Effects of Substrate and Time of Day on Fish Abundance in Two Upper Peninsula Lakes

Mia L. Stephen
November 1, 2002

INTRODUCTION

There is a good deal of literature that exists on the ecological importance of structure in aquatic habitats (France 1997). Structurally complex habitats may reduce predation rates by decreasing encounter rates between predator and prey, or by providing efficient prey refuges (Savino and Stein 1989). Increased structure may change the outcome of interspecific competition by favoring certain foraging strategies (Persson 1991). In general, the foraging efficiency of mobile predators is inversely related to the degree of structural complexity, and is due to decreased predator vision, increased possibility for prey to hide, and negative effects on predator mobility (Anderson 1984). Anderson (1984) also found, in ambush predators, an initial increase in foraging efficiency with increased structure, but a decrease at high levels of structural complexity.

This study is concerned with two kinds of structure in the littoral zone of North temperate lakes: aquatic macrophytes and woody debris.

Macrophytes are submerged aquatic vegetation that contribute to an energetic base for higher trophic levels (Randall et al. 1996). They serve as one source of oxygen within the lake, which is utilized by aquatic animals, other plants, and bacteria and decomposers (Eddy 1947). Littoral macrophytes support epiphytic algae and macroinvertebrates, and may provide refuge for large pelagic zooplankton (Lauridsen and Lodge 1996) and small fish (Cole 1994). In some lake systems, a positive relationship between macrophyte density and fish abundance has been identified (Randall et al. 1996). Small fish, many of which are zooplanktivores, use littoral habitats as daytime refuges from piscivores (Venugopal and Winfield 1993). At high densities, macrophytes tend to inhibit predatory fish's foraging activity (Lau and Lane 2001). In a study of macrophyte dominated littoral zones, Turner and Mittlebach (1990) showed there was no significant mortality on bluegill sunfish by largemouth bass. Low macrophyte densities do not provide sufficient refuge for prey populations (i.e. invertebrates, planktivorous fish) to persist under predation pressure (Lau & Lane 2001). Randall et al. (1996) also suggests that macrophyte density has a negative relationship with fish size. Presumably, this trend is related to the juvenile and small planktivore use of macrophytes as refuge, and the inability of larger fish to make a way into dense stands.

Studies on the ecological significance of woody debris have largely focused on lotic systems (France 1997). Despite this paucity of formal investigation, in some areas woody debris is routinely added to lakes for fish refuge and spawning sites (Illinois Parks and Recreation 1992). Many littoral macroinvertebrates also occupy woody debris, probably for its use as either a biofilm substrate or a predation refuge (France 1997).

This study looks at the habitat use of fish in a low-density versus a high-density macrophyte lake. Habitats were categorized by substrate, i.e. vegetation (macrophytes), open sand, or woody debris. Fish use of this habitat was determined from visual counts. We expected a differential usage of substrate, according to structure, within each lake, and differential usage of substrate between lakes, as well. In the low-density lake, we expected lower fish abundance, in general, and perhaps a forced redistribution onto less suitable substrates. Godin (1997) has shown that loss of habitat due to macrophyte destruction may cause a displacement of fish populations to less ideal lake habitat. It is possible that some fish species have been extirpated if they were unable to compensate for habitat and food losses. We also expected a difference in size structure between the two lakes. Specifically, without the refuge provided by macrophyte stands, predators are able to forage on all fish size-classes. This has been shown to potentially result in the extirpation of small-bodied fish (MacRae & Jackson 2000).

MATERIALS AND METHODS

Two lakes were selected for this study: (1) Crampton Lake on the UNDERC property, the high-density macrophyte lake, and (2) Lake Ottawa in the Ottawa National Forest, the low-density macrophyte lake. Lake descriptions are summarized in Table 1.

Three distinct littoral substrates are present in each lake: vegetated, open sand, and woody debris.

In both the low and high-density lakes, two 20 meter transects were selected in each of the three substrate types. Transects were preferentially placed in areas of high substrate homogeneity. The 20 m transect length was dictated by the limited length of naturally occurring patches of vegetation and woody debris. These substrate zones were identified based upon preliminary snorkeling of the lake perimeter, and unpublished data provided by Kreps and Rosenthal (*personal communication* 2002). For each transect, vegetation and woody debris were quantified in order to characterize the structure. The transects were divided into 4-meter intervals and vegetation was sub-sampled at a random location within each interval. A half-meter square quadrat was used to count number of stems. Percent cover was also estimated within the quadrat. Mean plant height was determined from five stem height measurements per quadrat, selected randomly. The data from the intervals were then averaged across each transect. Woody debris was sub-sampled at a random location within each interval and classified according to type (chips, branch, bole, brush), diameter, and degree of embeddedness (suspended, lying on the lake bottom, or embedded in sediment). These data are summarized in Table 2.

Observations were conducted in late June and July within two time periods: dawn/dusk and midday. An observer equipped with snorkel, fins, and a clipboard slowly swam the length of the transect. All transects were swum along a depth contour of 1 to 2 meters and demarcated with underwater flags at 4 meter intervals, to maintain a consistent line of sight and travel. Any fish swimming within the snorkeler's wingspan (1.5 m) was included in a tally of number, species, and size class. Only one snorkeler (Mia L. Stephen) conducted all surveys. For the purposes of this study, only two size classes were used: < 8 cm and > 8 cm. In the remainder of the paper, the former size class will be referred to as "prey" and the latter will be referred to as "non-prey." We will use "non-prey" rather than "predators" because not all > 8 cm fish are piscivorous (e.g. bluegill). When fish were encountered in schools (i.e. greater than 20 individuals swimming in close proximity, rendering an underwater count unreliable), individuals were not counted, but rather noted as a "school." Fish of the same species that were observed more than 1 meter away from the school were counted as individuals. For the purposes of data analysis, individuals and schools were handled separately, since their units are not comparable.

