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UTILIZATION OF AQUATIC MACROPHYTES BY
LARGEMOUTH BASS (Micropterus salmoides),
BLUEGILL SUNFISH (Lepomis macrochirus),
AND YELLOW PERCH (Perca flavescens)
IN DEVILS LAKE, OREGON

by

Steven Lawrence Thiesfeld

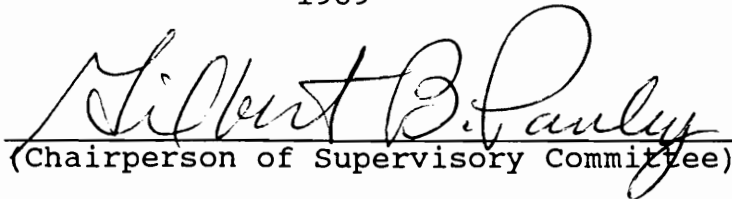
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of the requirements for the degree of

Master of Science

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1989

Approved by


(Chairperson of Supervisory Committee)

Program Authorized
to Offer Degree

School of Fisheries

Date July 21, 1989

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Abstract

UTILIZATION OF AQUATIC MACROPHYTES BY LARGEMOUTH BASS
(Micropterus salmoides), BLUEGILL SUNFISH (Lepomis
macrochirus), AND YELLOW PERCH (Perca flavescens) IN DEVILS
LAKE, OREGON

by Steven L. Thiesfeld

Chairperson of the Supervisory Committee: Gilbert B. Pauley

The influence of aquatic macrophytes on fish distributions was examined within in situ experimental plots in Devils Lake, Oregon. Devils Lake is a polymictic, coastal lake with a mean depth of 3.0 m. Sampling with gill nets, fyke nets, and electroshock gear suggested that largemouth bass (Micropterus salmoides) < 100 mm preferred intermediate levels of macrophytes, yellow perch (Perca flavescens) preferred dense macrophytes, and bluegill sunfish (Lepomis macrochirus) < 100 mm were not related to macrophyte cover. These relationships were observed during the fall in shallow water (1.5 m). No relationships between fish density and macrophyte cover were observed during the fall in deep water (3.0 m) or at either depth during the spring.

Additional sampling was conducted to determine if fish distributions in the lake could be predicted by macrophyte

density. Electroshock gear and fyke nets were used to capture fish from randomly selected quadrats in the lake. Catch per unit effort indices (C/f) were used to estimate fish abundance in five different areas of the lake and were examined with respect to macrophyte density and surface water temperature. Bass and perch distributions in the lake appear to be influenced by temperature, but not macrophyte density. Bluegill distributions were not influenced by either macrophyte density or temperature. Monthly C/f indices of separate size ranges of fish demonstrated the absence of small fish in the littoral zone during the spring and summer, and this absence might have been the result of predator avoidance. However, young of the year remained in the littoral zone during late summer and fall, and apparently were not avoiding predators.

TABLE OF CONTENTS

	Page
List of Figures	iii
List of Tables	iv
Introduction	1
Methods	5
Study Area.....	5
Experimental Design	5
Fish Sampling Within the Experimental Plots.....	8
Whole Lake Sampling Design.....	8
Fish Distribution and Relative Abundance.....	8
Macrophyte Density and Distribution.....	9
Water Temperature.....	10
Data Analysis	10
Experimental Plots.....	10
Whole Lake.....	11
Results	13
Abundance of Fish in Experimental Plots.....	13
Whole Lake Observations.....	17
Macrophyte Density and Distribution.....	17
Water Temperature.....	17
Fish Distribution and Relative Abundance.....	18
Discussion	29
Literature Cited	39

LIST OF FIGURES

Number	Page
1. Bathymetric map of Devils Lake	6
2. Numbers of fish captured in experimental plots in shallow and deep water during spring and fall.....	14
3. Macrophyte density plotted against surface water temperature in five areas of Devils Lake.....	19
4. Spring electroshock catch per unit effort (C/f) of largemouth bass plotted against macrophyte density..	21
5. Spring electroshock catch per unit effort (C/f) of largemouth bass plotted against water temperature...	21
6. Spring electroshock catch per unit effort (C/f) of bluegill plotted against macrophyte density.....	23
7. Spring electroshock catch per unit effort (C/f) of bluegill plotted against water temperature.....	23
8. Spring electroshock catch per unit effort (C/f) of yellow perch plotted against water temperature.....	24
9. Spring electroshock catch per unit effort (C/f) of yellow perch plotted against macrophyte density.....	24
10. Summer electroshock catch per unit effort (C/f) of bluegill plotted against macrophyte density.....	26
11. Summer electroshock catch per unit effort (C/f) of bluegill plotted against water temperature.....	26
12. Summer electroshock catch per unit effort (C/f) of yellow perch plotted against macrophyte density.....	27
13. Summer electroshock catch per unit effort (C/f) of yellow perch plotted against water temperature.....	27
14. Spring fyke net catch per unit effort (C/f) of bluegill plotted against macrophyte density.....	28
15. Spring fyke net catch per unit effort (C/f) of bluegill plotted against water temperature.....	28

LIST OF TABLES

Number	Page
1. Numbers and average length of fish captured in experimental plots from Devils Lake.....	14
2. Catch per unit effort for fish of different sizes captured in Devils Lake during 1987.....	20

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INTRODUCTION

Aquatic macrophytes play an important role in lake ecosystems, influencing every trophic level and potentially even the yield of the top level predators. Macrophytes are often the primary source of synthesized organic matter in lakes (Wetzel 1983), and the magnitude and turnover rate of nutrient cycles are influenced by macrophytes (Frodge et al. 1987). Macrophytes can accelerate the aging of lakes by trapping sediments (Welch 1980). In moderate quantities and suitable diversity, aquatic macrophytes stabilize ecosystems by providing diverse habitats and encouraging a more varied invertebrate and fish community (Boyd 1971; Strange et al. 1975).

Macrophytes affect fish distributions and yield by providing substrate for attachment of benthic invertebrates upon which juvenile fish feed, cover to protect juvenile fish from predation, and adult spawning habitat (Holcomb et al. 1975). Complex habitats reduce the encounter rate between prey and predator (Cooper and Crowder 1979) and modify their behavior toward each other (Savino and Stein 1982). Mittlebach (1981) and Werner et al. (1983a) showed that bluegill (Lepomis macrochirus) > 100 mm maximize energy intake by utilizing zooplankton in the limnetic zone, but bluegill < 100 mm remained near vegetation to reduce predation risk, and as a result exhibited reduced growth.

Johnson et al. (1988) found that bluegill prefer artificial structure with small-interstices over medium- and large-interstices. Crowder and Cooper (1979) postulated that prey density would increase as structural complexity increased, but foraging efficiency would decline due to a decrease in the visual field of the predator. They suggested that intermediate structural complexity offered the maximum opportunity for energy intake by largemouth bass. Savino and Stein (1982) showed that predation efficiency of largemouth bass (Micropterus salmoides) in laboratory conditions decreased with increasing structural complexity because bass sighted fewer prey.

Researchers have estimated fish production based on predator-prey relationships and theorized that predators maximize production in habitat with intermediate structure, and that prey maximize production in densely structured habitat. Wiley et al. (1984) examined fish production (kg/ha/yr) in a series of Illinois ponds containing varying densities of macrophytes and developed a model which incorporated the contrasting relationships of prey density and predator efficiency to structural complexity. Their model predicted that piscivore production would be highest in ponds with intermediate macrophyte densities, and that insectivore production would increase linearly with increasing macrophyte density. Durocher et al. (1984) showed that both standing crop (kg/ha) of largemouth bass

and numbers being recruited to harvestable size were positively correlated with percent submerged vegetation, when submerged vegetation covered up to 20% of the substrate. Some authors suggest that trophic level is the primary factor which determines standing crop of fish in water bodies (Oglesby 1977; Hanson and Legget 1982; Jones and Hoyer 1982; Bays and Crisman 1983). Hoyer et al. (1985) felt that aquatic macrophytes are important only in determining fish production at a given trophic state, but that trophic state was the major factor in determining fish standing crops.

These models proposed for predicting fish yield usually are the result of regressing fish yield or standing crop against predictor variables for numerous lakes, often over wide geographic areas. The relationship between fish distribution or yield and macrophyte density within a single system where trophic level, morphometry, and other covariates are constant or nearly so, has not been widely addressed. If the predictions of Wiley et al. (1984) can be generalized for other areas and for Devils Lake in particular, then the highest abundance of bass in Devils Lake should have occurred in areas with intermediate macrophyte densities. In this study, macrophytes were manipulated to achieve five levels of structural complexity at two depths, and fish abundance was measured during spring

and fall. In addition, distributions of fishes throughout the system were measured and plotted against macrophyte density and surface water temperature to determine if fish distribution could be predicted.

METHODS

Study Area

The experiment was conducted in Devils Lake, Oregon, a 275 ha, polymictic, coastal lake which supports healthy populations of bluegill, yellow perch (Perca flavescens), and largemouth bass. Devils Lake has a history of excessive macrophyte growth with the plant community dominated by Elodea densa, Ceratophyllum demersum, and Myriophyllum spicatum. Peak mean macrophyte biomass was 1690 g/m² (spun weight) in 1986, with macrophytes covering over 50% of the lake bottom (Pauley et al. 1988). The lake was divided into five different areas which separated the lake into four arms and a central basin (Figure 1). These divisions were based upon assumptions of differences in the distribution of largemouth bass and macrophyte biomass in those areas, developed while sampling in 1986. All of the four arms were believed to be morphometrically similar, and each had a gently sloping bottom, a mean depth of about 2 m, and a convoluted shoreline. The central basin was steeper with a mean depth of about 4 m, but had a similarly convoluted shoreline.

