	-0.88*	0.50
Mean depth (m)	-0.47	-0.70	0.07	-0.46	-0.40	-0.55	-0.50
Maximum depth (m)	-0.71*	-0.83*	-0.18	-0.47	-0.70	-0.80*	-0.12
SDI	-0.79*	-0.64	-0.70	-0.39	-0.80*	-0.75*	0.62
Volume ($m^3/10^6$)	-0.78*	-0.75*	-0.22	-0.15	-0.92*	-0.94*	0.24
THV ($m^3/10^6$)	-0.55	-0.43	0.10	0.19	-0.79*	-0.75*	0.42
MEI	0.70	0.74	0.28	0.34	0.76	0.83*	-0.12
ELC	0.91	0.81	0.91*	0.60	0.92*	0.91	0.73

Table 15. Pearson correlation coefficients (*r*) for lake trout winter angling catch descriptors versus fish community attributes. Harvest descriptors were $\log_{10}$ transformed means from creel surveys. Sample size is eight lakes. Smallmouth bass are found in four lakes. Asterisk (*) indicates $p < 0.05$.

	Total harvest		Harvest per unit effort		Yield per winter		Mean weight
	(no)	(kg)	(no/h)	(kg/h)	(no/ha)	(kg/ha)	(kg)
No. of major species	-0.49	-0.38	-0.03	0.24	-0.72*	-0.68	0.38
No. of other predators	-0.26	-0.33	0.20	0.04	-0.44	-0.50	0.06
Presence or Absence:							
Smallmouth bass	-0.85*	-0.78*	-0.51	-0.37	-0.90*	-0.90*	0.39
Coregonines	-0.41	-0.45	0.18	0.09	-0.54	-0.59	-0.09
Smelt	-0.09	-0.10	-0.04	-0.02	0.08	-0.09	0.12
Coregonines or smelt	-0.43	-0.40	-0.05	0.03	-0.59	-0.60	0.25

Table 16. Pearson correlation coefficients (r) for fish community attributes versus angling effort and abiotic variables. For ELC, r is taken from ANOVA and has no sign. Mean effort from creel surveys and abiotic variables, except ELC, were $\log_{10}$ transformed. Sample size is eight lakes (six for MEI). Smallmouth bass are found in four lakes. Asterisk (*) indicates $p < 0.05$. "na" indicates r was not applicable.

	No. of major species	No. of other predator species	Presence or absence: Smallmouth bass	Coregonines	Smelt	Coregonines or smelt
Total effort (h)	-0.50	-0.36	-0.82*	-0.63	0.14	-0.53
Relative effort (h/ha)	-0.74	-0.43	-0.87*	-0.66	0.10	-0.65
Lake area (ha)	0.86	0.44	0.83*	0.61	-0.06	0.69
Mean depth (m)	0.03	0.58	0.49	0.53	0.01	0.43
Maximum depth (m)	0.40	0.70	0.68	0.67	-0.08	0.56
SDI	0.68	0.40	0.58	0.14	-0.42	0.16
Volume ($m^3/10^6$)	0.73	0.64	0.86*	0.69	-0.08	0.72*
THV ($m^3/10^6$)	0.79	0.49	0.79*	0.51	-0.01	0.72*
MEI	-0.60	-0.80	-0.64	-0.74	0.37	-0.57
ELC	0.81	0.67	na	na	na	na

Table 17. Pearson correlation coefficients (r) for winter angling effort versus abiotic variables. For ELC, r is taken from ANOVA and has no sign. Effort measures are means from winter creel surveys. All measures except ELC were $\log_{10}$ transformed. Sample size is eight lakes (six for MEI). Asterisk (*) indicates $p < 0.05$.

	Surface area	Volume	THV	Mean depth	Max. depth	SDI	MEI	ELC
Total effort (h)	-0.80*	-0.90*	-0.66	-0.66	-0.82*	-0.62	0.83*	0.83
Relative effort (h/ha)	-0.96*	-0.96*	-0.85*	-0.47	-0.73*	-0.70	0.82*	0.87

Discussion

There were morphometric and water quality differences among the three lake types. The sympatric lakes, as a group, are the largest and deepest. The LAT lakes have the least area and shoreline development. The SMB lakes, as a group, have the greatest shoreline development, the highest MEI, and the least suitable habitat for lake trout.