The values obtained from repeated observation periods in individual transects were averaged to improve the accuracy of the count. Each transect then served as one replicate, resulting in two replicates per substrate. Due to this low replication, data analysis was limited.

We performed the following G-tests ($\alpha=0.05$) to determine dependence between pairs of variables: lake vs. substrate, time vs. substrate, and lake vs. time. Results are summarized in Table 3. Expected values were derived from the data. The total number of fish observed was divided equally across factors, to simulate the null hypothesis result. Observed G-values greater than critical G-values indicate that the effects of the two variables upon fish abundance are not independent. That is to say, the observed abundances are not random with respect to the variables compared.

RESULTS

Electroshocking data has identified the fish assemblage in Lake Ottawa to include smallmouth bass (*Micropterus dolomieu),* yellow perch (*Perca flavescens),* walleye (*Stizostedion vitreum),* rock bass (*Ambloplites rupestris),* white suckers (*Catostomus commersoni),* northern pike (*Esox lucius),* and lake trout (*Salmo trutta lacustris*) (*unpublished data,* Rosenthal et al. 2002). Snorkeling data, however, revealed a predominance of smallmouth bass, yellow perch, and only the occasional northern pike and young walleye. No electroshocking data was available for Crampton, but the predominant observed species were largemouth bass (*Micropterus salmoides),* bluegill (*Lepomis macrochirus),* and the occasional yellow perch. Ottawa was characterized by smallmouth bass and schools of perch, while Crampton was characterized by largemouth bass and schools of bluegill. Fish abundance was strikingly different between the two lakes. Corrected for the number of observation periods, the average "whole-lake" (this term will be used to refer to the sum of the three transect averages, so it does not literally refer to the fish abundance in the entire lake) abundance of individual fish observed in Ottawa was a mere 5.41, compared to 38 in Crampton. Similarly, the average "whole-lake" abundance of schools observed in Ottawa was 0.684, compared to 4.75 in Crampton. From these data, we can say little more than that the abundance of individual fish and schools in Ottawa appears lower than in Crampton.

Lake and substrate:

Given the large difference in overall abundance, we normalized the data for each lake in order to compare abundances among substrates. Normalizing the data consisted of dividing each abundance value by the total number of fish observed in the lake.

A G-test indicated that lake and substrate type interact non-randomly. In other words, the abundance of individuals varied with substrate type, lake sampled, or some interaction between those two factors. Looking at Fig. 1A, we can see that the differences occur in the vegetated and open substrates. Vegetation in Ottawa, compared to that of Crampton, supports a greater relative abundance of individuals. Ottawa's open areas, as expected, are devoid of fish. Open areas in Crampton can support a low relative abundance of individuals.

The same G-test performed for school abundance revealed an independence between lake and substrate type, meaning there was no non-random effect on school abundance. The distribution pattern in Crampton resembles its distribution pattern of individuals (Fig. 1B). All observed schools in Ottawa were found in vegetated transects.

Time and substrate:

A G-test on time versus substrate for individuals indicated a non-random interaction (Table 3). In other words, either the abundance of individuals varied with time, substrate, or some interaction between the two. Looking at Figure 2A, we can see that the vegetated substrate supports a greater abundance of individual fish in the mid-day hours. The same is true of the open substrate. Abundance did not vary with time of day in the wood transects.

The same G-test performed on school abundances also indicated a non-random interaction. Figure 2B shows a large increase in abundance in the vegetated transects in the mid-day hours, and a complete evacuation of the open transects at this time.

Lake and time:

A G-test on lake versus time data indicated that there was no dependence between the two factors. The total number of individuals in each lake was random with respect to time. In other words, the time factor alone was not sufficient to produce significant differences in "whole-lake" abundance.

Size and abundance:

In Crampton, the "whole-lake" abundance of non-prey was greater than the abundance of prey individuals. This normalized Crampton non-prey abundance was also greater than the non-prey abundance in Ottawa (Fig. 3). Ottawa had a greater abundance of prey than non-prey individuals.

Lake, substrate, and time:

In Ottawa, more individuals utilized the vegetated transects at dawn/dusk than mid-day (Fig. 4A). Far more schools, on the other hand, utilized the vegetated transects in mid-day hours (Fig. 4B). No schools were found on open transects in either lake at mid-day hours.

Lake, substrate, and size:

A greater abundance of prey-sized individuals occupied vegetated transects in Ottawa than in Crampton (Fig. 5A). In Crampton, a greater abundance of non-prey-sized individuals occupied vegetated transects than prey-sized individuals. All schools in

Ottawa were prey-sized (Fig. 5B). Only a small portion of Crampton's schools were prey-sized, occupying only the vegetated transects.

DISCUSSION

Though Ottawa and Crampton were similar in water clarity and littoral species diversity, several important differences should be noted. Ottawa was a large lake that experienced a good deal of human use including fishing, water skiing, and power boating. Campsites, public access, a public beach, and a large pier were present along the shoreline. The littoral areas experienced frequent disturbance, and woody debris can be removed by campers or hikers. Crampton, on the other hand, was a small lake that experienced relatively little activity. There is no public access and the shoreline is completely undeveloped, aside from one access point.

There were notable differences between lake transects as well. The structure of the vegetation was distinct in each lake. Ottawa contained macrophytes with broad leaves, 20 to 30 cm tall. Crampton's vegetation was of a similar percent cover, but 10 to 20 cm taller, with narrower leaves and dramatically more stems per 0.5 m^2 (refer to Table 4). If we take percent cover to be the primary index of density, however, Ottawa and Crampton's vegetated transects can be considered structurally equivalent. The open sand transects in Ottawa supported no vegetation. There were no such barren stretches in Crampton, but the vegetation in those open transects was less than 3 cm high and less than 7% cover. The amount and type of wood in each of the lakes was similar, but the wood transects in Crampton also contained some vegetation. Relative to the rest of the lake, however, the vegetation in the woody transects was nearly as minimal as in open sand.