Experimental Design

To evaluate vegetation use by fish, macrophytes were manipulated in experimental plots to achieve five levels of structural complexity from which fish were sampled. To

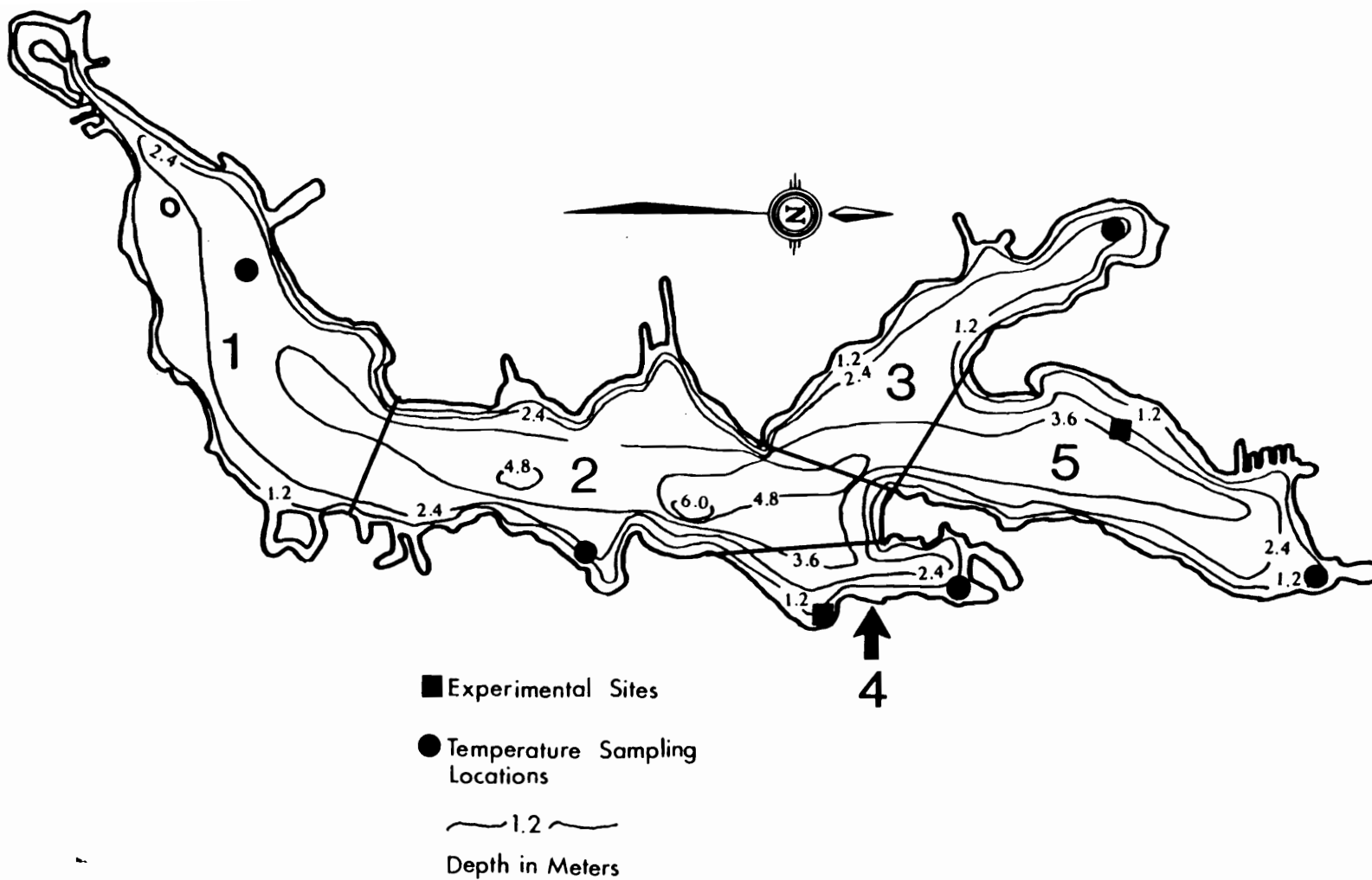


Figure 1. Bathymetric map showing location of temperature sampling sites and areas used in fish distribution analyses.

provide a large range of macrophyte levels and to increase the probability that bass would inhabit the experimental plots, two sites with high macrophyte densities and high densities of largemouth bass were identified from previous research in Devils Lake. Sites were chosen with a uniform depth of 1.5 m and 3.0 m to evaluate the effect of depth on fish use of macrophytes. Five experimental plots of 7.6 m by 8.5 m were designated at each site for elimination of 0, 25, 50, 75, and 100 percent of the macrophytes. Aquascreen was marked with 0.61 m squares, except that a 0.3 m border around the perimeter of the aquascreen sheet was retained to preserve the rectangular shape of the Aquascreen. From three sheets in each site, 25, 50, and 75 percent of the squares were removed at random, except that a strip of squares running diagonally across the sheet was retained to facilitate setting sampling the experimental plot with nets. A fourth sheet had no squares removed. Four experimental plots received treatment with Aquascreen and the fifth plot was maintained as a baseline control. The Aquascreen was laid over the experimental plot, with SCUBA divers pulling weeds through the removed squares and securing the intact portion of the sheet to the bottom. Plants underneath the intact Aquascreen were eliminated from the water column.

Fish Sampling Within The Experimental Plots

Experimental plots were not disturbed for two weeks. Between September 9, 1987 and October 25, 1987, all experimental plots were sampled with gill nets five times, fyke nets three times and electroshocking gear three times. Also plots were sampled with fyke nets once, gill nets twice and electroshocking gear twice between May 20, 1988 and June 10, 1988. Gill nets were 9.1 m long with six randomly placed 1.5 m panels. Panels were of 25.4 mm to 89 mm stretched mesh monofilament in 12.7 mm increments. Fyke nets were constructed with 20 mm stretched mesh multifilament nylon and had openings of 0.9 m by 1.8 m and a single perpendicular lead of 10.4 m. A five meter jon boat with two forward projecting anodes was used for electroshocking. The electroshock boat was equipped with a Smith-Root GPP 5.0 electrofisher and generator. Between two and eight amperes were used while electroshocking, depending on the conductivity of the water. Fish were measured for fork length to the nearest millimeter in order to evaluate possible differences in fish distributions due to size.

Whole Lake Sampling Design

Fish Distribution And Relative Abundance

The entire lake was sampled to examine the distribution of fish and their relationships with macrophyte density and water temperature. The lake was divided into 112 quadrats of

200 m². Quadrats were randomly sampled May through August in 1987 by electroshocking or fyke nets. Forty seven quadrats were electroshocked and 16 were sampled with fyke nets during May and June. During July and August, 34 quadrats were sampled by electroshocking and 14 with fyke nets. Additional samples were collected during March, April, and September to determine the relative abundance of fishes over time.

Three quadrats were sampled with fyke nets each week, one net in each quadrat. Nets were placed offshore with the lead anchored on the shore. Fyke nets were set in each quadrat where no underwater structure would keep the net and lead line from resting on the bottom. Fyke nets were fished for three days consecutively and checked each morning.

Electroshocking was generally conducted for a six hour period two nights per week, with four to ten quadrats sampled each week. The immediate shoreline and all available cover or structure in each quadrat were electroshocked first, followed by a transect which generally ran parallel to the shore but which tended to follow along the edges of milfoil (M. spicatum) or lily pad (Nuphar sp. and Nymphaea sp.) habitats.

Macrophyte Density and Distribution

The lake was divided into 180 quadrats and macrophyte samples were collected from 90 randomly selected quadrats on

May 25, 1987 and again on July 25, 1987. Macrophytes were sampled with a 0.25 m² quadrat sampler patterned after one designed by Purkerson and Davis (1975). Samples were sorted by species, spun in a washing machine to remove excess moisture, and weighed for fresh spun weight. A detailed description of the sampling design can be found in Bonar et al. (1989).

Water Temperature

Temperature (°C) was measured weekly with a Hydrolab series 4000 at 0.5 m below the surface at one location in each area (Figure 1). Temperature was assumed to be homogeneous throughout each area.

Data Analysis

Experimental Plots

Total numbers of bluegill, yellow perch, and largemouth bass were calculated for each experimental plot. Average length was determined for each species in each experimental plot. Distributions of fish with respect to macrophytes were examined by species, depth and season. To determine if fish preferred any level of macrophyte cover, total catch of each species was compared among the experimental plots using a Chi-square analysis. Average length of each species was compared among macrophyte levels using analysis of variance.

Whole Lake

A species catch per unit effort (C/f) was determined for each quadrat sampled. Electroshock C/f was equal to the number of fish of a given species divided by the number of seconds shocked. Fyke net C/f was equal to the number of fish captured in 24 h. To examine possible differences in fish distribution due to size, catch per unit effort was also calculated for three size ranges of fish: < 100 mm, 100-200 mm, and > 200 mm. These size ranges were chosen because in Devils Lake bass and perch < 100 mm are usually young of the year (YOY), and perch and bluegill > 200 mm are rare (Thiesfeld et al. 1989). Also, male bass can mature when they reach 220 mm, while female bass may mature at 250 mm (Heidinger 1976).

Macrophyte density (g/m^3) was calculated for each quadrat. Spun fresh weight is an accepted measure of macrophyte density (ASTM 1985) and was used for analysis. Mean areal macrophyte density was calculated as the mean of the quadrat densities within that area. Seasonal mean temperature for each area was computed as the simple mean of the weekly temperatures.

A one-way analysis of variance was used to determine if there were differences in temperature, macrophyte density and C/f of each fish species among areas. If C/f was different at or near standard levels of statistical significance, it was plotted against temperature and

macrophyte density to visually assess the potential presence of any relationships. Temperature was also plotted against macrophyte density to visually assess the potential presence of any relationships.

