TROPHIC EFFECTS OF MACROPHYTE REMOVAL ON FISH POPULATIONS IN A BOREAL LAKE

Robert Rabasco

A thesis submitted to the Faculty of Graduate Studies of the
University of Manitoba in partial fulfilment of the Requirements
of the degree of Master of Natural Resources Management

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The University of Manitoba
Winnipeg, Manitoba, Canada
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ABSTRACT

Northern pike (*Esox lucius*), yellow perch (*Perca flavescens*), and pumpkinseed (*Lepomis gibossus*) rely on vegetated littoral zones as spawning substrate, foraging areas, and refuge from predation. However, the removal of littoral zone habitat has increased in the past twenty-five years. This led Department of Fisheries and Oceans Canada (DFO) researchers to study the effects of habitat loss on northern pike production in Lake 191 in the Experimental Lakes area (ELA) in northwestern Ontario. The removal of 50% of littoral zone macrophytes led to a 50% reduction of northern pike abundance, increases in yellow perch and pumpkinseed abundance, and changes in the size structure and biomass of the zooplankton community. The present study was initiated to help determine underlying causes for changes in the fish and zooplankton community in Lake 191.

Fish from Lake 191 were examined for feeding patterns. Northern pike sampled did not effectively exploit alternative prey fish species in Lake 191. Only three (out of twenty) northern pike stomachs contained yellow perch and none contained pumpkinseed. Further, yellow perch made up only 12% of northern pike diet. Instead, the northern pike in Lake 191 ate small northern pike. Northern pike fingerlings and/or remains made up 49% of the diet of larger northern pike. Northern pike preference for conspecifics helps to explain both the decreases in northern pike abundance, and the increases in preyfish abundance. Northern pike in Lake 191 may prefer cannibalism because of differences between young-of-the-year (YOY) northern pike, yellow perch, and pumpkinseed habitat selection, fin morphology, and predator avoidance behaviors.

Yellow perch and pumpkinseed ate mostly benthic invertebrates and zooplankton. Further, preyfish in Lake 191 selected only large species of zooplankton. Macrophyte harvesting may have increased preyfish access to benthic invertebrates, and thus contributed to the increases in preyfish abundance. Preyfish preference for large zooplankton coupled with the increase in preyfish abundance may be responsible for the shifts in zooplankton community structure observed by Salki (in prep. 2000). Thus, macrophyte harvesting may be indirectly responsible for the changes in zooplankton community structure.

The policies of Manitoba, Ontario, Minnesota, Wisconsin, and Michigan for the control and /or removal of aquatic macrophytes were reviewed. Fish habitat protection in Canada is administered by the DFO via the Federal Fisheries Act and habitat protection provisions of the No Net Loss Policy (NNLP). In the United States, regulations relating to fisheries habitat are administered by individual state agencies. The regulations that Minnesota, Wisconsin, and Michigan adopted to administer macrophyte removal include Minnesota Rules Chapters 6280 & 6216, Wisconsin Codes Chapters NR 107 and 19.05, and Michigan State Codes Chapter PA 004199, Section 12562 and Michigan Compiled Laws PA 324.48735 & R 299.1052.

Regulations governing macrophyte removal in these jurisdictions are not an effective tool to protect fish populations. Four of the five jurisdictions lack specific guidelines on how to apply the regulations to the physical control of macrophytes. The permitting processes that the jurisdictions utilize to regulate chemical control do not integrate enough biological information about the application sites to insure habitat protection. Finally, the jurisdictions do not directly regulate the biological control of macrophytes. The relevant government agencies should adopt new macrophyte control regulations based on the results of adaptive management experimentation.

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1. INTRODUCTION

1.1 Background

The main focus of this research project was to determine the effects of habitat modification on the trophic dynamics of a boreal lake. Of particular interest were the effects of harvesting littoral zone macrophytes on the relationships between pumpkinseed sunfish (*Lepomis gibbosus*), yellow perch (*Perca flavescens*), northern pike (*Esox lucius*), and associated zooplankton communities. The importance of macrophytic habitat for fish populations is well established (Crossman and Casselman 1987). Macrophytes are used for spawning, for nursery habitat for young, and for feeding areas. Although macrophytes are critical to fish populations, harvesting by management agencies and landowners attempting to reduce eutrophication and remove exotic macrophyte species is widespread in North America (Nicholson 1981).

Fish use macrophytic habitat for a variety of life history activities (Crossman and Casselman 1987). Radio-telemetry studies indicate that adult northern pike select microhabitats, such as logs, creek channels, and moderately dense macrophytes (Diana 1979, Headrick 1985). Northern pike select dense vegetation for egg deposition, and emergent fry use these areas for nursery habitat (Farrell and Werner 1996). The most important predictor of a lake's northern pike carrying capacity is the percentage of near-shore area that has vegetation (Simpson 1995). Finally, the relationship between macrophyte cover and northern pike foraging area selection has been well researched (Roos et al. 1994). Diehl and Ekloev (1995) found a strong positive correlation between macrophytic cover and the selection of foraging habitat by northern pike. Forage fish populations also rely on vegetated habitat for spawning, nursery, and feeding areas (Diehl and Ekloev 1995). These fish increase their use of macrophytic vegetation in the presence of predators (Savino and Stein 1989, He 1990).