Upon analysis of the data, we found that many observed trends were not significant. Low replication substantially limited our statistical power. What follows is a discussion of the few differences that were statistically significant.

Overall abundance:

We expected lower abundance of fish in Ottawa, the low-density macrophyte lake. The "whole-lake" abundance data affirmed this trend, but cannot speak to causality.

The low and high-density lake were different in pH and presence of rusty crayfish (*Orconectes rusticus*). It is possible that Crampton's low pH, relative to Ottawa, could have directly affected fish abundance. But we would expect lower abundances with lower pH, and since Crampton actually had higher observed abundances, any impact of pH in this study is overwhelmed by other factors. The presence of rusty crayfish in Ottawa is likely to have impacted fish abundance indirectly, through alteration of habitat. In general, the consumptive and non-consumptive activity of the rusty crayfish contributes to a reduction in macrophyte density (Lodge et al. 2000; Nystrom et al. 1999). In effect, this is a reduction in habitat for herbivorous or small fish (Crowder & Cooper 1982) or a displacement of fish populations to less ideal habitat (Godin 1997). One reasonable explanation for the low fish abundance in Ottawa, relative to Crampton, is such rusty-induced reduction in habitat.

But vegetation is not the only useful structure in a lake. Woody debris can function as refugia for small fish (Godin 1997). So in the face of macrophyte destruction, we might expect small fish to (1) concentrate in remaining vegetation patches or (2) increasingly utilize areas with woody debris. If these adjustments were totally efficient, we wouldn't expect a change in "whole-lake" abundance, just a change in distribution within the lake. Because there was no available abundance data pre-invasion, we could not draw any direct conclusions. If (1) or (2) were the case, we would expect to see at least similar whole-lake abundances between Ottawa and Crampton, with higher abundances of fish in Ottawa's vegetated and woody areas. Thus, given the disparity in surface area between Ottawa and Crampton, the very low abundance in the much larger, low-density lake probably indicates either displacement to deeper waters, or an increase in mortality for small or herbivorous fish.

Effects of substrate:

As noted earlier, vegetated transects in Ottawa, as compared to those of Crampton, supported a greater abundance of individuals and schools relative to the open or woody transects (Fig. 1). In fact, the only observed substrate that supported schooling fish in Ottawa was vegetation. Should rusty-induced decline in macrophyte density have occurred, we have hypothesized that there would be no suitable littoral habitat for schooling fish. Crampton lacked a difference in abundance between the vegetated and woody transects. Perhaps this can be accounted for with the heterogeneity of each area (i.e. the vegetated transects were not without wood, and the woody transects were not without vegetation). The co-occurrence of these two types of structure may have masked the relative importance of each. It is of great interest that minimal vegetation (of similar percent cover as open areas), interspersed with woody debris, supported similar abundances of individuals and schools as heavily vegetated areas with little wood. This may shed some light on rehabilitation efforts in low macrophyte or rusty-infested lakes. Current methods for wide-scale revegetation will likely require huge amounts of time and labor. And, as discussed earlier, the addition of only wood may be easy but unsuccessful at restoring schooling fish populations. But the abundance data from Crampton indicated that the efficacy of added woody debris may be greatly enhanced by the presence of even minimal vegetation.

Effects of time:

Though it was not a primary focus of this study, the effect of time of day on fish distribution was of interest. In Crampton, there was a significantly greater usage of vegetated habitat during the mid-day hours than in the dawn/dusk portion of the day. The same is true of schools in both Ottawa and Crampton. We hypothesize that since (1) mid-day light is the brightest of the day, (2) fish are visual feeders, (3) vegetation is common refugia, and (4) predators must locate themselves near their food source, the prey species hid in areas of macrophyte density and their predators followed. In other words, the vegetative cover was more necessary for prey species at times of the day when they were most detectable. Even with camouflage, the prey species still attracted predators to the vicinity of their refuge, which thereby increased the abundance of both schools and individuals in vegetated patches in the mid-day hours.

We also looked at time effects across the whole-lake. The G-test of time versus lake, in failing to disprove the null hypothesis, was of interest. When all the substrates were lumped together, there was no difference in abundance with time of sampling. But the previous paragraph just highlighted a significant difference in usage of vegetation with time. This indicates that time of day influences the distribution of fish across the substrate types, but not the total number of fish present in the littoral zone.

Effects on fish size classes:

We should also say a word about the patterns found in size class in the two lakes. There was a significantly larger abundance of non-prey individuals and schools in vegetation in Crampton than of prey-sized individuals or schools. On the other hand, Ottawa supported no non-prey-sized schools. At first glance, this data seems to contradict out expectations. We had hypothesized that the loss of habitat (due to rusty crayfish induced loss of macrophytes) would not support small or herbivorous fish, yet there were more prey-sized individuals in Ottawa than Crampton. The lack of non-prey sized schools in Ottawa may help to explain such unexpected results. If there were no schooling fish larger than 8 cm, this may have indicated that small fish did not survive long enough to grow to the next size class. In fact, with the loss of macrophyte density might also come a loss in food resources. As mentioned earlier, vegetation supports macroinvertebrates, which is a dietary component of many-prey sized fish. One possible result of this loss in food resources is a reduction in fish abundance or lower growth rates. It is possible, however, that once they reached a non-prey size, the fish in Ottawa no longer maintained the school structure. If this were the case with Ottawa's yellow perch, we would still expect to see a number of non-prey sized yellow perch individuals. These larger-sized perch were not observed, and thus we might hypothesize that mortality rates were higher for small fish in Ottawa than in Crampton.