RESULTS

Relationships between Macrophyte Density, and Abundance and Size of Fish in Experimental Plots

The number of bass captured differed among macrophyte cover levels only during the fall in shallow water ($p < 0.001$), when bass abundance exhibited a quadratic relationship with macrophyte level. The greatest catches of bass occurred in the plot with 50% macrophyte cover, and the smallest catches in the plot with no macrophytes (Figure 2). Bass abundance was not different among the experimental plots during autumn in deep water. Too few bass were captured in the spring to determine if abundance differed at that time among macrophyte levels (Table 1).

Largest bass were captured in the experimental plots during the spring, but too few were captured to determine if length differed by depth or macrophyte level. Average length of bass during the fall was greater at 3.0 m than at 1.5 m ($p < 0.001$), and was not related to macrophyte level at 3.0 m (Table 1). At 1.5 m, average length of bass appeared to fit a concave quadratic relationship with macrophyte level; the largest bass were captured in the plots with 0 and 100% macrophyte cover ($p = 0.016$), and smaller bass were captured in plots with intermediate levels of cover (Table 1). However, this relationship was not conclusive. Bass averaged 91 mm in the fall because large numbers of YOY were present at that time, and 250 mm in the spring (Table 1).

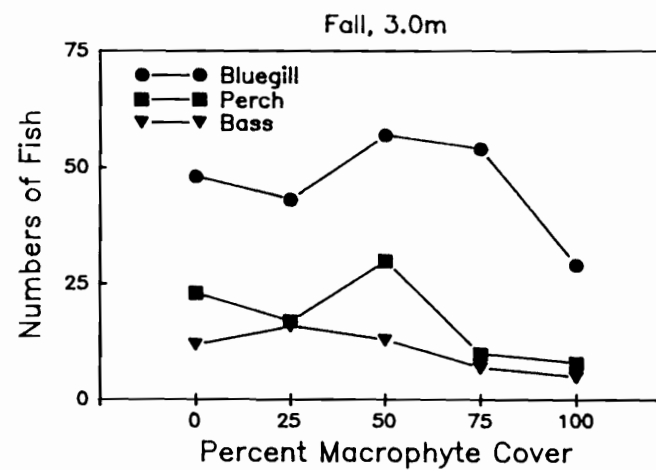
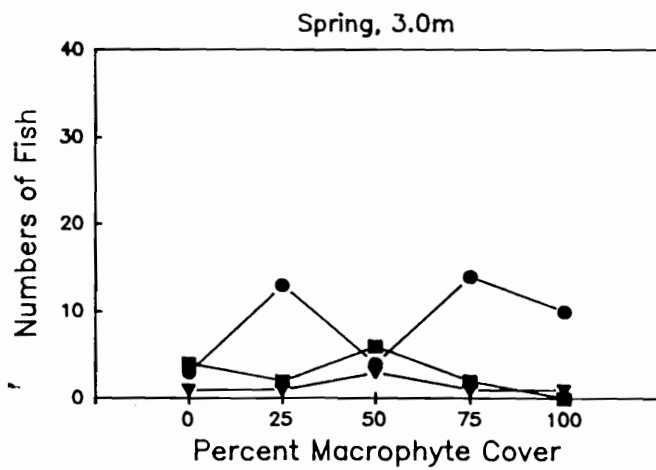
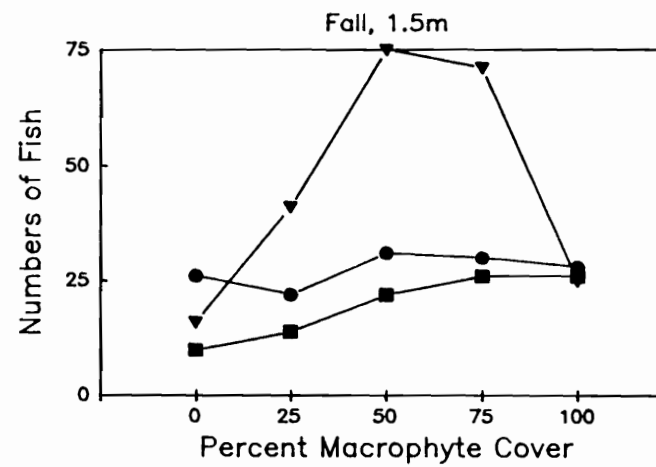
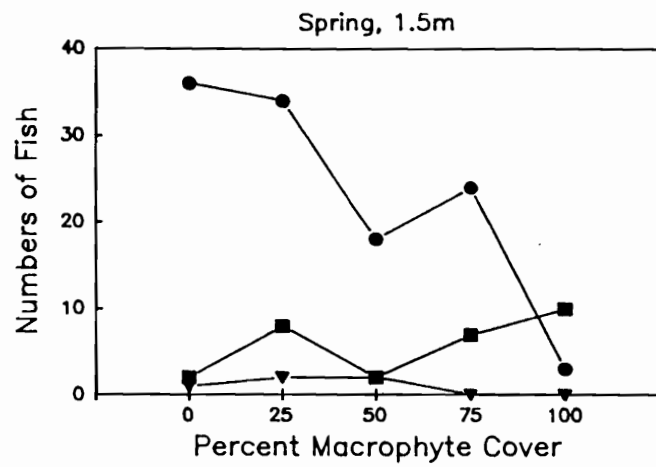


Figure 2. Numbers of fish captured in experimental plots in shallow and deep water during spring and fall.

Table 1. Total numbers and average length of fish captured with electroshock gear, fyke nets and gill nets from experimental plots in Devils Lake.

Season	Depth	Cover	Bluegill		Perch		Bass	
			L	#	L	#	L	#
Fall	1.5	0	120	26	147	10	117	16
		25	92	22	159	14	77	41
		50	99	31	159	22	78	75
		75	98	30	166	25	75	71
		100	105	28	137	26	94	25
	3.0	0	108	48	171	23	164	12
		25	99	43	152	16	114	16
		50	97	57	163	30	138	13
		75	105	54	153	10	142	7
		100	87	29	150	8	73	5
Spring	1.5	0	150	35	179	2	188	1
		25	155	34	164	8	133	2
		50	156	18	173	2	211	2
		75	153	24	159	7	---	0
		100	143	3	170	10	---	0
	3.0	0	156	3	204	4	440	1
		25	141	13	186	2	230	1
		50	154	4	167	6	264	3
		75	142	14	246	2	323	1
		100	154	10	---	0	344	1

During spring, abundance of large bluegill (> 100 mm) in the shallow water experimental plots appeared to decline as macrophyte cover level increased. Bluegill abundance differed among macrophyte levels during the spring in both shallow ($p < 0.001$) and deep water ($p = 0.020$), and during the fall in deep water ($p = 0.032$). During spring, bluegill abundance in the shallow experimental plots was lowest in those plots with the greatest macrophyte cover (Figure 2); whereas 35 bluegill were captured in the plot with no macrophytes, only 3 were captured in the plot with 100% macrophyte cover (Table 1). No trend in bluegill abundance was observed with respect to macrophyte level in the deep water plots in either the spring or the fall (Figure 2), and average length was not different between depths or among percent macrophyte cover. In the spring bluegill were more abundant in deep water than in shallow water (Table 1). Bluegill were larger during spring than during fall ($p < 0.001$), but were more abundant during fall than during spring (Table 1). Bluegill captured in all areas during the fall were generally < 100 mm, or YOY, while bluegill captured in the spring averaged 141-156 mm, or about 2 or 3 years old.

Yellow perch abundance was related to macrophyte level only during the fall in shallow water when perch abundance increased as percentage of macrophyte cover increased (Figure 2). Yellow perch abundance was different among

macrophyte levels in both shallow ($p=0.029$) and deep water ($p=0.001$) in the fall, and in deep water during the spring ($p=0.037$). Yellow perch were more abundant in autumn than in spring, and there was no difference in perch abundance by depth during any season (Table 1). Average length of perch captured in autumn was not different between depths or among levels of macrophyte cover. Average length of perch captured in the spring was not statistically tested because the sample size was small.

Whole Lake Observations

Macrophyte Density

Mean springtime macrophyte density over the entire lake was 764 g/m^3 . Mean springtime macrophyte density varied among the five areas ($p=0.009$), and was highest in area 3 at 1356 g/m^3 , and lowest in area 2 at 448 g/m^3 . Macrophyte density during the summer averaged 951 g/m^3 for the entire lake. Mean summer density was also different among the five areas ($p=0.016$); it was highest in area 3 at 1597 g/m^3 and lowest in area 1 at 576 g/m^3 .

Water Temperature

Mean surface water temperature during the spring was highest in area 5 at $18.8 \text{ }^\circ\text{C}$, and lowest in area 1 at $17.5 \text{ }^\circ\text{C}$ ($p=0.364$). Mean surface water temperature in the summer was highest in area 5 at $22.1 \text{ }^\circ\text{C}$, and lowest in area 3 at $20.0 \text{ }^\circ\text{C}$ ($p=0.002$).

Mean macrophyte density was plotted against mean surface water temperature in the spring and summer for each of the five areas of the lake (Figure 3). However, no trends were evident to suggest that macrophyte density was related to surface water temperature.

Fish Distribution and Abundance in the Entire Lake

Fish Captured in the Spring by Electroshocking

The mean spring electroshock C/f of bass differed among the five areas ($p=0.023$). For all sizes of largemouth bass combined, mean C/f was highest in area 5 (0.0172 bass/s) and lowest in area 1 (0.0072 bass/s). Mean C/f of bass between 100 and 200 mm ranged from 0.0014 in area 1 to 0.0050 in area 5 ($p=0.117$). Bass > 200 mm had C/f's which ranged from 0.0040 in area 1 to 0.0114 in area 4 ($p=0.061$). Most of the bass observed in the littoral region during the spring were spawners larger than 200 mm (Table 2).