There are three broad categories of macrophyte harvesting: physical harvest (i.e. mechanical and non-mechanical), chemical control (i.e. herbicide use), and biological control (i.e. stocking of herbivorous fish and/or aquatic invertebrates). Resource management agencies and private landowners have increased macrophyte harvesting over the past twenty years (Wilcox and Meeker 1992). North American habitat managers use macrophyte removal for lake rehabilitation in a number of different circumstances. In the United States macrophytes are harvested from lakes where high densities are thought to contribute to the stunting of gamefish populations (i.e. smaller than average sexually mature individuals) (Olson et al. 1998). In these situations a reduction in predator efficiency due to high macrophyte density is the proposed mechanism of stunting (Olson et al. 1998). Although there is no doubt that macrophyte removal results in increased fish growth, actual fish production (the product of growth and change in abundance) may be substantially reduced due to a decrease in fish abundance resulting from increased predation. Whether fish production actually decreases or how much it decreases is not known (Olson et al. 1998, pers. comm., K.H. Mills, Freshwater Institute, Winnipeg, Mb. 1998).

Management agencies harvest macrophytes to mitigate eutrophication, stop the spread of invasive exotic macrophyte species, improve water quality, and increase angler access (Nicholson 1981, McKee et al. 1986, Wynne 1992, VanEeckhout and Quade 1994). Macrophytes sequester nutrients that would otherwise be quickly recycled by phytoplankton. Therefore, the recycling of these nutrients by algae is decreased. The decrease in nutrient recycling leads to a decrease in water clarity. Thus, management agencies have adopted macrophyte removal techniques to increase/maintain water clarity (VanEeckout and Quade 1994).

Habitat managers across the United States use macrophyte harvest to increase angler access (Wynne 1992). Littoral zones are cleared of vegetation to increase shoreline angling opportunities in urban centers. Additionally, triploid (sterile) grass carp (*Ctenopharyngodon idella*) are stocked to prevent re-growth of aquatic vegetation (Elder and Murphy 1997). Landowners often view near-shore vegetation beds as a detriment to recreational pursuits such as swimming and boating (Bryan and Scarnecchia 1992). Therefore, macrophyte beds are harvested to establish swimming beaches and improve the aesthetic and recreational value of their property.

Historically, there have been several common methods employed to clear shorelines of aquatic vegetation. The use of herbicides was a popular technique until legislation was passed in the United States and Canada that restricted non-commercial use of such chemicals (VanEeckhout and Quade 1994, Ontario Ministry of Natural Resources 2000). Physical control techniques include raking, pulling, and cutting using hand held tools, as well as specially designed harvesting machinery (Engel 1998). The whole lake impact of these types of removal is not well documented or understood.

1.2 The Experimental Lakes Area

This study was conducted in The Experimental Lakes Area (ELA), which is located 52 km east of Kenora, Ontario (Fig. 1), at 93°30 - 94°00′, 49°30′ - 49°45′N