Implications:

Looking at the low-macrophyte density Lake Ottawa versus the high-density macrophyte Crampton, this study supports differential use of habitat by fish. It further indicates that different substrates/habitats are more or less suitable at different times of the day. Finally, it suggests that the addition of structure (woody debris) without some presence of macrophytes may not promote an increase in fish abundance.

ACKNOWLEDGEMENTS

Sadie Rosenthal, Tim Kreps, and David Lodge were tremendously helpful in their contributions to experimental design, sampling, and data analysis. They deserve many thanks for their generous time commitment to this project. Andrew Borden and Margaret Kulwicki were valuable assistants during the sampling process. I appreciate the ever-benevolent Gary Belovsky and Joe Caudell for the use of UNDERC vehicles and supplies. And finally, thank you to the Land O' Lakes Dairy-Maid, without which we couldn't possibly have found the will to triumph over inclement weather and the menacing *Orconectes rusticus*.

LITERATURE CITED

Anderson O. 1984. Optimal foraging by largemouth bass in structured environments. *Ecology* 65:851-861.

Cole GA. 1994. *Textbook of Limnology.* Waveland Press: Prospect Heights, IL. 412 pp.

Crowder LB and Cooper WE. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63: 1802-1813.

Eddy S. 1947. *Northern fishes.* University of Minnesota Press: Minneapolis. 276 pp.

France RL. 1997. Macroinvertebrate colonization of woody debris in Canadian shield lakes following riparian clearcutting. *Conservation Biology* 11:513-521.

Godin J-GJ. 1997. *Behavioral Ecology of Teleost Fishes.* Oxford University Press: Oxford. 384 pp.

Illinois Parks and Recreation. 1992 Jan. *Illinois Periodicals Online.* < http://www.lib.niu.edu/ipo/ip9201tc.html>. Accessed 2002 Oct. 31.

Lau SSS and Lane SN. 2001. Continuity and change in environmental ecosystems : the case of shallow lake ecosystems. *Progress in Physical Geography.* 25 : 178-202.

Lauridsen TL and Lodge DM. 1996. Avoidance by Daphnia magna of Fish and Macrophytes: Chemical Cues and Predator-Mediated Use of Macrophyte Habitat. *Limnology and Oceanography* 41: 794-798.

Lodge DM, Taylor CA, Holdich DM, Skurdal J. 2000. Nonindigenous crayfishes threaten North American freshwater biodiversity. *Fisheries.* 25 :7-20.

MacRae PSD and Jackson DA. 2001. The influence of smallmouth bass (*Micropterus dolomieu*) predation and habitat complexity on hte structure of littoral zone fish assemblages. *Can. J. Fish Aquat. Sci.* 58:342-351.

Nystrom P, Bronmak C, and Graneli W. 1999. Influence of an exotic and a native crayfish species on a littoral benthic community. *OIKOS* 85: 545-553.

Randall RG, Minns CK, Cairns VW, Moore JE. 1996. The relationship between an index of fish production and submerged macrophytes and other habitat features at three littoral areas in the Great Lakes. *Can. J. Fish. Aquat. Sci.* 53 :35-44.

Persson L. 1991. Behavioral response to predators reverses the outcome of competition between prey species. *Behavioral Ecology and Sociobiology* 28: 101-105.

Savino JF and Stein RA. 1989. Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. *Environmental Biology of Fishes* 24:287-293.

Turner AM and Mittlebach GG. 1990. Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. *Ecology* 71:2241-2254.

Venugopal MN and Winfield IJ. 1993. The distribution of juvenile fishes in a hypereutrophic pond: Can macrophytes potentially offer a refuge for zooplankton? *Journal of Freshwater Ecology* 8: 389-396.

TABLE AND FIGURE LEGEND

Table 1. Lake characteristics (*unpublished data,* Rosenthal 2001, *unpublished data,* UNDERC 2002)

Table 2. Transect characterization.

Table 3. G-test results summary.

Table 4. Listing of macrophyte species present in transects.

Figure 1.

- **A.** Average individual abundance summed over all three substrate types. Data has been normalized for each lake. Error bars represent standard error (n=2).
- **B.** Average school abundance summed over all three substrate types. Data has been normalized for each lake. Error bars represent standard error (n=2).

Figure 2.

- **A.** Average individual abundance summed over substrate, both lakes combined. Data has been normalized for each lake. Error bars represent standard error (n=2).
- **B.** Average school abundance summed over substrate, both lakes combined. Data has been normalized for each lake. Error bars represent standard error (n=2).

Figure 3. Average individual abundance of prey and non-prey size classes, grouped by lake. Data has been normalized for each lake. Error bars represent standard error (n=2).

Figure 4.

- **A.** Average individual abundance for substrate and time period. Data has been normalized over each lake. Error bars represent standard error (n=2).
- **B.** Average school abundance for substrate and time period. Data has been normalized over each lake. Error bars represent standard error (n=2).

Figure 5.

- **A.** Average individual abundance for substrate and size class. Data has been normalized over each lake. Error bars represent standard error (n=2).
- **B.** Average school abundance for substrate and size class. Data has been normalized over each lake. Error bars represent standard error (n=2).

TABLES

1.

Characteristics	**Lake Ottawa**	**Crampton**
Location	Iron River, MI	Land O' Lakes, WI
Size	550 acres	72 acres
Elevation	1660 ft.	1654 ft.
PH	8.58	6.0
Secchi Depth	4.8 m	4.25 m

2.