The mean spring electroshock C/f of all bass combined and of each of the three size ranges were plotted against both macrophyte density and surface water temperature to determine if either parameter could explain differences in bass distributions. Trends were not evident in C/f plotted against macrophyte density (Figure 4), but C/f of bass of all sizes combined increased with increasing temperature as did C/f for bass > 200 mm (Figure 5).

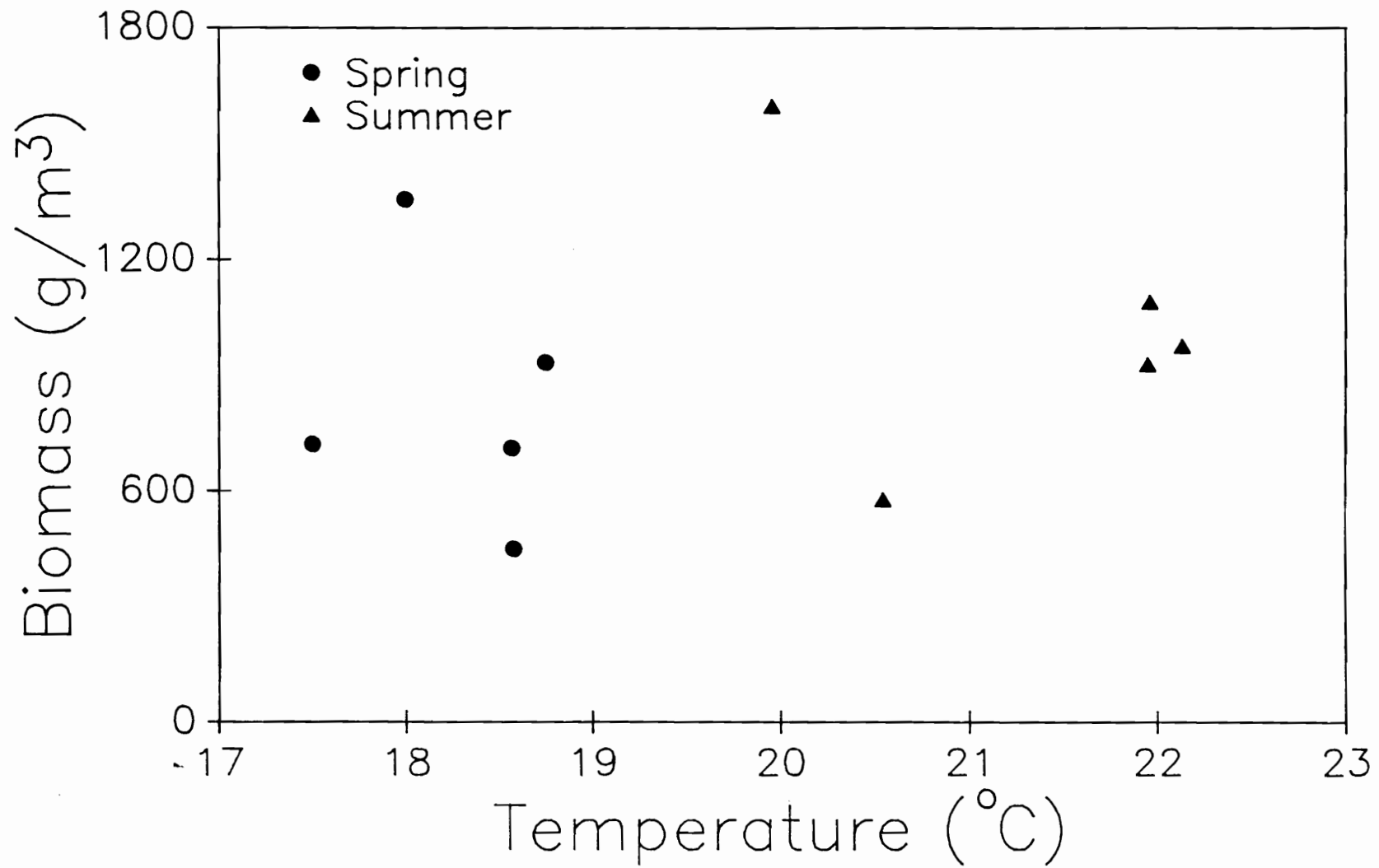


Figure 3. Macrophyte density versus surface water temperature in five areas of Devils Lake.

Table 2. Catch per unit effort for fish of different sizes captured in Devils Lake during 1987.

Largemouth Bass

Electroshock

<u>Month</u>	<u>L<100</u>	<u>100<L<200</u>	<u>L>200</u>
March	0.0017	0.0052	0.0120
April	0.0008	0.0030	0.0104
May	0.0014	0.0036	0.0080
June	0.0043	0.0057	0.0070
July	0.0059	0.0020	0.0030
August	0.0396	0.0077	0.0076
Sept.	0.0137	0.0026	0.0039

Bluegill

Electroshock

Fyke Nets

<u>Month</u>	<u>L<100</u>	<u>L>100</u>	<u>L<100</u>	<u>L>100</u>
March	0.0035	0.0059	0.0833	2.9286
April	0.0065	0.0082	0.0732	2.0244
May	0.0059	0.0076	0.3333	7.3571
June	0.0072	0.0084	0.1905	16.9091
July	0.0011	0.0023	0.4545	17.2059
August	0.0176	0.0066	0.8889	0.2222
Sept.	0.0226	0.0034	-----	-----

Perch

Electroshock

Fyke Nets

<u>Month</u>	<u>L<100</u>	<u>L>100</u>	<u>L<100</u>	<u>L>100</u>
March	0.0002	0.0377	0.0833	14.4286
April	0.0002	0.0633	0.0000	14.7805
May	0.0005	0.0437	0.0000	0.5357
June	0.0002	0.0231	0.0000	0.5909
July	0.0006	0.0091	0.0000	0.5000
August	0.0091	0.0328	0.0000	2.1111
Sept.	0.0052	0.0115	-----	-----

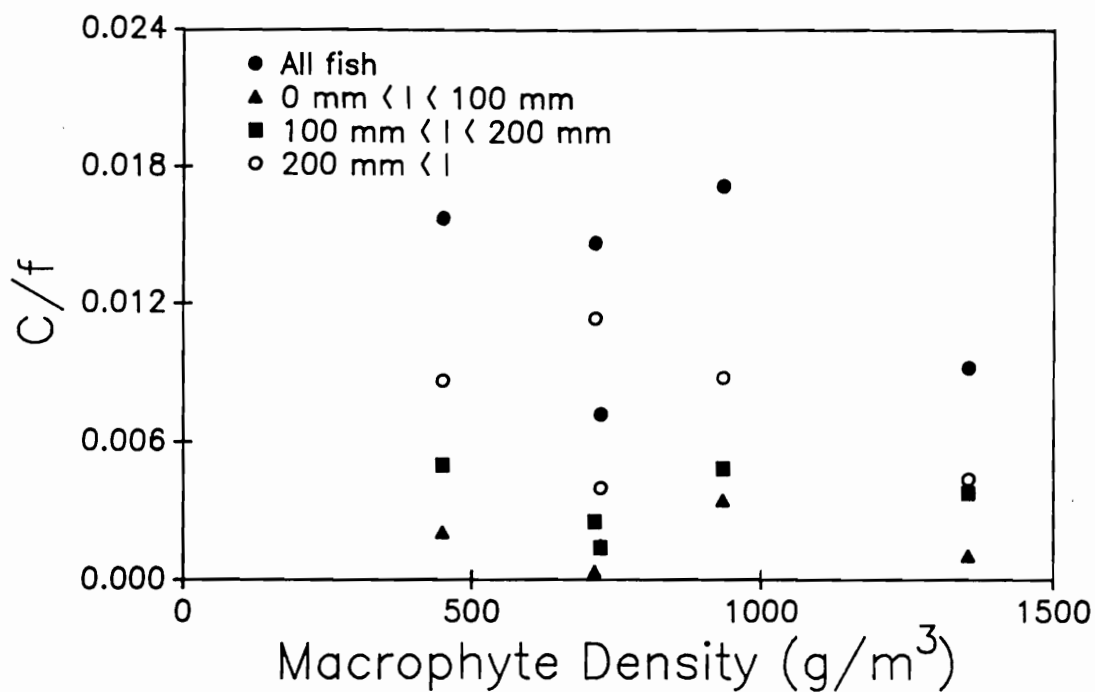


Figure 4. Spring electroshock catch per unit effort (C/f) of largemouth bass versus macrophyte density.

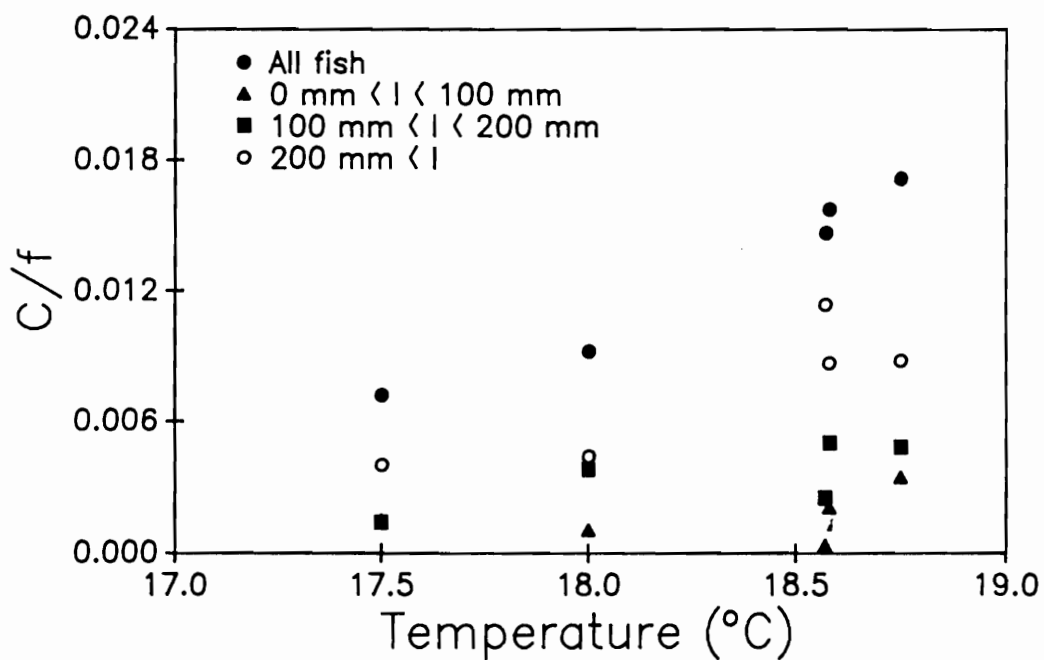


Figure 5. Spring electroshock catch per unit effort (C/f) of largemouth bass versus water temperature.