ELC separated lakes in a way that was consistent with the three lake types based on allopatry or sympatry, with the exception that Birch Lake (a LAT lake) shared the same class (ELC 03) as two SMB lakes. While this may seem to indicate a lack of refinement of the classification model, only 9 of the 24 Cook County lakes in this class contain lake trout. Birch Lake's THV on 21 August 1989 was zero when the criteria of Payne et al. (1990) were strictly applied, and included a layer only 7 cm deep by the modified criteria used here. A profile taken 5 August 1982 was used to compute the THV used in this study. Observations by Siesennop (personal communication 1992) are that this lake may be undergoing eutrophication and its suitability to lake trout may be declining. With this exception, ELC provides additional evidence that the three lake types are different limnologically.

The phylogeny of the fish community of each lake type is consistent with its limnological characteristics. The greatest phylogenetic diversity occurs in the sympatric lakes, which, based on their greater size, depth, and at least moderate shoreline development, are expected to have the greatest habitat diversity. Carl et al. (1990) and OMNR (1982) noted the increase in number of species present with increasing surface area of Ontario lakes. However, fewer and phylogenetically more primitive species are a likely result of reclaiming the three smallest (LAT) lakes, and may not be conditions that inherently follow from ELC or small lake size.

Whether or not causal relationships exist between limnological and fish community variables, these variables differ sufficiently among lake types to warrant their consideration when comparing lake types to determine species interactions. Fisheries managers recognize that the SMB lakes warrant different management than the other lakes. The SMB lakes are stocked with walleye, whereas the sympatric and LAT lakes are stocked with lake trout. The particular LAT and sympatric lakes considered in this study are currently managed similarly, except that lake trout stocking is considered to be unnecessary in Trout Lake, and has been discontinued. Management of these lakes may diverge in the future as ELC or other information is considered.

Lake trout CPUE from gill nets was significantly higher in the LAT lakes, which is in general agreement with the overview for Ontario lakes presented by Carl et al. (1990), namely, that this measure was greatest in small transparent lakes with few predator species and few major species, possibly resulting from reduced interspecific competition. Lake trout CPUE from 13-mm and 19-mm trap nets set in fall was significantly higher in the two sympatric lakes. This contradiction may be an artifact of the more precipitous shoreline in Mayhew Lake, and, hence, less suitable sites for trap netting in the LAT lakes. Stocking lake trout in only some years undoubtedly contributes to annual fluctuations in CPUE. For this reason, CPUE data from only two or three years may not be sufficient to draw general conclusions about the relative abundance of lake trout in lakes of each type.

Drawing conclusions about relative abundance is more difficult for smallmouth bass than for lake trout. Electrofishing CPUE data were highly variable and failed to show significant differences in relative abundance of smallmouth bass between SMB lakes and sympatric lakes. Assessment reports characterize smallmouth bass as abundant in Flour, Two Island (SMB lakes), Greenwood, and Loon (sympatric lakes) Lakes, moderately abundant but variable in Caribou Lake, and low in numbers in Poplar Lake (SMB lakes).

The fact that ELC in ANOVA explained more of the variation in gill net catches than did smallmouth bass status might have been predicted based upon its greater number of levels. However, it illustrates that smallmouth bass status is a simplification and that ELC may more accurately classify lakes with respect to CPUE.

Fall trap net CPUE data and scant information from fisheries assessment records suggest that abundance of minnows may have been greatest in three of the four LAT lakes (Birch, Mayhew, and Trout), intermediate in one SMB lake (Caribou), and least in the remaining lakes. Coupled with each lake's (limited) abundance information for lake trout and smallmouth bass, this pattern is consistent with both intra- and interspecific competition.

There is some evidence that growth rates of young lake trout are greater in the LAT lakes than in the sympatric lakes. Siesennop (1992) applied Schnute's growth model (Schnute 1981) to lake trout collected during spring, fall, and winter from four of the study lakes. Growth rates were highest in Birch Lake, followed in order by Mayhew, West Bearskin, and Duncan Lakes, consistent with the ranking based on size and age at fall-capture examined here. This could suggest competition with smallmouth bass, as smallmouth bass were present in West Bearskin and Duncan lakes, but may also be explainable by differences in forage fish.