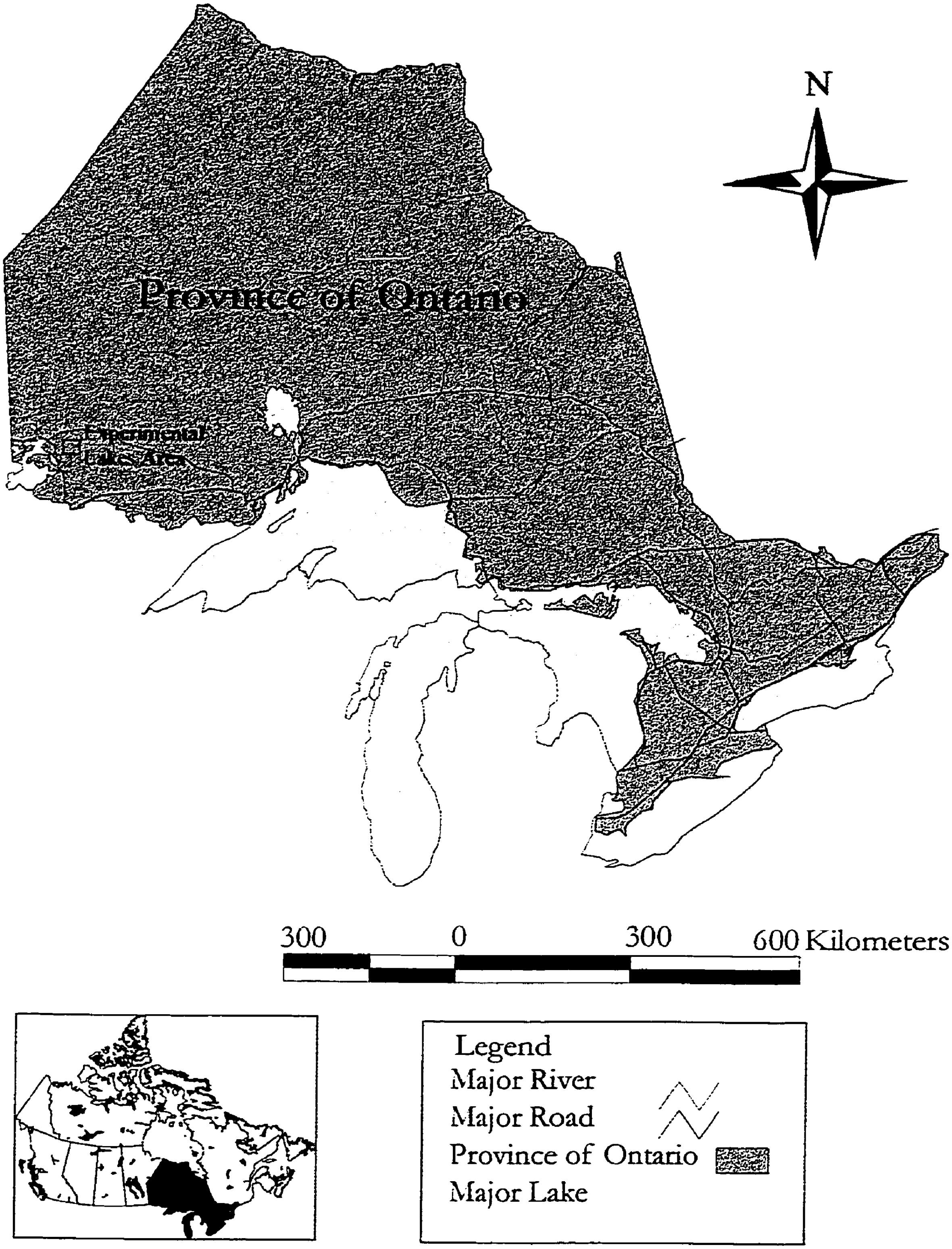


Figure 1: Location of the Experimental Lakes Area.

(Brunskill and Schindler 1971). There are two reasons why the ELA was the ideal location for this study. First, the ELA represents a rare opportunity where whole-lake experimentation takes place (Johnson and Vallentyne 1971). The founding principles of the ELA are entrenched in the basic tenets of adaptive management. Specifically, experiments at the ELA involve perturbing a natural system to study the responses. This study is centred around the idea that littoral habitat modification has an effect on the entire ecosystem of a lake. Second, this study was designed as part of an ongoing ELA experiment.

1.3 The Lake 191 Macrophyte Removal Experiment

Lake 191 is a small (16.3 ha), shallow (4 m Z_{max}), brown-water lake that contains northern pike (abundant), white sucker (*Catostomus commersoni*) (rare), yellow perch (moderately abundant), and pumpkinseed (moderately abundant). The Lake 191 macrophyte removal experiment was initiated as part of the Canadian Green Plan program (1993 – 1996). The primary purpose of the experiment was to quantify the relationship between loss of macrophyte cover and changes in northern pike production. Secondary purposes include quantifying changes in northern pike habitat usage, changes in abundance of other fish species, and changes in other trophic levels in the lake when macrophyte cover is removed. The experiment was initiated as a result of discussions with local Kenora OMNR staff about fish habitat issues. Macrophyte removal by cottage owners is a local concern and macrophyte enhancement is a technique in its infancy as a measure to compensate for loss of fish habitat [No Net Loss Policy (1986) of DFO].

DFO scientists collected two years of pre-manipulation data on Lake 191 (1994 – 1995), and harvested macrophytes for three years (1996 – 1998) (Table 1). No macrophyte harvesting occurred in 1999, which was the first year of the recovery phase of the experiment. However, little re-growth of macrophytes in harvested areas had occurred in 1999, making this year similar to other years in which macrophytes were reduced. Data collected during all years of the study included the following components: mark-recapture methods to assess abundance and survival of northern pike, catch-per-unit-effort (CPUE) methods to assess abundance of yellow perch, pumpkinseed, YOY northern pike, macrophyte biomass and species composition, water chemistry, and phytoplankton and zooplankton species diversity and abundance. Fish capture occurred using three types of gear: small-mesh trap nets, small-mesh seines, and angling.

The removal of shoreline macrophytes was extremely successful (Table 1). In 1996, macrophyte biomass and percent cover in the harvested areas of the littoral zone of Lake 191 were reduced by 93% and 88% of the original pre-harvest values, respectively. By 1998 macrophyte biomass and percent cover in the harvested areas of the littoral zone of Lake 191 were reduced by 96% of the original pre-harvest values. In unharvested areas, the biomass and percent cover in 1999 were similar to 1994 – 1997 values.

Table 1 Percent littoral zone cover and biomass of aquatic macrophytes in the littoral zone of Lake 191, ELA, 1994 – 1999. * No harvesting occurred in 1994 – 1995, and 1999, the first year of recovery. (Adapted from Jansen 2000).

	Harvested Littoral Zone Areas	
Year	**Biomass**	**% Cover**
*1994	100%	100%
*1995	100	100
1996	7	12
1997	3	10
1998	4	4
*1999	< 5	< 5

Northern pike abundance decreased by over 50% in the three years that macrophytes were harvested (Fig. 2). The decrease in northern pike abundance could be due to cannibalism because refuge areas were reduced for young northern pike. The abundance of age-0 northern pike in cut and uncut areas decreased when harvesting began in 1996 and continued through 1999 (Jansen 2000). The abundance of smaller size classes (> 60 mm) of yellow perch and pumpkinseed has increased (Figs. 3 & 4) (Jansen 2000). Determining the role that feeding relationships had in the abundance changes of these species was the first goal of this study.