The mean spring electroshock C/f of all sizes of bluegill differed among the five areas ($p=0.007$). Mean bluegill C/f was highest in area 5 at 0.0202 bluegill/s and lowest in area 1 at 0.0032 bluegill/s. Catch per unit effort of bluegill < 100 also differed among areas ($p=0.101$). Highest C/f of bluegill 100-200 mm occurred in area 5 at 0.0135 bluegill/s, which was more than twice the C/f in any other area ($p=0.003$). No bluegill larger than 200 mm were captured. Plots of bluegill C/f versus water temperature and macrophyte density suggest that bluegill distributions were not related to either parameter (Figures 6 and 7).

Spring electroshock C/f for all sizes of yellow perch was highest in area 3 (0.568 perch/s) and lowest in area 5 (0.210 perch/s) ($p=0.104$). Catch per unit effort for perch 100-200 mm was highest in area 5 (0.014 perch/s) and lowest in area 1 (0.001 perch/s) ($p=0.122$). Spring electroshock C/f of all perch combined and perch 100-200 mm declined as temperature increased (Figure 8). The abundance of perch was not related to macrophyte density (Figure 9).

Fish Captured in the Summer by Electroshocking

The mean C/f of bluegill captured by electroshocking during the summer ranged among areas from 0.012 bluegill/s to 0.068 bluegill/s ($p=0.089$). Most bluegill captured by electroshocking during the summer were < 100 mm (Table 2)

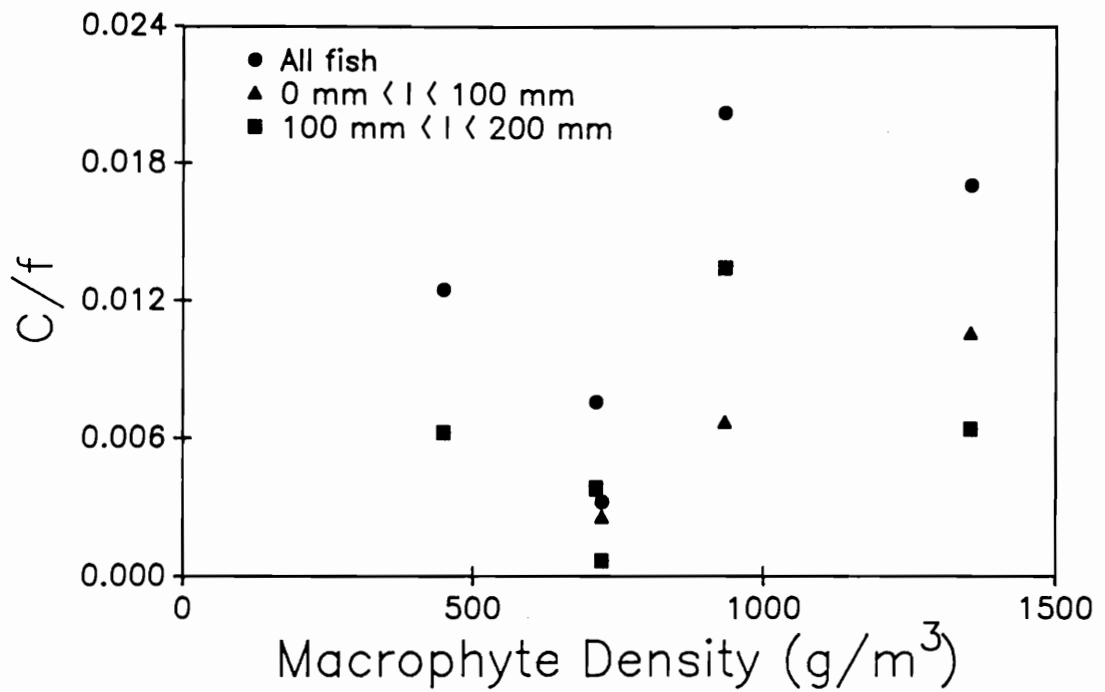


Figure 6. Spring electroshock catch per unit effort (C/f) of bluegill versus macrophyte density.

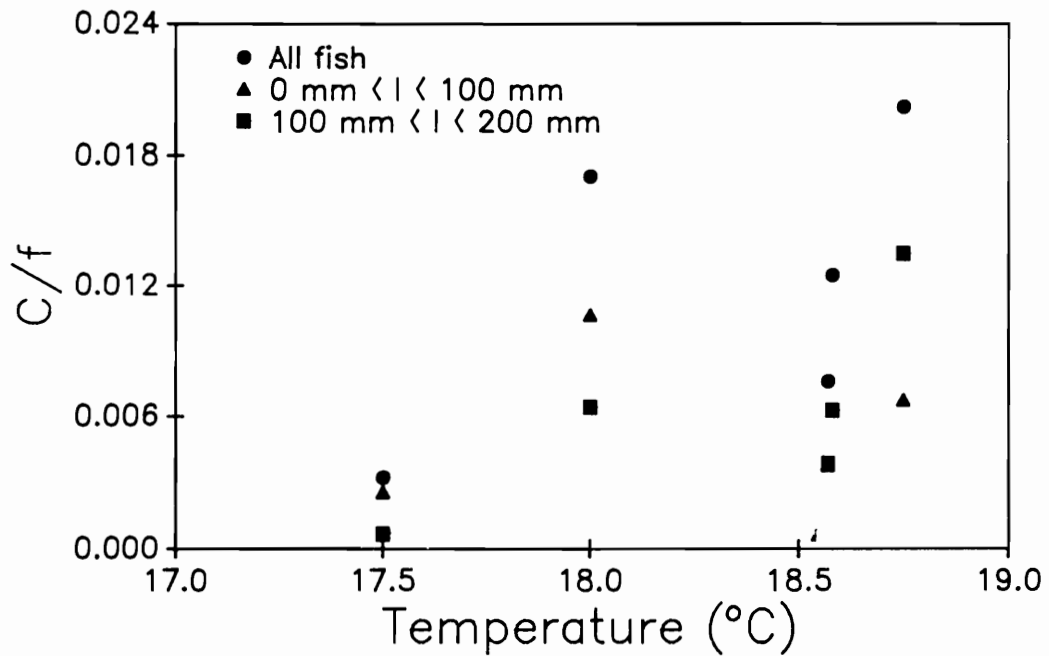


Figure 7. Spring electroshock catch per unit effort (C/f) of bluegill versus water temperature.

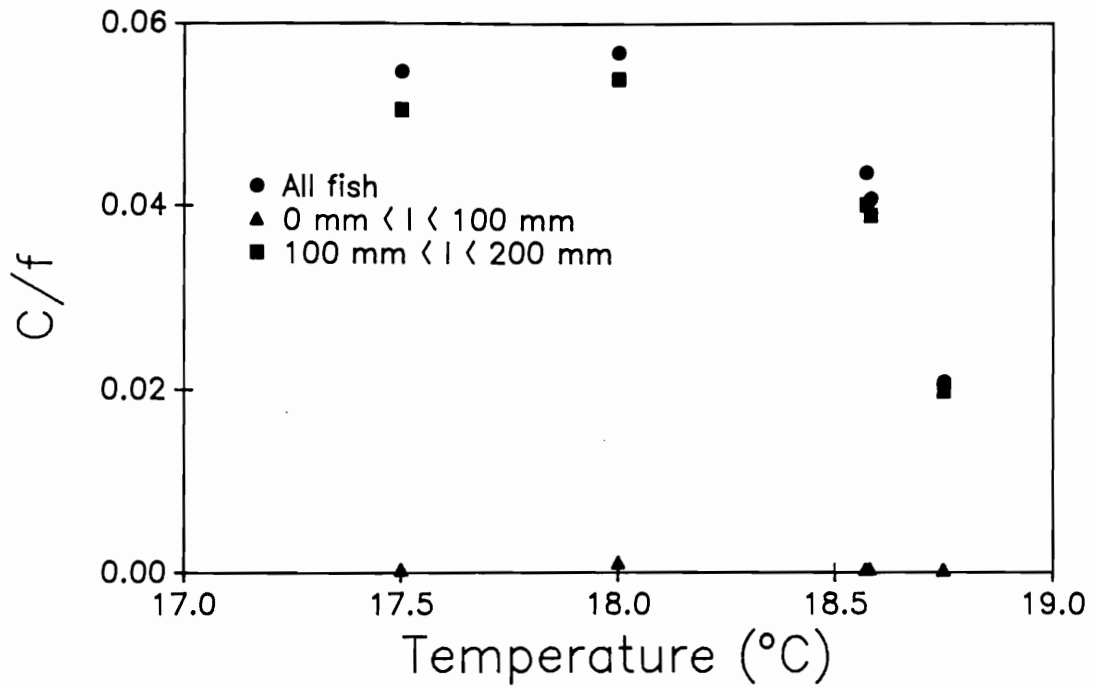


Figure 8. Spring electroshock catch per unit effort (C/f) of yellow perch versus water temperature.