The ultimate size attained by lake trout appeared to be greater in the sympatric lakes, and is explainable by their having more large forage fish. Cisco are abundant in Greenwood, Loon, and Duncan Lakes. West Bearskin Lake has an abundance of rainbow smelt. These species are absent from the LAT lakes, except that both are found, along with *Mysis relicta*, in Trout Lake. Cisco, in the absence of *Mysis relicta*, apparently reduced the growth rate of young lake trout but increased the growth rate and fecundity of older lake trout in Lake Opeongo, Ontario (Colby et al. 1987). Assessment records characterized growth rates of lake trout in Trout Lake as average through age 3, but slow for ages 4-8, compared to other county lakes. Notably, the cisco population may be senile. In 1990 the lake contained an abundance of small lake trout, but cisco were too large to serve as forage, since all those sampled were greater than 480 mm total length. The effect of *Mysis relicta* in Trout Lake is potentially complex, but is likely to include competition with zooplanktivorous fishes, and could result in decreased growth rates for these fishes and lake trout (Carl et al. 1990). Data available to Siesennop (1992) suggested that ultimate size was greatest in Duncan Lake, followed in descending order by West Bearskin, Mayhew, and Birch Lakes. This is nearly the same order as the elevation of the weight-length regressions, and the reverse order compared to growth rates of young lake trout. These growth characteristics parallel those of two classes of Ontario lakes, based on their fish communities. Lake trout populations lacking coregonines as prey exhibit rapidly declining growth efficiency and small maximum size (Carl et al. 1990).

To the extent that pooling lakes is biologically and statistically valid, the linear growth model clearly indicates that growth rates of smallmouth bass are reduced in the sympatric lakes. This is consistent with interspecific competition, but ignores relative abundance information needed to measure intraspecific competition. The highest growth rates among lakes electrofished occurred in Caribou and Poplar Lakes, where smallmouth bass populations were probably least dense. Assessment records characterized growth as slow in Flour, Two Island, and Loon Lakes, apparently as a result of high bass density and low forage availability. Based on the scant relative abundance information available from assessment records, growth rates of smallmouth bass are consistent with intraspecific competition.

The occurrence of cisco is coincident with slow growth of smallmouth bass in Flour and Loon Lakes, and moderately slow growth in Greenwood Lake. These results are consistent with Emery's (1975) findings that growth rates of smallmouth bass younger than age 3 declined following introduction of cisco to Lake Opeongo, Ontario. Emery further stated that growth of adult smallmouth bass was limited by crayfish abundance. The abundance of rainbow smelt, in the absence of cisco, might explain slow growth of smallmouth bass in West Bearskin Lake. Being absent from Two Island Lake, these two apparent competitors cannot be responsible for the slow growth of smallmouth bass there after age 1.

Differences in sampling methods may confound the comparison of lake trout and smallmouth bass diets. Prey digestion may have been more complete in stomachs of lake trout collected with overnight gill net sets than in stomachs of smallmouth bass collected by angling and electrofishing.

Smallmouth bass diet composition may vary with sampling date, and may do so more in some lakes than in others (Clady 1974; Serns and Hoff 1984). Different sampling dates therefore confound the comparison of lake trout and smallmouth bass diets, but such comparisons are still useful. One predator may deplete prey from a particular depth zone during a period of stratification that would otherwise have become available to the other predator during periods of overturn. Shuter et al. (1987) assumed that smallmouth bass in Lake Opeongo remained in the epilimnion during summer, and that lake trout remained in the hypolimnion. This segregation would seem to prevent direct competition, but could allow smallmouth bass to deplete minnows that were restricted to the epilimnion, possibly having a negative impact on lake trout in fall and explaining the apparently reduced abundance of minnows in the sympatric lakes. At the same time, lake trout might deplete some deepwater prey to the subsequent detriment of smallmouth bass, though an example of this seems less straightforward.

The high number and volume of insects and other invertebrates in the lake trout diet is consistent with the relatively small size of the study lakes (Carl et al. 1990). Our observations that smallmouth bass relied on similar invertebrates and that larger bass increased consumption of crayfish are patterns documented in other lakes (Fedoruk 1966; Clady 1974; Emery 1975; Johnson and Hale 1977; Serns and Hoff 1984).

Diet descriptions did not always reflect prey occurrence or abundance, since, in some cases, prey known to occur in a lake were not identified in stomachs. To the extent that diet descriptions represent prey availability, there is considerable variation in prey availability among lakes within a type.