Lake	**Transect**	**Stems (#/ $0.5m^2$)**	**Cover (%)**	**Mean Height (m)**	**Wood Structure**
Ottawa	Veg1	8.6	21	0.3	none
	Veg2	4.6	7	0.25	chips
	Open1	0	0	0	branches
	Open2	0	0	0	none
	Wood1	0	0	0	boles, branches, chips
	Wood2	0	0	0	boles, branches, chips
Crampton	Veg1	52	20.6	0.438	none
	Veg2	21.6	13.8	0.346	boles, branches, chips
	Open1	47.2	1.6	0.024	branches
	Open2	44.4	6.2	0.026	branches
	Wood1	15.2	7.2	0.33	boles, branches, chips
	Wood2	52.8	6.4	0.028	boles, branches, chips

3.

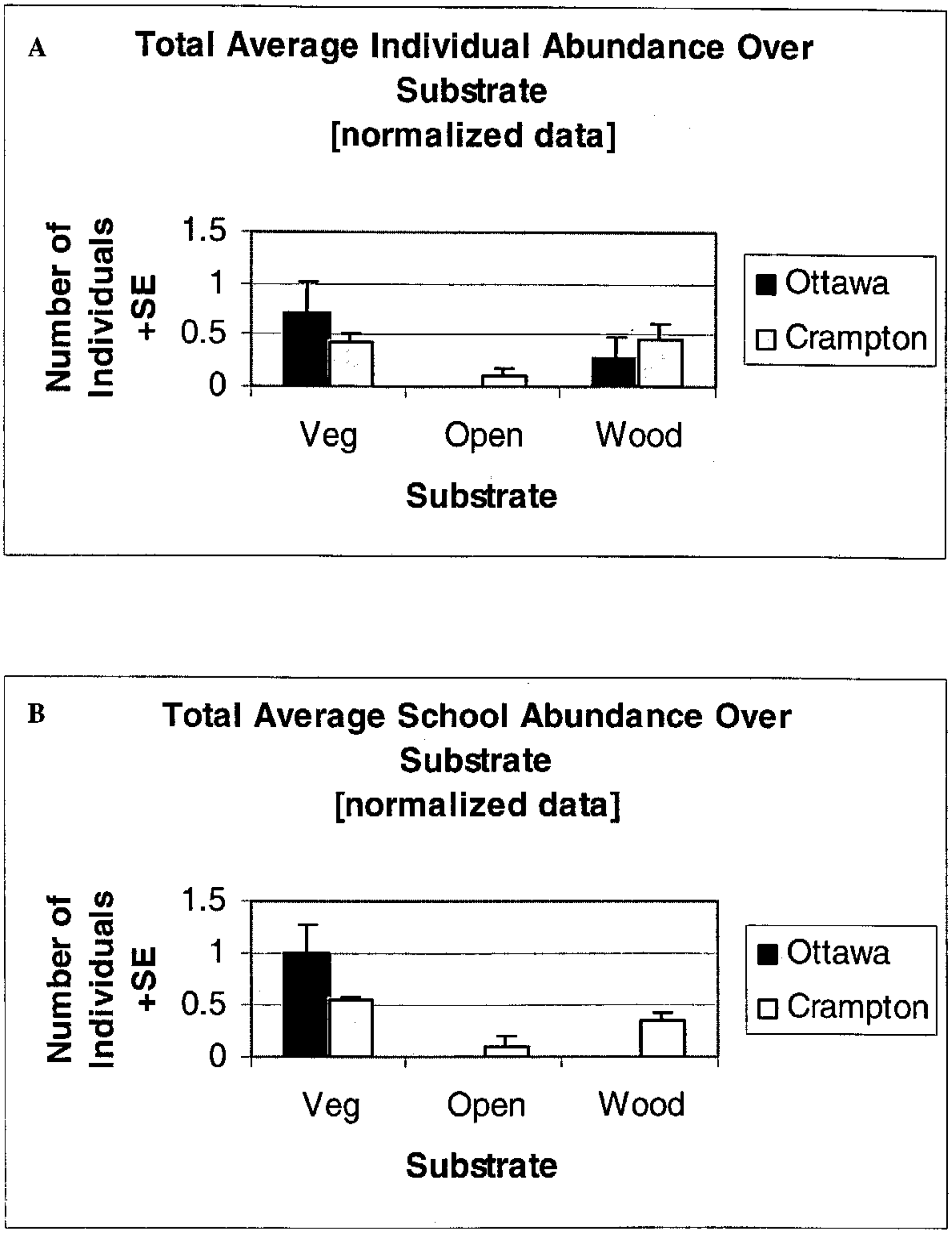
Factors Compared		**G-critical**	**G-observed**
lake vs. substrate	Individuals	5.991	16.85
	Schools	5.991	3.113
time vs. substrate	Individuals	5.991	30.97
	Schools	5.991	24.367
lake vs. time	Individuals	3.841	1.6866
	Schools	3.841	0.7866

4.