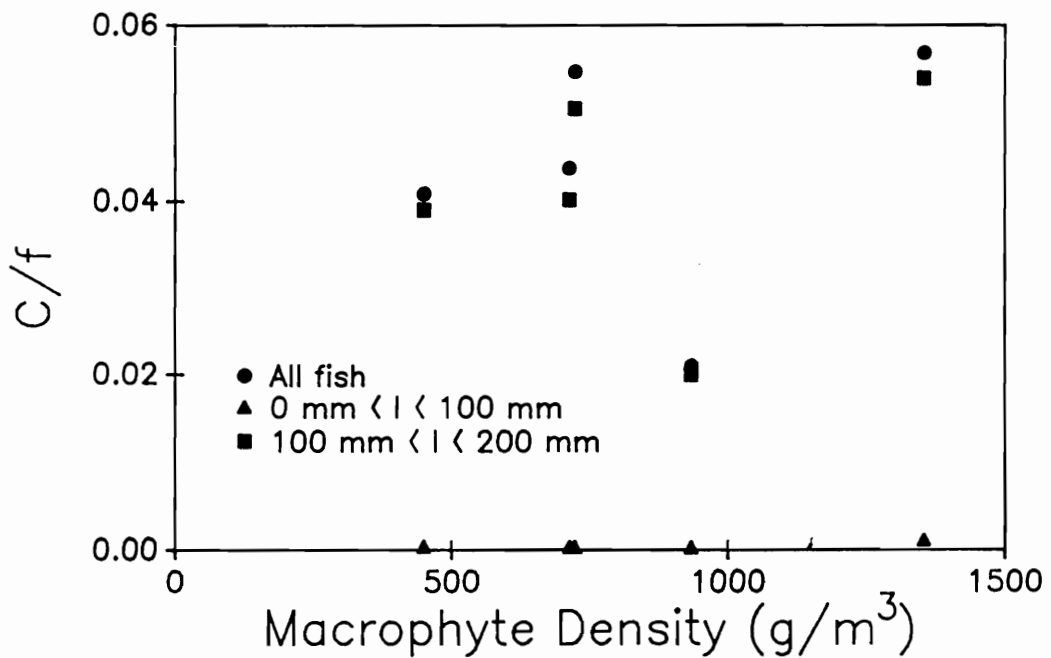


Figure 9. Spring electroshock catch per unit effort (C/f) of yellow perch versus macrophyte density.

and C/f of these fish ranged from 0.0082 in area 2 to 0.0582 in area 4 ($p=0.063$). The abundance of small bluegill was not related to either macrophyte density (Figure 10) or water temperature (Figure 11).

The mean electroshock C/F of yellow perch captured during the summer differed among the five areas, with highest C/f in area 4 at 0.0851 perch/s and lowest in area 3 at 0.0154 perch/s ($p=0.007$). The mean C/f of perch < 100 mm also differed among areas ($p<0.001$). The highest C/f was in area 4 at 0.0305 perch/s and the lowest C/f was in area 3 at 0.0033 perch/s. The mean summer electroshock C/F of perch 100-200 mm ranged from 0.0132 in area 3 to 0.540 perch/s in area 4 ($p=0.050$). The abundance of perch was not related to macrophyte density (Figure 12). The mean summer C/F of all perch combined and perch 100-200 mm appeared to increase with temperature (Figure 13).

Fish Captured by Fyke Nets

Fyke nets were not effective for sampling largemouth bass or yellow perch, but were reasonably effective for sampling bluegill > 100 mm. Few bluegill reach 200 mm and thus fish this large were rarely captured. Springtime fyke net C/f of bluegill 100-200 mm ranged from 1 bluegill/day in area 1 to 51 bluegill/day in area 4 ($p<0.001$). However, mean springtime fyke net C/f of bluegill 100-200 mm was not related to macrophyte density (Figure 14) or temperature (Figure 15).

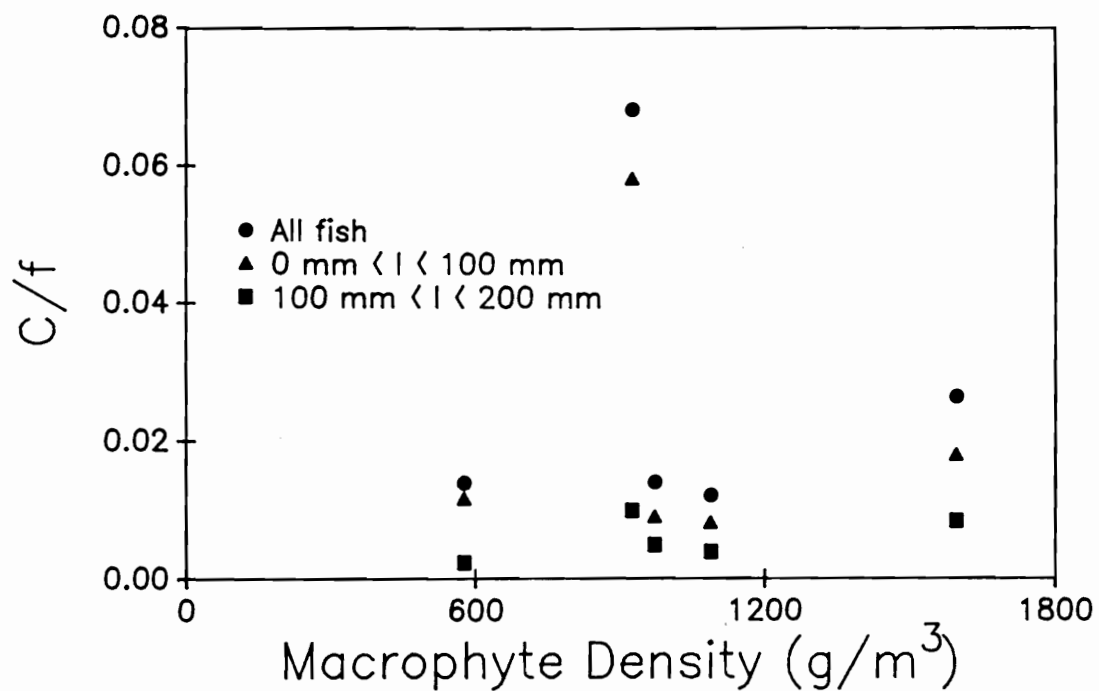


Figure 10. Summer electroshock catch per unit effort (C/f) of bluegill versus macrophyte density.

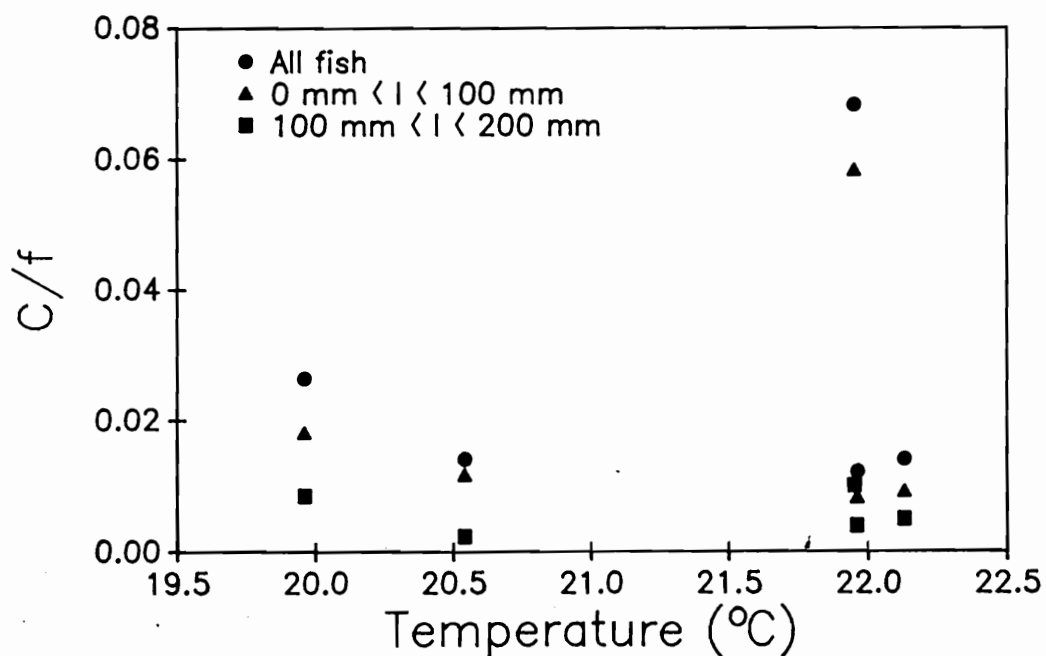


Figure 11. Summer electroshock catch per unit effort (C/f) of bluegill versus water temperature.