Between-lake diet similarity values for lake trout sampled in May 1989 did not appear to be higher within lake type than between lake type, in contrast to expectations if smallmouth bass controlled lake trout diet. Between-lake diet similarities of smallmouth bass did not appear to be lower when one lake contained lake trout, suggesting that lake trout did not control smallmouth bass diet. These results may reflect variations in forage species abundance, or else too few lakes and stomachs were sampled to test this. The two species in sympatry exhibited a moderate amount of diet overlap. Some of the similarities presented may be underestimates, since diet compositions (percent of total volume) often did not sum to 100%. Because it is not known whether demand for prey exceeds supply, similar lake trout and smallmouth bass diets indicate only that the potential for interspecific competition exists.

Both species may compete for food with other species. Walleye may compete with smallmouth bass in the SMB lakes, though Johnson and Hale (1977) concluded that intraspecific competition outweighed interspecific competition. From mid-June through August smallmouth bass stomachs contained primarily crayfish, insects, and fish, in descending order of percentage total volume, while the order for walleye stomachs was the reverse. Serns and Hoff (1984) determined that diets of smallmouth bass and yellow perch (the latter species being found in most of our study lakes) overlapped for several insect orders, depending on sampling date, but because smallmouth bass concentrated on crayfish, which were not an important food for adult perch, competition did not appear to be severe. White sucker are present in all lakes except Trout Lake. They have been shown to outcompete yellow perch (Tremblay and Magnan 1991) and brook trout *Salvelinus fontinalis* (Hayes 1990) for benthos, and might do the same for both lake trout and smallmouth bass. Hodgson et al. (1991) demonstrated that largemouth bass *Micropterus salmoides* became more generalist feeders and rainbow trout *Oncorhynchus mykiss* became more planktivorous when in sympatry. Schneidervin and Hubert (1987) found *Daphnia* in 500-mm-long lake trout, and cited evidence from other studies that lake trout structure the zooplankton communities in arctic lakes, indicating that adults maintain a capability for substantial consumption of zooplankton.

If salmonids, including lake trout and cisco, outcompete smallmouth bass for zooplankton, and white sucker are the dominant benthivores, then, smallmouth bass may be more negatively affected by sympatry than lake trout. This scenario suggests that smallmouth bass diets would include relatively more benthos and less zooplankton in sympatric lakes compared to SMB lakes. The scarcity of zooplanktors enumerated in smallmouth bass stomachs precludes such a comparison.

The methods used to predict harvests and yields may not be appropriate for these study lakes. Both models (MEI and THV) were developed for large lakes and self-sustaining commercially fished populations that are not obviously overexploited. The THV model assumed not only a stable summer thermal regime, but stable harvest and population attributes. In contrast, our study lakes are relatively small, dependent upon stocking, and support sport fisheries that often have high exploitation rates. Siesennop (1992), considering only four of our study lakes, showed a cycling of annual lake trout harvests that reflected stocking years, growth rates, and angling effort. The high exploitation rate in Birch Lake may have prevented the observation of lake trout approaching maximum potential size.

The MEI formula may be conservative when used to predict sport fisheries yields (OMNR 1982). In addition, some judgement is required in using number of species to partition the total fish yield into yield for lake trout only. This analysis included at least one additional species (rainbow smelt), and possibly others, not included in the Ontario partition model (OMNR 1982). These were found in more sympatric lakes than LAT lakes, and therefore tended to reduce predicted yields more in the sympatric lakes. In spite of these two potential biases, ratios of observed angling yield to MEI-predicted yield were generally less than one for the sympatric lakes and greater than one for the LAT lakes.

Payne et al. (1990) suggested that the THV model may be a better predictor of lake trout harvest than MEI for lakes in the same geographic area that have very similar total dissolved solids, such as the lakes in this study. However, lakes less than 100 hectares are inadequately represented in the model, and tend to have fewer species, fewer competing predators, dense populations of planktivorous/ benthivorous lake trout, and relatively high yields (Carl et al. 1990). These conditions apply more to the LAT lakes included in this study than to the sympatric lakes, suggesting that THV-predicted yields for the LAT lakes may be too low.

In a full regression model attempting to explain species-specific yields in northern Finnish lakes, Ranta and Lindstrom (1990) found that none of 16 water quality variables remained after stepwise elimination. For six species the corresponding effort variable was accepted into the model, with coefficients of determination approaching 50%. They, too, concluded that variation in water quality variables over a small geographic area was insufficient to explain yield.