Zooplankton abundance in Lake 191 has changed as a result of macrophyte harvesting (A. Salki Freshwater Institute, pers. comm., Winnipeg, Manitoba 1999). In

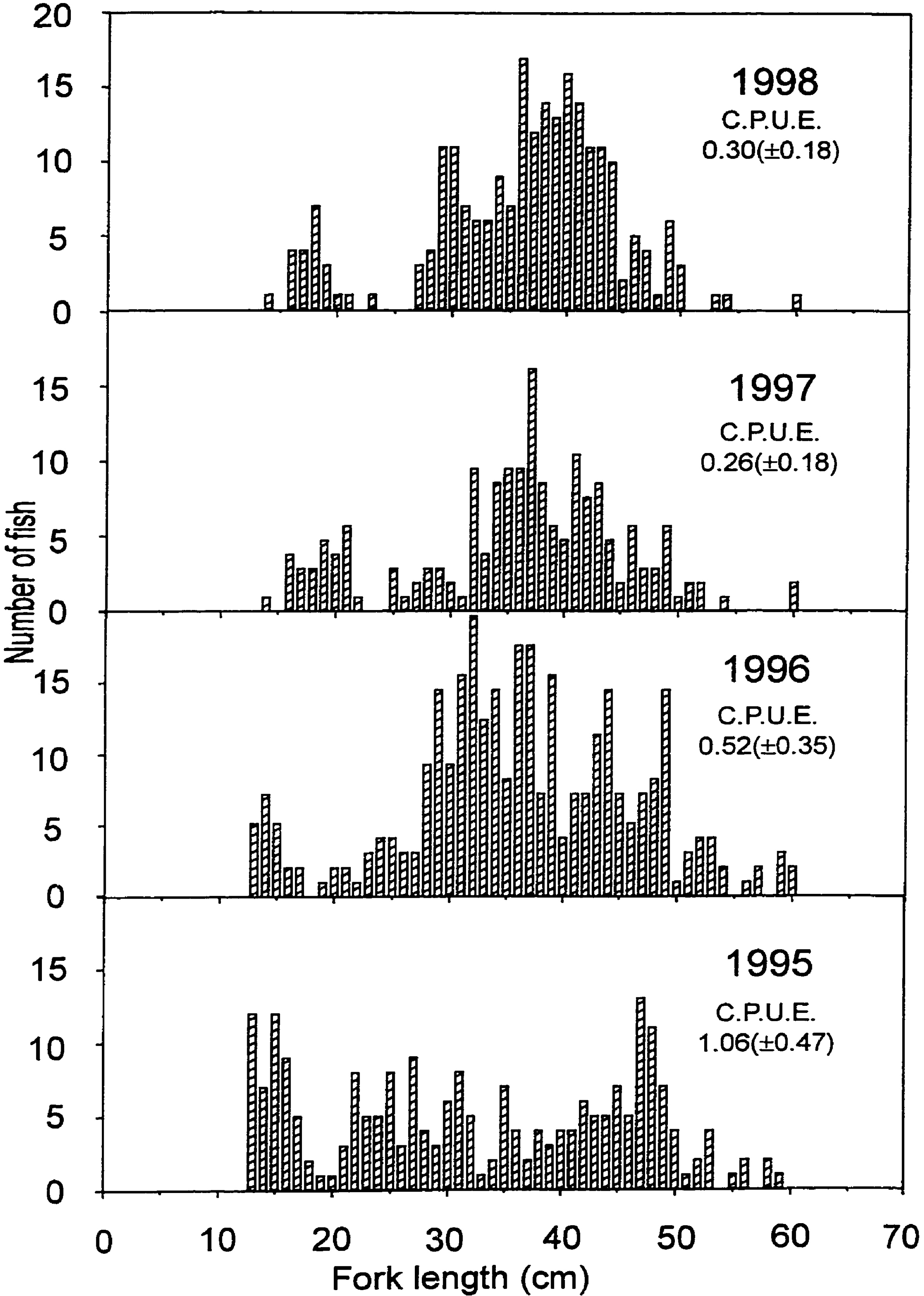


Figure 2 : Length frequency distributions for northern pike sampled 1995 - 1998 in ELA Lake 191. Mean Catch-Per-Unit-Effort (C.P.U.E.)and 95% confidence intervals are included for each year.