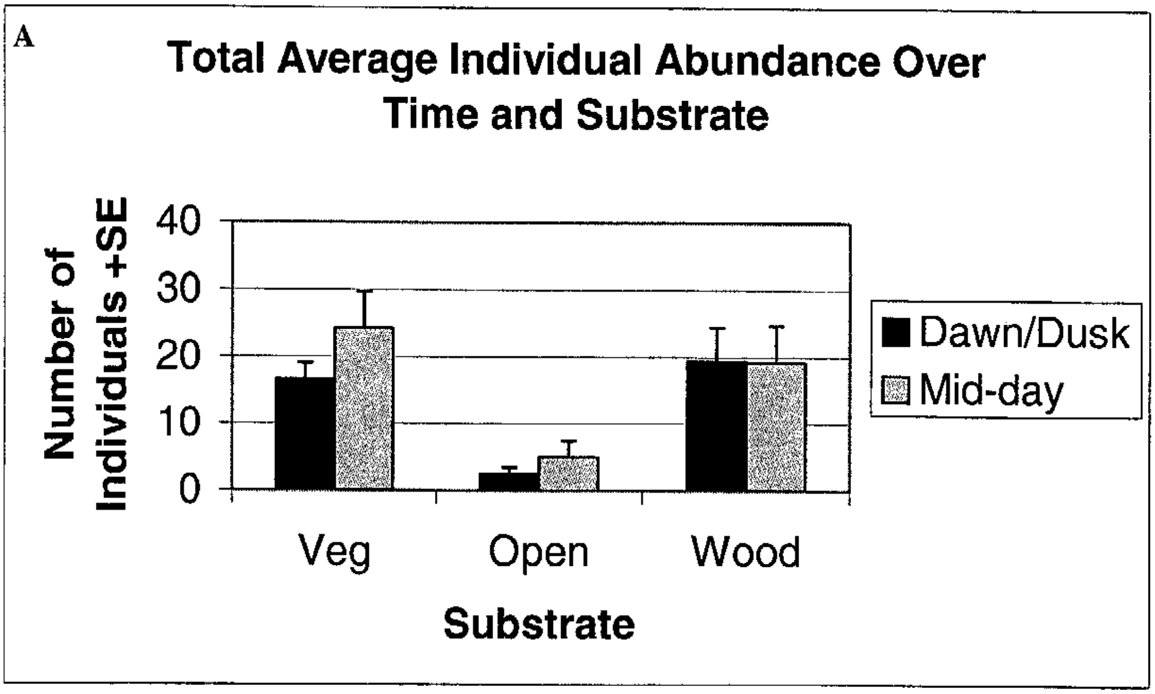
	Ottawa	**Crampton**
Macrophyte species present	*Potamogeton amplifolius*	*Eriocaulon septangulare* *Pontederia cordata* *Sparganium omersum* *Nuphar luteum* *Nymphaea odorata*

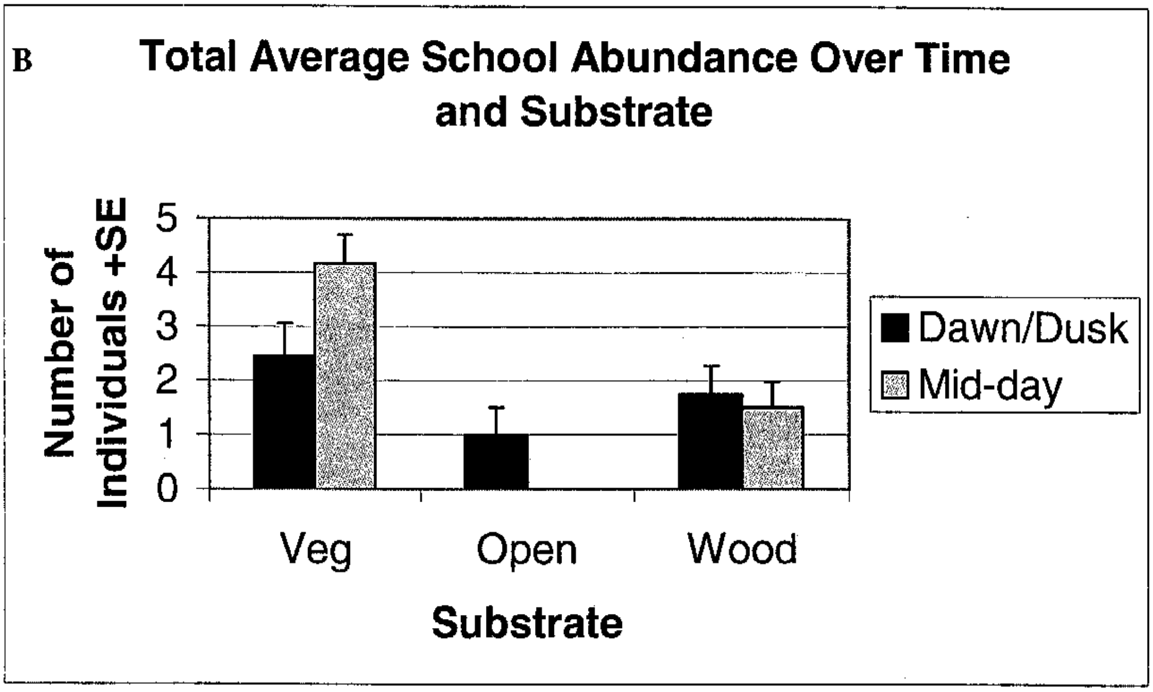
FIGURES

1.