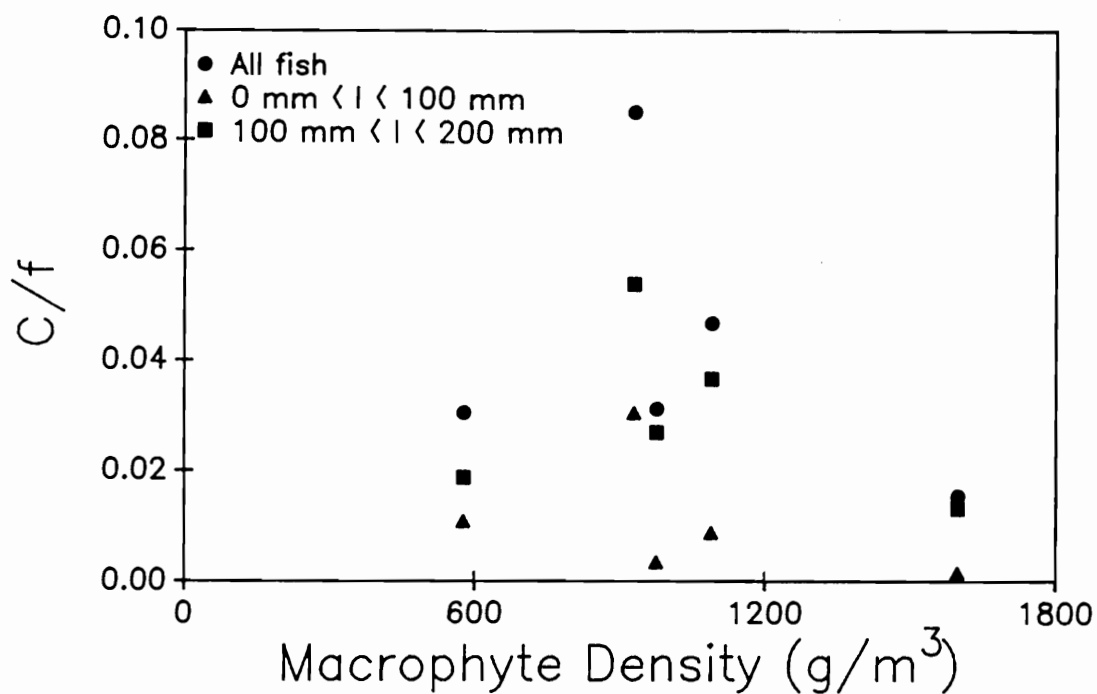


Figure 12. Summer electroshock catch per unit effort (C/f) of yellow perch versus macrophyte density.

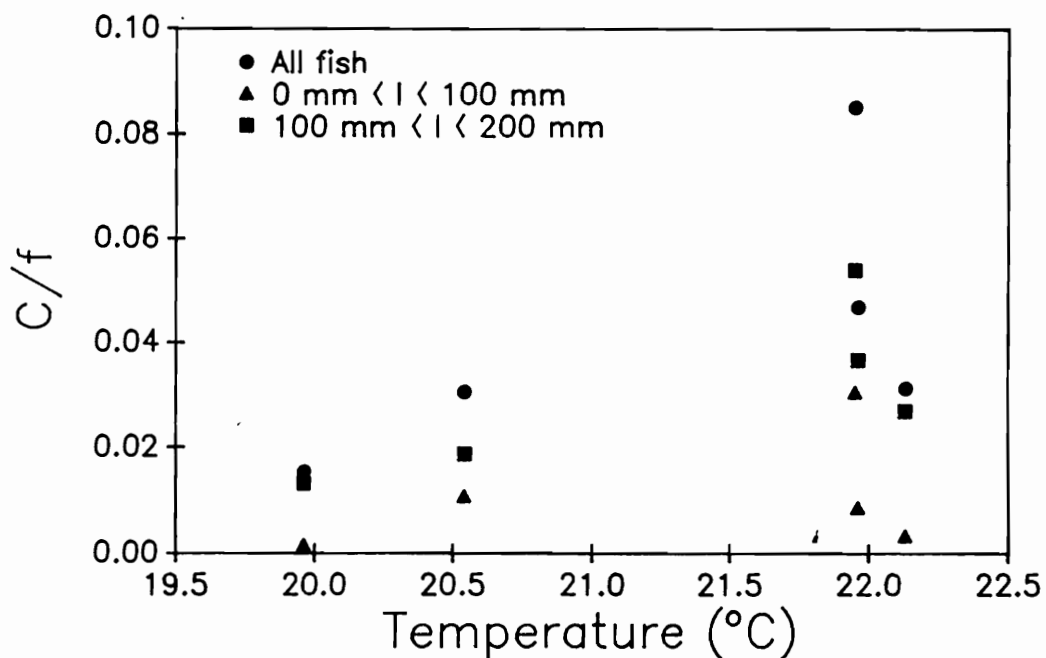


Figure 13. Summer electroshock catch per unit effort (C/f) of yellow perch versus water temperature.

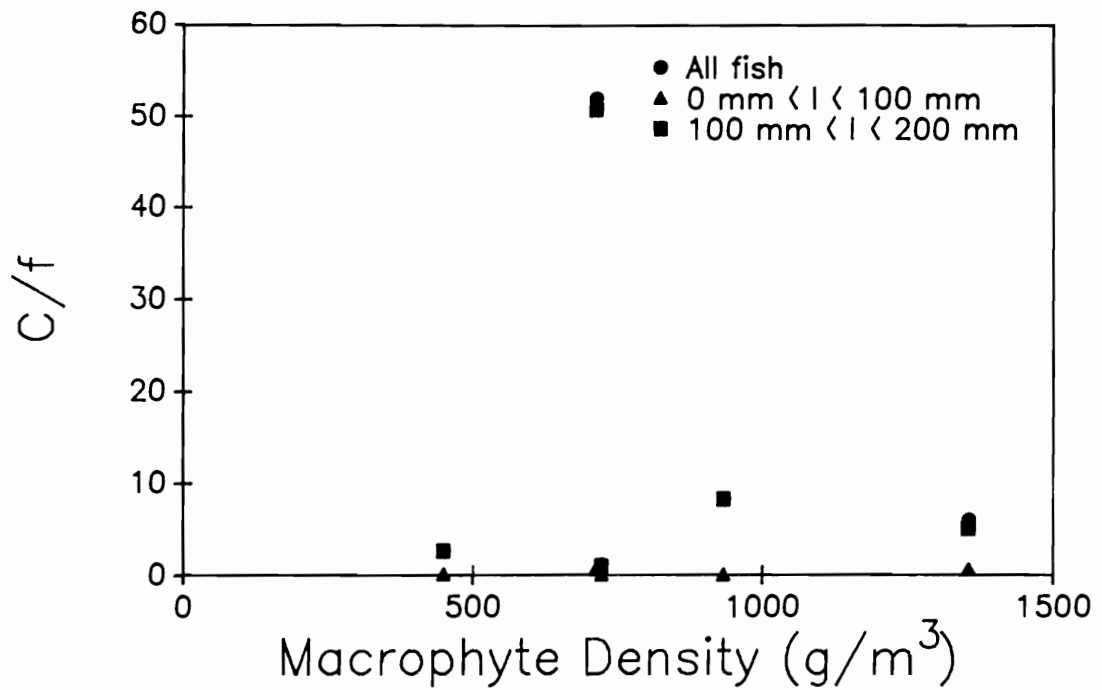


Figure 14. Spring fyke net catch per unit effort (C/f) of bluegill versus macrophyte density.

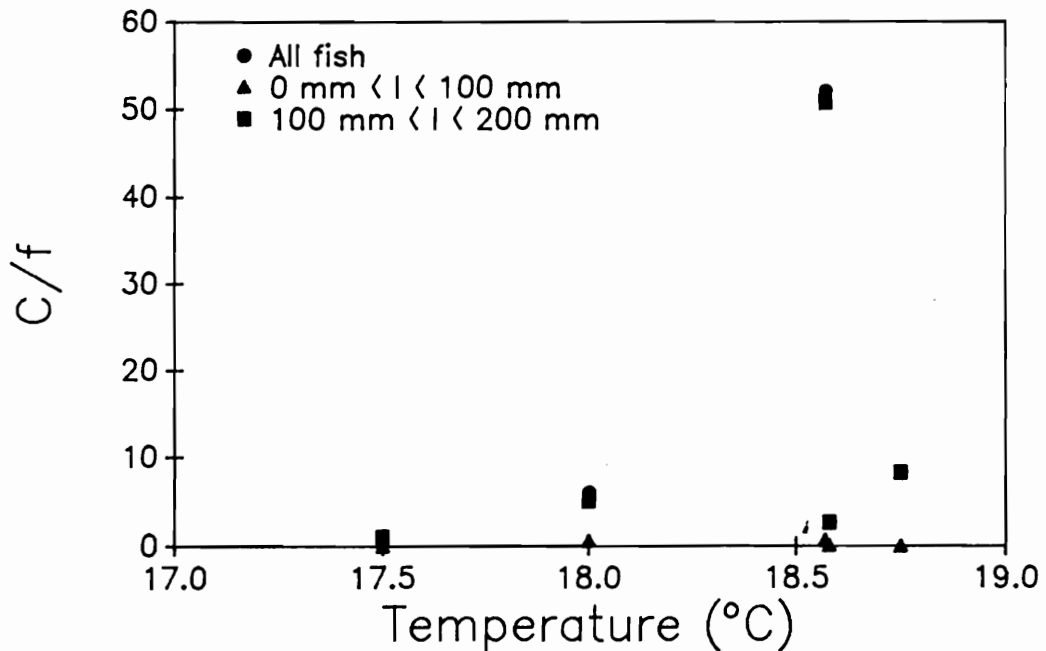


Figure 15. Spring fyke net catch per unit effort (C/f) of bluegill versus water temperature.

DISCUSSION

The density distribution of largemouth bass in Devils Lake did not fit the patterns predicted by the model proposed by Wiley et al. (1984). In the experimental plots, the highest density of bass only occurred at intermediate levels of macrophytes during the fall, and only occurred with small bass (< 100 mm) in shallow water. As with the experimental plots, bass distributions in the lake were not related to macrophyte density, and intermediate macrophyte densities were not preferred. Wiley et al. (1984) concluded that macrophyte density was a good predictor of bass yield based on their data from small experimental ponds in Illinois. The results from my study, however, suggest that the model by Wiley et al. (1984) cannot be applied to lakes in the Pacific Northwest perhaps due to differences in climate, the species composition of macrophytes, fish community structure, or size of the lake.