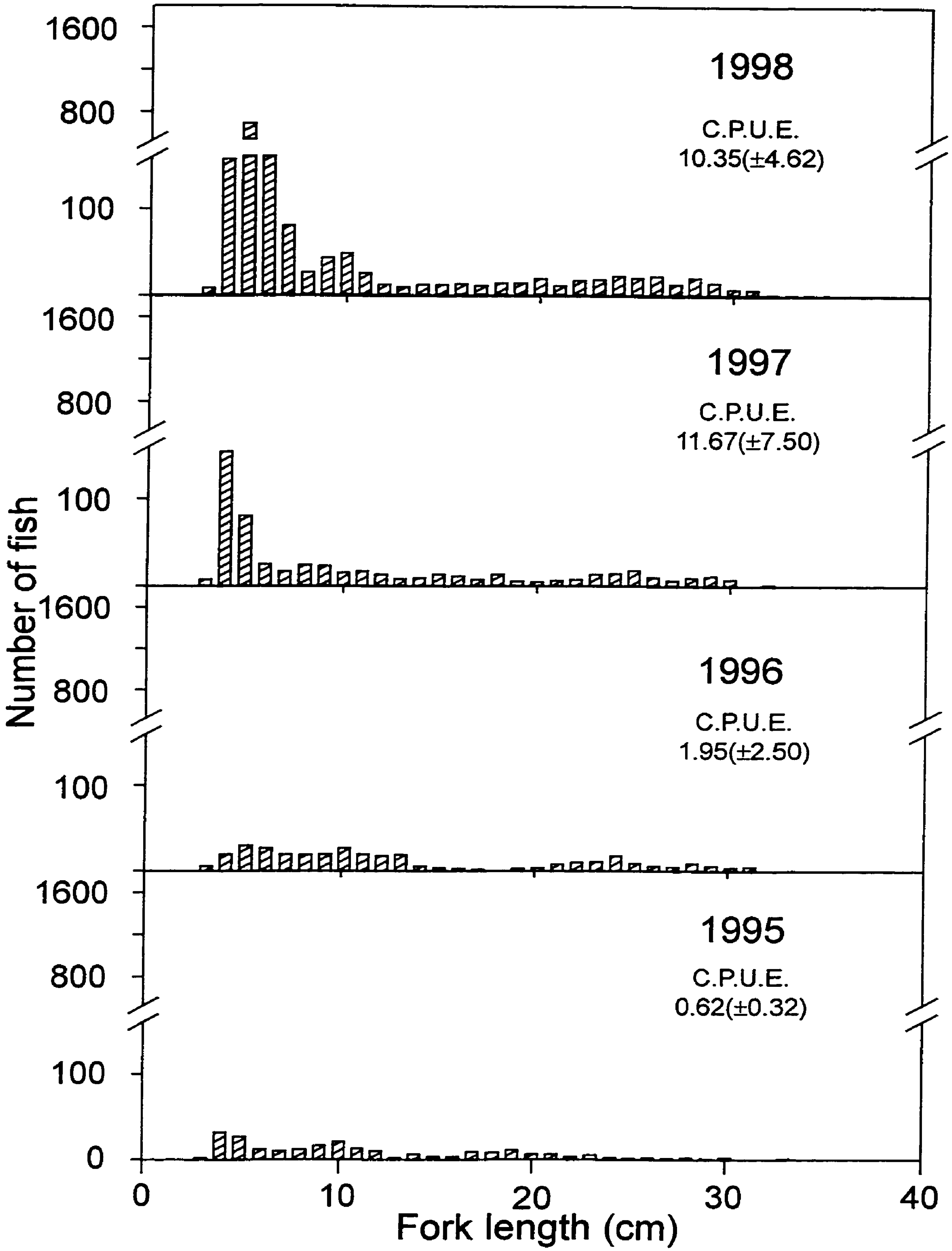


Figure 3 : Length frequency distributions for yellow perch sampled 1995 - 1998 in ELA Lake 191. Mean Catch-Per-Unit-Effort (C.P.U.E.)and 95% confidence intervals are included for all years.