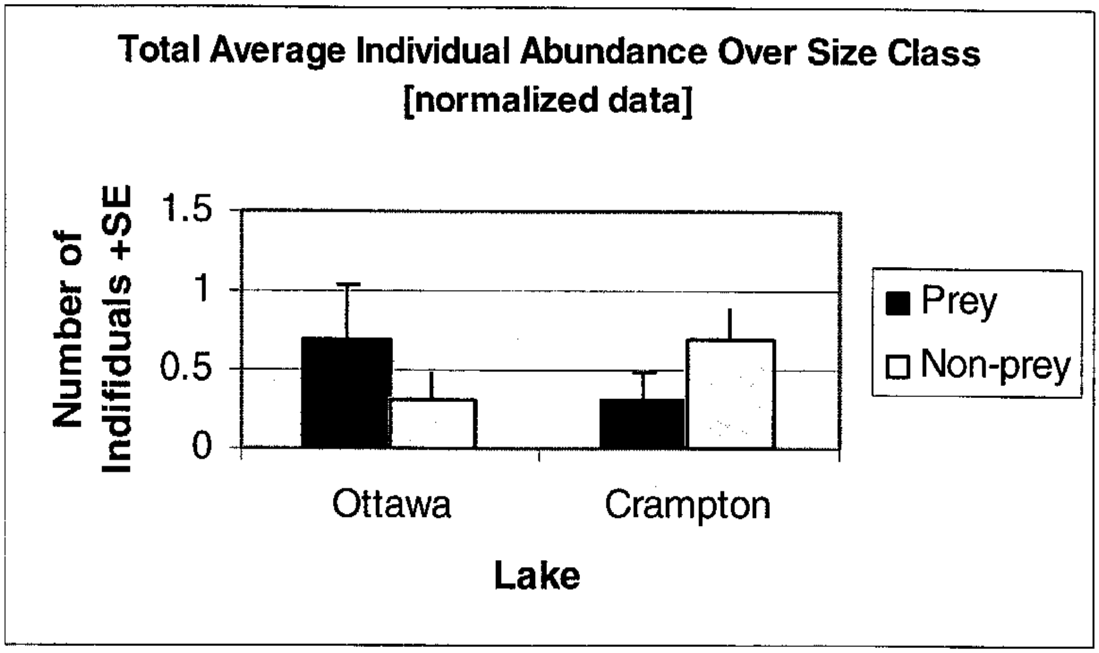

A
Total Average Individual Abundance Over Substrate [normalized data]
Number of Individuals +SE
1.5
1
0.5
0
Veg
Open
Wood
Substrate
■ Ottawa
□ Crampton
B
Total Average School Abundance Over Substrate [normalized data]
Number of Individuals +SE
1.5
1
0.5
0
Veg
Open
Wood
Substrate
■ Ottawa
□ Crampton

2.

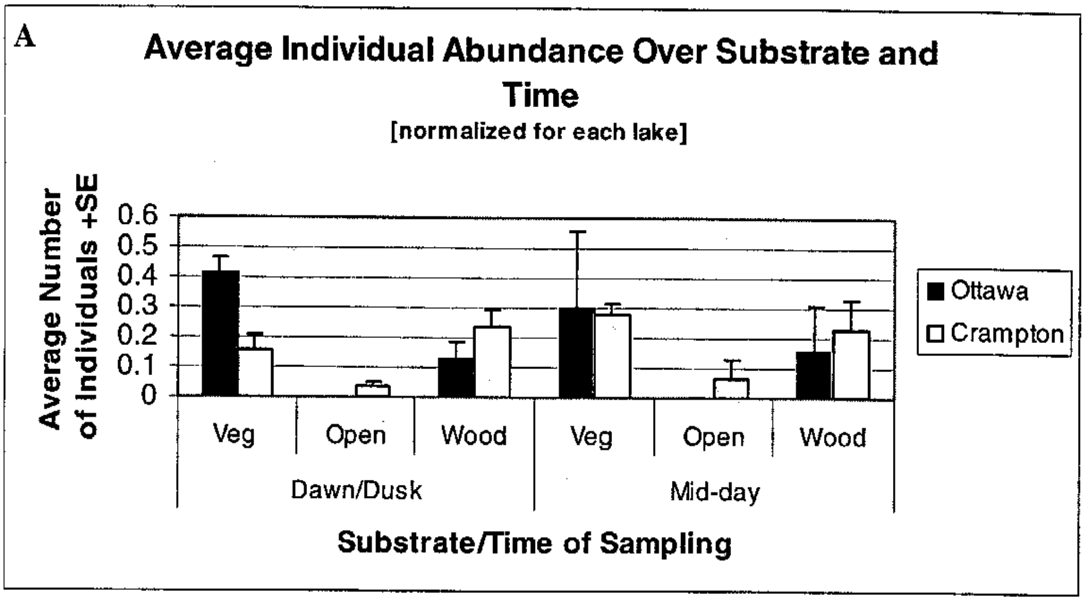

A
Total Average Individual Abundance Over Time and Substrate
Number of Individuals +SE
40
30
20
10
0
Veg
Open
Wood
Substrate
■ Dawn/Dusk
▨ Mid-day

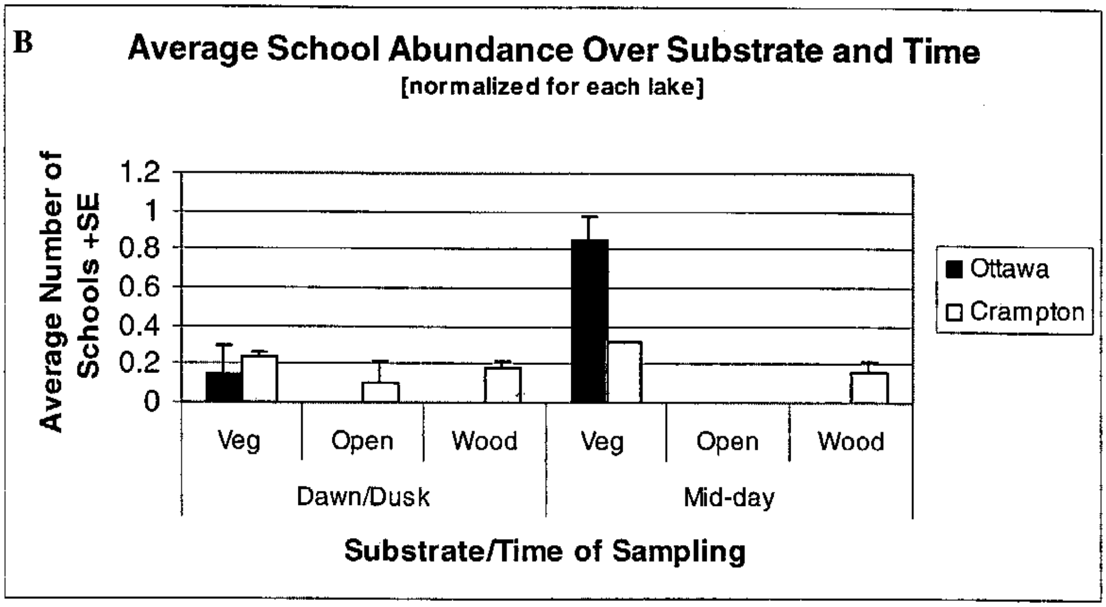

B
Total Average School Abundance Over Time and Substrate
Number of Individuals +SE
5
4
3
2
1
0
Veg
Open
Wood
Substrate
■ Dawn/Dusk
▨ Mid-day

3.