Electroshock C/f of bass appeared to be related to surface water temperature in the spring although such results are tenuous since the probability level for significant differences in water temperature among the five areas of the lake was only 0.364. Devils Lake is polymictic throughout the summer because the mild marine temperatures preclude strong thermal stratification and the marine winds cause periodic mixing of the water column. These conditions

create transient pockets of warmer water in particular areas. For instance, after a couple of days with minimal wind, surface water temperature varied by 2.4 °C among the five areas. However, after a windy period, water temperature varied by only 0.5 °C among the five areas. The difference in mean water temperature was real and probably affected bass distributions, but temperature changed too frequently to be adequately measured with my sampling design. Miller and Kramer (1971) report that a surface water temperature difference of 0.6 to 1.6 °C among sites was sufficient to cause bass to select certain shorelines or coves over others for spawning. The prevailing winds on Devils Lake originated from the northwest. Areas 4 and 5 at the north end of the lake received less wind because of their orientation, hence water temperature was probably higher in these areas during certain weeks.

If water temperature truly differed among areas, then the differences in abundance among areas as indicated by electroshocking C/f may have been temperature related. Because bass do not feed aggressively while spawning (Heidinger 1976), their distribution during spawning probably would not be related to food abundance. Since bass were more abundant in the areas with the warmest water during the spring, this distribution was probably due to spawning, not feeding requirements. The increase in

accumulated temperature units from these short-term increases in water temperature would be beneficial to bass because their eggs would hatch sooner and thus be less vulnerable to predation.

Bluegill were apparently not restricted to vegetated littoral areas in Devils Lake. Observations within the experimental plots and the lake indicate that most of the bluegill in the littoral region during the spring were mature, prespawning fish; most juvenile bluegill (< 100 mm) were absent from the shoreline littoral zone. Similar results were seen in small, temperate, Michigan lakes, where bluegill leave dense vegetation and move into open water when they are between 50 and 100 mm (Hall and Werner 1977; Werner et al. 1977). However, the absence of small bluegill in the littoral zone is contrary to bluegill distributions in other lakes where largemouth bass were present. Mittlebach (1984) felt that bluegill should feed on Daphnia in limnetic areas to maximize their feeding rate, but the presence of largemouth bass in these small lakes restricted them to dense shoreline vegetation (Mittlebach 1981; Werner et al. 1983a). Since the density of piscivorous yellow perch and largemouth bass in the littoral zone was highest during the spring in Devils Lake, small bluegill probably stayed in the limnetic zone to feed on zooplankton while minimizing their exposure to predators.

The distribution of bluegill in Devils Lake shifted during the summer as foraging opportunities and the distribution of predators changed. Small bluegill (<100 mm) became more abundant in the littoral zone during the summer after perch and many of the bass had left this area, but abundance of these small bluegill was not related to macrophyte density. Thiesfeld et al. (1989) suggested that YOY bluegill in Devils Lake recruited into the electroshock fishery during August and September, and as a result, C/f of bluegill < 100 mm increased at that time. The fact that so few age 1 bluegill were captured nearshore in the summer indicates that these small bluegill probably remained in the limnetic zone. Adult bluegill (> 100 mm) migrated to the littoral zone to spawn during June and July when densities of large bass and perch in littoral areas were less than half the density of these same bass and perch during March and April. Their onshore movement after piscivore densities dropped probably reduced their vulnerability to predation, although they were less vulnerable than younger year classes. Large bluegill were not selecting habitats based on macrophyte level, probably because of their low vulnerability to predators.

In the fall, bass and bluegill < 100 mm were more abundant in experimental plots with intermediate levels of macrophytes which was different than expected from previous

research. Mittlebach (1981) and Werner et al. (1983a) suggest that if the risk of predation is high in the littoral area, bluegill should inhabit the densest macrophyte beds. Small bass and bluegill in Devils Lake were found in low and intermediate levels of macrophytes during the fall, where the risk of predation was more prevalent (Savino and Stein (1982). Perhaps there are advantages from foraging in habitats with medium macrophyte densities for insects and cladocerans, their major food groups (Carlander 1977), that are similar to the advantages incurred by larger fish when they forage in habitats with medium density structure.

Bluegill in Devils Lake utilized macrophytes differently than described for other lakes perhaps because the macrophyte species composition, distribution and densities were different. Research by Werner et al. (1983a) determined the influence of predators in small ponds on the utilization by bluegill of a 3 m wide border of cattails (Typha spp.) when all other macrophytes had been removed. Werner et al. (1983b) used the same ponds to conduct their research on optimal foraging by bluegill. Hall and Werner (1977) described Lawrence Lake as covered almost exclusively with a dense littoral stand of Scirpus subterminalis about 0.5 m tall. Structure in these environments was restricted to shoreline areas. In Devils Lake aquatic macrophytes cover approximately 55% of the lake bottom (Pauley et al. 1988)

including much of the limnetic zone, which greatly increases the amount of edges and pockets for valuable fish habitat. In Devils Lake, bluegill were not restricted to a small patch of structure in the littoral zone, but were free to utilize all habitats with macrophytes because refuge from predators was always available. Therefore, bluegill could forage in the limnetic zone as predicted by Mittlebach (1984), even though predators were present which should have restricted bluegill to nearshore vegetation (Mittlebach 1981; Werner et al. 1983a). Bass could not forage optimally in intermediate levels of macrophyte cover if prey were not concentrated, because the encounter rate of prey would be low.

While a relationship between yellow perch abundance and macrophytes has not been described in the literature, their distribution should be similar to that of bluegill, because most perch in Devils Lake are < 200 mm and potentially vulnerable to bass predation for most of their life. Perch abundance during the fall in the shallow water experimental plots increased as macrophyte level increased, and this was the only time I observed an apparant linear relationship between prey density and macrophyte density, This was the relationship predicted between prey fish and structural complexity by Crowder and Cooper (1979), and is similar to the relationship between prey fish production and macrophyte

density developed by Wiley et al. (1984) for Illinois ponds. However, perch abundance over the entire lake was not related to macrophyte density. Instead, surface water temperature appeared to be a better predictor of perch abundance. Scott and Crossman (1973) report that perch prefer a temperature range of 20 to 24 °C. The highest temperature recorded during my study was 22 °C. Perhaps perch seek out spawning areas with the coolest water temperature in the spring. These cooler areas had fewer bass and thus lower potential for predation mortality. As bass density in the littoral zone declined during the summer, perch could seek out habitats or areas with water temperatures closer to their optimum.

My research has suggested that temperature might influence the distribution patterns of perch and bass, and that macrophyte density might influence distribution patterns of small bass and bluegill under very specific conditions. However, several relationships predicted by other research did not apply to the fish populations in Devils Lake. Inadequacies in the sampling design might explain why some relationships between fish density and macrophyte density were not found. Macrophyte density often changed within any individual quadrat. Also, within a quadrat, fish often formed dense aggregations in small areas such as near docks, submerged logs, or small patches of macrophytes. The size of the quadrats was too large relative

to the spatial heterogeneity of fish and macrophyte densities; therefore, the sampling design was not sensitive enough to accurately measure the exact habitat occupied by the fish. A better sampling design could be achieved by establishing four or five small and homogenous habitats with increasing densities of macrophytes, analogous to the experimental plots used in this study, but larger. These areas would be sampled every third or fourth day for perhaps two weeks, and four or five macrophyte samples would be collected from each homogenous habitat during one day.

Woody structure might have influenced the distributions of fish in Devils Lake, but this source of structure was not measured. Devils Lake has many fallen trees in the water and numerous docks in various stages of deterioration. Woody structures were usually associated with the best habitat for capturing adult bass while electroshocking, and the amount of woody structure might have influenced the abundance of bass in a quadrat. However, the amount of woody structure in each quadrat was not quantified in the sampling design used for this study. It appears that no research has examined the relationship between woody structure and macrophytes, or how these two elements interact to effect predator and prey distributions. While woody structure is preferred by bass, its value as habitat might increase as macrophyte density decreases.

Prediction of fish yields has been a concern of fish managers for many years. Recent estimates of general fish yield are based on one or two predictor variables because other variables were not measured, or the purpose of the research was to determine the single best predictor. Oglesby (1977) demonstrated that chlorophyll a (mg/m^3) predicted fish yield ($\text{g dry wt.}/\text{m}^2$) better than annual primary production and the morphoedaphic index (MEI). Hanson and Leggett (1982) found that total phosphorous concentration and macrobenthos density/mean depth were adequate predictors of fish yield (kg/ha), and that both indices were stronger predictors than MEI, total dissolved solids or mean depth. Jones and Hoyer (1982) found that annual harvest (kg/ha) of sportfish correlated better with chlorophyll a (mg/m^3) than with total phosphorous (mg/m^3), alkalinity ($\text{mg}/\text{l CaCO}_3$), or MEI. Durocher et al. (1984) found a positive correlation between percent coverage of macrophytes and standing crop (kg/ha) of largemouth bass, but Hoyer et al. (1985) felt that chlorophyll a was as good a predictor as macrophyte cover, even though macrophyte cover had a higher correlation coefficient with standing crop of bass.

Devils Lake provided an opportunity to determine if fish density varied with macrophyte density, and if so, were these patterns comparable to those for centrarchids elsewhere (e.g., Crowder and Cooper 1979, Wiley et al. 1984). By analyzing the distribution of fishes within a

single body of water, the problems associated with multiple lake correlations might be avoided. In the latter, the many factors effecting abundance such as depth, total dissolved solids, total phosphorous, chlorophyll a and secchi disk transparency can interact in complex ways and make analysis difficult.

Results of this study show that distributions of bass, perch, and bluegill vary seasonally in Devils Lake; and that care must be taken to sample characteristics of the fish and macrophyte community (e.g. density, species composition, size composition) at the correct times of the year. Obviously much research is needed to determine when significant changes in these characteristics occur so that sampling can be allocated accordingly. This research showed that macrophytes and temperature were two variables which helped explain fish distributions in Devils Lake. However, other variables should be measured as well to predict fish distributions and yield elsewhere.

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