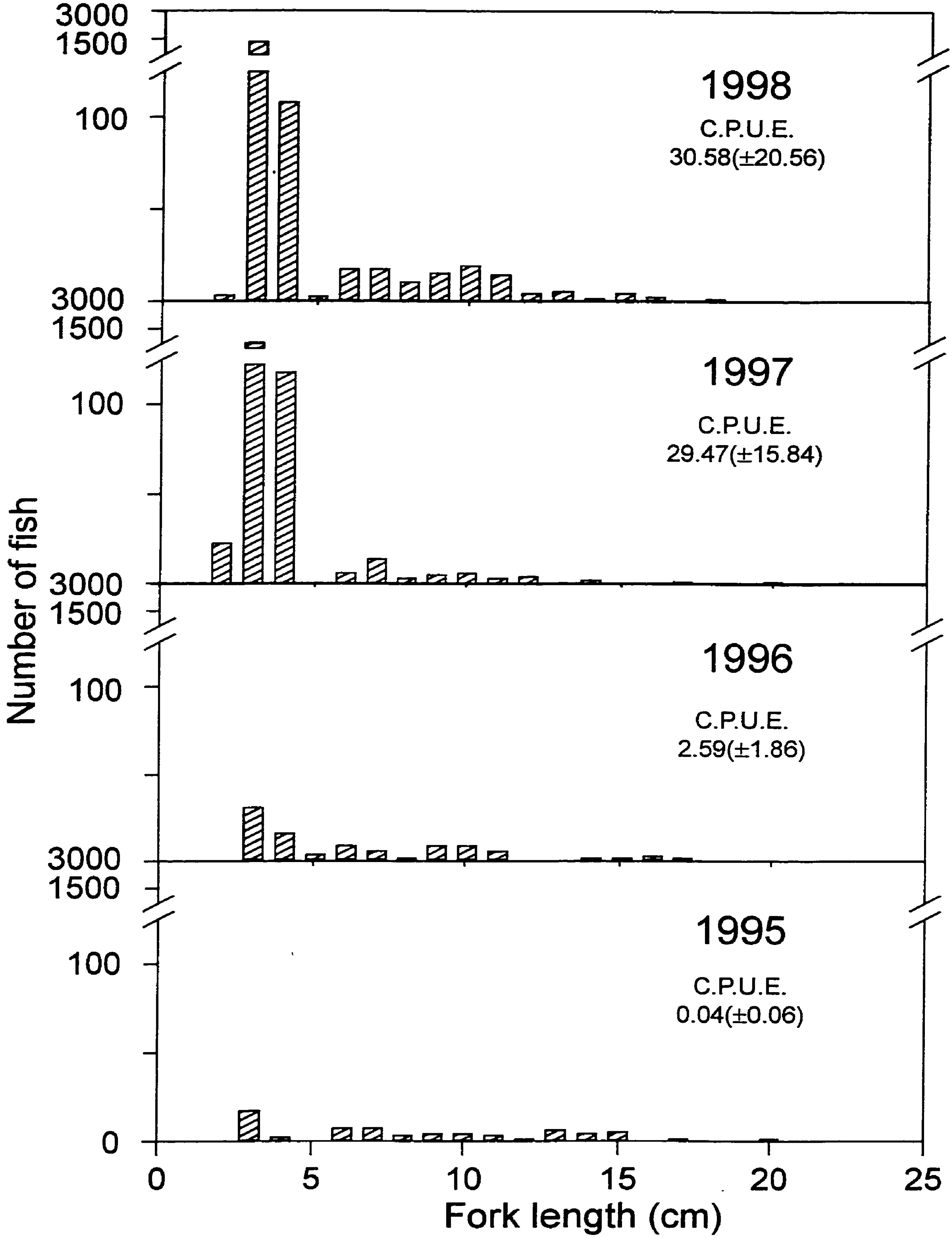


Figure 4 : Length frequency distributions for pumpkinseed sampled 1995 - 1998 in ELA Lake 191. Mean Catch-Per-Unit-Effort (C.P.U.E.) and 95% confidence intervals are included for each year.

1999 zooplankton abundance increased (Salki, in prep. 2000). However, the abundance of large zooplankton (i.e. *D. pulex*) decreased in 1999. The zooplankton community shifted from a community made up of cladocerans, copepods, and cyclopoids to one made up mostly of copepod nauplii, small cyclopoids, and *Holopedium gibberum* (Salki, in prep. 2000). The second goal of this study was to examine the feeding relationships between fish and zooplankton communities.

DFO Fish Habitat Management is already using results of the removal experiment as supporting data for evaluating macrophyte removal proposals (K.H. Mills, pers. comm., Freshwater Institute, Winnipeg, Mb. 1998). Under Section 35(1) of the Fisheries Act "the harmful alteration, disruption, or destruction (HADD) of fish habitat is prohibited", but there is a non-compliance problem, and macrophyte removal remained in the top five concerns by habitat managers at the 1997 Fish Habitat Workshop (sponsored by the DFO and OMNR). There is a need for research on the ecological effects of macrophyte removal on predatory game fish such as northern pike as well as associated forage fish (K.H. Mills, pers. comm., Freshwater Institute, Winnipeg, Mb. 1998).

1.4 The Trophic Effects of Macrophyte Removal

There were two main components to this project. The first component involved the determination of some of the underlying ecological mechanisms for changes in fish and zooplankton communities in lakes when macrophytes are removed. The second component involved an examination of the policy implications of macrophyte removal. Ecological reasons for changes in fish populations subject to macrophyte removal were determined by sampling Lake 191 fish populations. Stomach content analysis was used to determine the effects of macrophyte removal on feeding relationships between northern pike and preyfish. Policy implications were explored via a review and critique of macrophytic habitat legislation for Ontario, Manitoba and several U.S. states (Minnesota, Wisconsin, and Michigan) with similar ecosystems.

1.5 Research Objectives

There were two main goals to this project. The first was to determine the feeding relationships between fish species in Lake 191 after macrophytes were removed. The second was to evaluate management prescriptions for macrophyte management. These goals were achieved by addressing the following objectives:

1. To determine the feeding relationships between the fishes and lower trophic levels in Lake 191. This was achieved by sampling fish from Lake 191 and analysing the contents of their stomachs.
2. To link the results of the stomach content analysis to the changes in fish and zooplankton communities that were caused by macrophyte removal and observed by Mills (in Jansen 2000) and Salki (in prep. 2000).
3. To examine the current regulations that resource agencies administer to manage aquatic macrophytes and protect fish habitat.
4. To determine the implications of the results of this research on macrophyte removal regulations in Ontario, Manitoba, Michigan, Minnesota, and Wisconsin.

1.6 Methods

Field Sampling

Fish sampling consisted of a two-step process. The first step involved capture of northern pike, yellow perch, and pumpkinseed by shoreline seining and angling. The next step involved gut content analysis of the fish samples. Results from step two were used in conjunction with the results from the overall experiment to ascertain the importance of feeding relationships in determining the effects of macrophyte removal on northern pike abundance.

Literature Review

Ultimately, the results from field sampling were examined for their implications for habitat management. Information gathered from an intensive literature review (see Chapter 2) of relevant macrophyte and fish literature was compared to the results of this study. A three-step process was utilised to determine management implications from the field data. First, current regulations governing habitat modification were researched and summarised (Chapter 6). Second, conclusions generated from the field experiment were used to evaluate these regulations. Finally, pertinent management prescriptions were presented as alternatives to the current approach of habitat modification followed by habitat restoration.

1.7 Assumptions

There were two assumptions associated with this project. The first assumption is that the changes in Lake 191 fish populations are due to macrophyte removal rather than natural variation. This is likely true because the magnitude of abundance change of each fish species observed in Lake 191 has never been documented in any other ELA unmanipulated lake. The second assumption relates to the methodologies of the proposed experiment. This assumption is that the stomach samples gathered from a subset of each fish population during the field season were representative of each population.

2. LITERATURE REVIEW

2.1 Scope

This chapter is divided into three sections. The first covers the importance of macrophytes to the life histories of the fish that inhabit Lake 191, northern pike, yellow perch, and pumpkinseed sunfish (Fig. 5). The second provides information on the ecological relationships between these species. The final section explores the literature with reference to habitat modifications (i.e. macrophyte removal and/or reduction) and their implications for fish management.