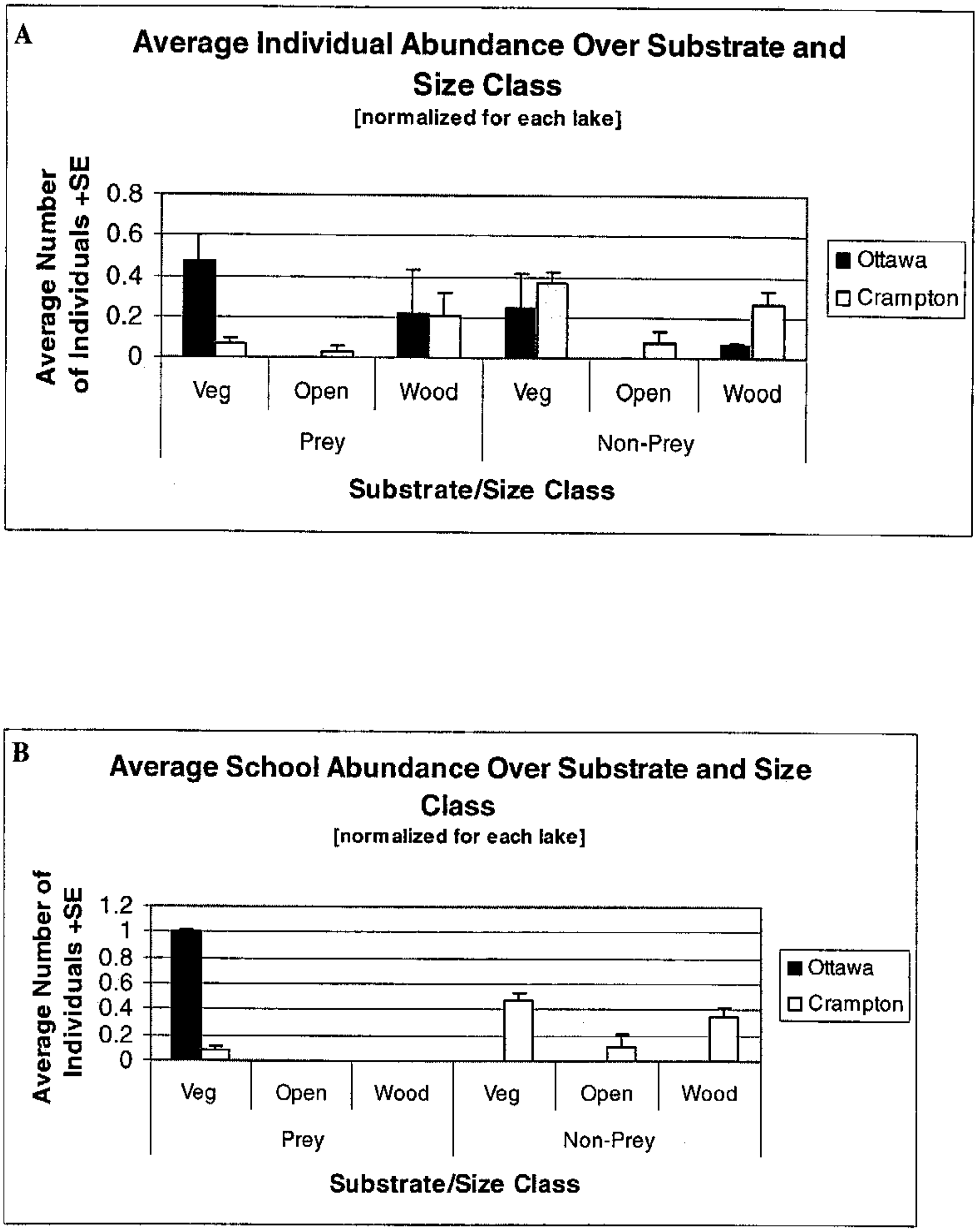

Total Average Individual Abundance Over Size Class
[normalized data]
Number of Indifiduals +SE
1.5
1
0.5
0
Ottawa
Crampton
Lake
■ Prey
□ Non-prey

4.


A
Average Individual Abundance Over Substrate and Time
[normalized for each lake]
Average Number of Individuals +SE
0.6
0.5
0.4
0.3
0.2
0.1
0
Veg
Open
Wood
Veg
Open
Wood
Dawn/Dusk
Mid-day
Substrate/Time of Sampling
■ Ottawa
□ Crampton


B
Average School Abundance Over Substrate and Time
[normalized for each lake]
Average Number of Schools +SE
1.2
1
0.8
0.6
0.4
0.2
0
Veg
Open
Wood
Veg
Open
Wood
Dawn/Dusk
Mid-day
Substrate/Time of Sampling
■ Ottawa
□ Crampton

5.



A
Average Individual Abundance Over Substrate and Size Class
[normalized for each lake]
Average Number of Individuals +SE
0.8
0.6
0.4
0.2
0
Veg
Open
Wood
Veg
Open
Wood
Prey
Non-Prey
Substrate/Size Class
■ Ottawa
□ Crampton
B
Average School Abundance Over Substrate and Size Class
[normalized for each lake]
Average Number of Individuals +SE
1.2
1
0.8
0.6
0.4
0.2
0
Veg
Open
Wood
Veg
Open
Wood
Prey
Non-Prey
Substrate/Size Class
■ Ottawa
□ Crampton