The variation in lake trout harvest and yield estimates observed among our lakes can be explained by their significant positive correlations with total angling effort (r = 0.92) and relative angling effort (r = 0.97), respectively. The greater harvests and yields from the LAT lakes can be explained by the greater effort (order of magnitude) expended on the LAT lakes, without invoking competition from smallmouth bass in the sympatric lakes. Conversely, it might be argued that smallmouth bass, as a competing species, had reduced lake trout abundance and angling harvest per unit effort (HPUE), which then caused reduced effort and yield. This confounding argument is not as strong as the former argument for two reasons. The negative association between the presence of smallmouth bass and lake trout HPUE was not statistically significant. Secondly, correlations of HPUE with effort were weak and not significant.

Goddard (1987) determined that fish community groupings had little or no effect on the angling yield of lake trout from 87 Ontario lakes, when the influence of effort and lake size was controlled. Carl et al. (1990) found that very small differences in angling harvest were attributable to community composition, but these differences were overshadowed by effects of lake area and effort. They concluded that angling data do not allow for a valid test of community effects because of strong correlation between harvest, angler effort, and lake surface area. Though our correlations with lake area were negative rather than positive, the same must be said for the lakes examined here.

Fausch (1988), in reviewing studies of competition between stream salmonids, emphasized that without manipulations the differences apparent between sympatric and allopatric populations may be indistinguishable from effects of stream or site differences, unless other evidence from a large number of sites is considered. This should apply equally to lakes. It may or may not have been possible to find lakes more similar than our study lakes. The ecological lake classification may have contributed in this regard had it been available when this study began. Sampling additional lakes would not have been logistically feasible. The number of lakes considered here may have been sufficient to test the effects of lake trout and smallmouth bass status if fewer limnological and fish community differences had occurred and data collection had been more rigorous.

Fausch (1988) further stated that the central idea in competition studies is to test the strength of interspecific competition versus that of intraspecific competition by manipulating densities of the two competitors. The limited abundance data for lake trout and smallmouth bass did not allow for a determination of the relative degree of each type of competition. Diet overlap between lake trout and smallmouth bass showed a potential for interspecific competition, but prey availability data was not obtained for most prey taxa and was therefore insufficient to determine if prey was limiting. For these reasons, observed differences in abundance, growth rates, and diet composition between allopatric and sympatric populations can only circumstantially be attributed to interspecific competition.

Summary

The four lakes having sympatric populations of lake trout and smallmouth bass had the greatest volume and (with one exception) maximum depth, and the most phylogenetically diverse fish community. The four SMB lakes had the greatest shoreline development and the least mean depth. The four LAT lakes had the least surface area and shoreline development, and the fewest major and predator species (three of these lakes had been poisoned and restocked with desired species). Cisco or rainbow smelt were present in all sympatric lakes, one SMB lake, and one LAT lake. These limnological and fish community differences may have influenced measures of abundance, growth rates, and diet composition that we had hoped would indicate effects of interactions between lake trout and smallmouth bass.

Abundance and growth results are consistent with interspecific competition. Lake trout CPUE from gill nets was higher in LAT lakes, consistent with literature citing higher catch rates and yields from simpler communities. Young lake trout grew faster in LAT lakes, where small forage fish may have been more abundant. Maximum size attained by adult lake trout was greatest in sympatric lakes, probably as a result of preying on cisco or rainbow smelt. Smallmouth bass CPUE from electrofishing was not significantly different between SMB and sympatric lakes, but this data may have been too imprecise to rigorously test this. Smallmouth bass grew fastest in the two SMB lakes that may have had the least dense populations, and faster in SMB lakes as a group than in sympatric lakes. Forage fish abundance information was insufficient to compare between SMB and sympatric lakes.

Diets of lake trout and smallmouth bass in sympatry overlapped about as much as diets of each single species overlapped between lakes, indicating a potential for competition. Insects, including Ephemeroptera, Odonata, and Diptera were important in the diet of both predators. Smallmouth bass over 256 mm in total length ate more crayfish than smaller bass. Lack of abundance information precluded determining whether invertebrate prey taxa limited either predator.

Harvest and yield of lake trout during winter angling was highly correlated with total and relative effort, respectively. Yields predicted from morphoedaphic index or July lake trout thermal habitat volume did not correlate significantly with winter angling yields.

Though abundance, growth, and diet results suggest that the potential exists for competition between lake trout and smallmouth bass, strong inferences about interspecific competition are precluded by confounding limnological and fish community variables, lack of fish population density manipulations, limited diet data, and insufficient abundance data for predators and prey.

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