2.2 The Importance of Macrophytes to Fish Communities

The importance of vegetated areas to northern pike is well documented (Franklin and Smith 1963, Osterberg 1985, Cook and Bergersen 1988, Headrick and Carline 1993, Farrell and Werner 1996). Macrophytes are important to the following activities of northern pike: spawning, habitat partitioning, and foraging (Franklin and Smith 1963). Northern pike are benthic spawners whose eggs adhere to aquatic macrophytes. Spawning habitat consists of water depths from 0.5m to 1.5 m with abundant patches of dense macrophytes (Farrell and Werner 1996). Northern pike spawning success is dependent on a high proportion of vegetated littoral zone habitat (Dube and Gravel 1980, Moyle and Cech 1996). Dube and Gravel (1980) found that northern pike spawning success was lowered when macrophyte areas were absent or degraded.

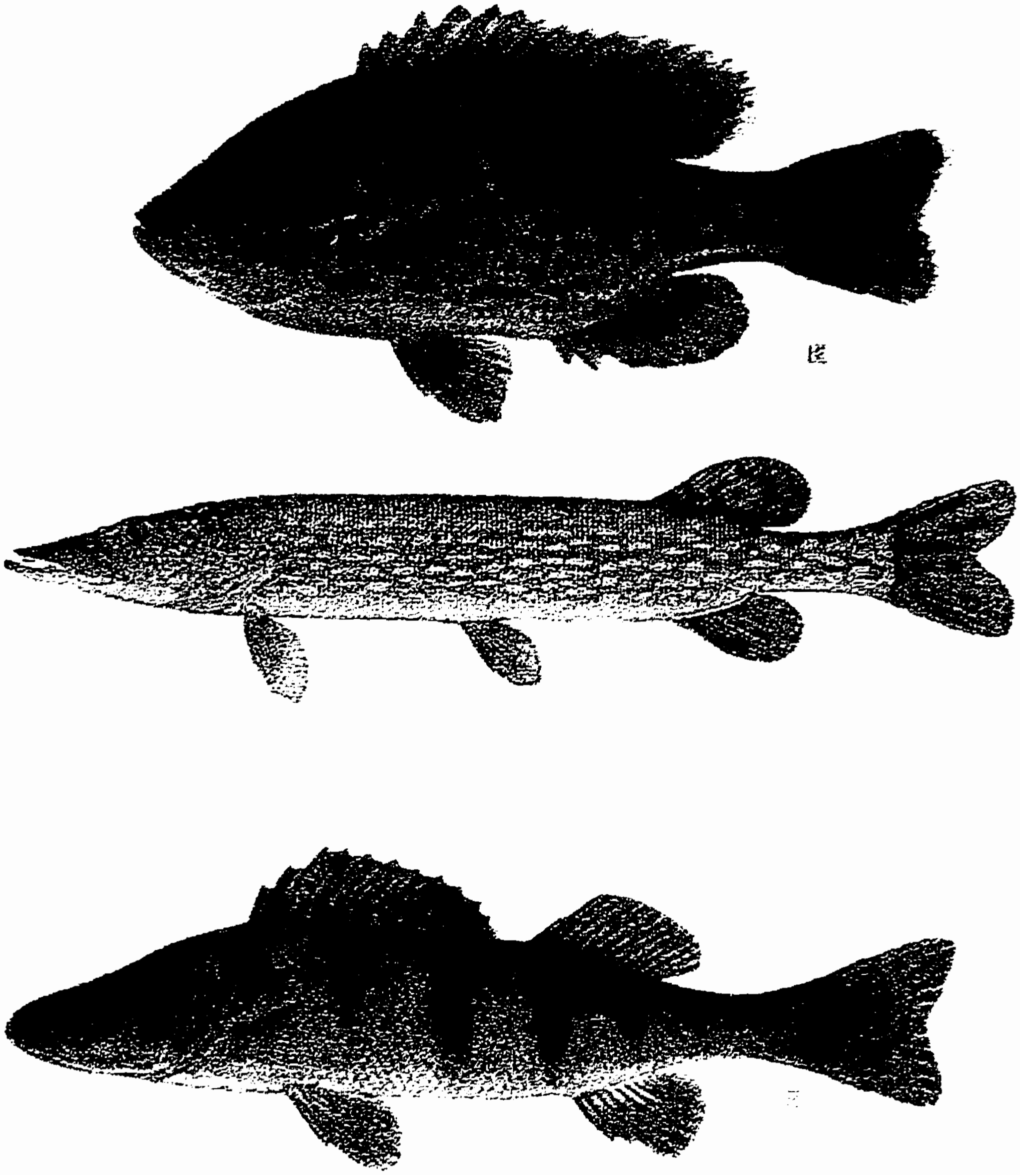


Figure 5: The fish of Lake 191, pumpkinseed sunfish (*Lepomis gibbosus*), northern pike, (*E. lucius*), and yellow perch (*Perca flavescens*), from www.nativefish.org. The pictures above are not to scale.

Northern pike associate with medium to high macrophyte densities in littoral zone habitats (Diana 1977, Chapman and Mackay 1984, Cook and Bergersen 1988, Headrick and Carline 1993). Diana (1977) used radio-telemetry equipment to determine northern pike distribution. Northern pike were found most frequently in shallow water (< 4m) associated with aquatic macrophytes. Further, Chapman and Mackay (1984) found that 80% of sampled northern pike were found in < 2m water depth. Headrick and Carline (1993) found that at the onset of summer thermal stratification northern pike moved to inshore locations associated with macrophytes. Additionally, young northern pike prefer vegetated littoral zones (Osterberg 1985). Cook and Bergersen (1988) conducted radio-telemetry studies on pike in Eleven Mile Reservoir, Colorado. Northern pike movements paralleled shoreline areas during summer stratification in this reservoir. Additionally, Cook and Bergersen (1988) concluded that although northern pike did not usually occupy distinct home ranges, they preferred vegetated littoral zone areas. Further, aquatic vegetation was often the key factor in northern pike habitat selection.

Northern pike frequently associate with aquatic macrophytes to acquire prey (Diana 1979, Savino and Stein 1989, Moyle and Cech 1996). Consumption of vertebrate prey starts as early as day 11, when young northern pike begin to exhibit cannibalism (Gres 1994). At this stage northern pike spend most of their time in shallow vegetated areas (Gres 1994). The increased ability of northern pike to capture prey may explain their associations with these areas (Savino and Stein 1989). Additionally, there is evidence that northern pike abundance is closely associated with the availability of suitable forage (Snow and Kendall 1978).

Yellow perch and pumpkinseed also have well-documented relationships with macrophytes (He 1990, Dionne and Folt 1991, Wilcox and Meeker 1992, Kubecka and Svatora 1993, Flesch et al. 1994, Osenberg et al. 1994, Coleman and Wilson 1996, Fisher and Willis 1997, Cobb and Watzin 1998). Yellow perch utilize macrophyte areas for reproduction, acquiring prey, and avoiding predators (He 1990, Dionne and Folt 1991, Wilcox and Meeker 1992, Kubecka and Svatora 1993, Flesch et al. 1994, Coleman and Wilson 1996, Fisher and Willis 1997, Cobb and Watzin 1998). Pumpkinseed use vegetated areas to acquire prey and seek refuge from predation (Dionne and Folt 1991, Coleman and Wilson 1996).

Yellow perch are benthic spawners whose eggs adhere to aquatic vegetation (Kubecka and Svatora 1993, Flesch et al. 1994). Flesch et al. (1994) used population survey techniques and angling creel data to examine yellow perch distribution patterns. In both cases, gravid females and new recruits were associated with vegetated littoral zones (Flesch et al. 1994). Kubecka and Svatora (1993) examined the efficiencies of mark-recapture techniques for yellow perch populations. All subsets of the population aggregated in dense patches of macrophytes during spawning (Kubecka and Svatora 1993). Wilcox and Meeker (1992) investigated the effects of macrophyte loss on fish abundance in a Minnesota lake regulated for water level. The loss of structurally diverse macrophyte beds led to decreased yellow perch reproduction (Wilcox and Meeker 1992).

Yellow perch depend on macrophytes to acquire prey items (Fisher Willis 1997, Cobb and Watzin 1998). Fisher and Willis (1997) studied the early life history of yellow perch in two lakes in South Dakota. Cladocerans and macro-invertebrates associated with aquatic vegetation dominated yellow perch diet in these two lakes (Fisher and Willis

1997). Cobb and Watzin (1998) studied yellow perch growth rates and abundance in Northern Lake Champlain, Quebec. The yellow perch population in Lake Champlain was stunted (consisting of many small and slow-growing fish) due to resource limitations (Cobb and Watzin 1998). The population was divided and placed into vegetated and non-vegetated fish enclosures. Growth rates were calculated for each set of enclosures (Cobb and Watzin 1998). The non-vegetated group was slow growing relative to the vegetated group. The lack of suitable vegetative habitat for prey items was the proposed mechanism limiting the sub-population (Cobb and Watzin 1998).

Pumpkinseed use aquatic macrophytes to capture prey and avoid predators (Dionne and Folt 1991, Osenberg 1994). Dionne and Folt (1991) examined the importance of macrophyte growth form, plant density, and prey abundance on pumpkinseed foraging rates. Foraging rates increased by two orders of magnitude when a sufficient quantity and composition of vegetation was present (Dionne and Folt 1991). Osenberg et al. (1994) investigated differences in population structure of two members of the *Lepomis* genus, bluegill (*Lepomis macrochirus*) and pumpkinseed. Pumpkinseed were characterised as littoral zone fish that depended on aquatic vegetation to acquire prey (Osenberg et al. 1994).

2.3 Population Interactions Between Northern Pike, Yellow Perch, and Pumpkinseed Sunfish

The majority of research on northern pike, yellow perch, and pumpkinseed population interactions has focused on the examination of predator-prey relationships

(Wolfert and Miller 1978, Snow and Kendall 1978). Prey species usually modify their behaviour to avoid predation (He 1990, Weaver et al. 1997, Jacobsen and Perrow 1998). Yellow perch prefer macrophytic habitat when predators are present (Weaver et al. 1997, Jacobsen and Perrow (1998). Weaver et al. (1997) studied the importance of macrophytes as habitat for yellow perch populations in Wisconsin. Yellow perch were more abundant where vegetation was species rich and structurally complex (Weaver et al. 1997). Jacobsen and Perrow (1998) studied the effects of predator presence on the diel migration patterns of yellow perch. Yellow perch spent the majority of daylight hours hiding in macrophytes. This was interpreted as evidence of predator avoidance behaviour. Migration from macrophytes changed from 13% during the day to 90% at night (Jacobsen and Perrow 1998).

Pumpkinseed displayed similar patterns of behaviour to yellow perch (Coleman and Wilson 1996). Specifically, pumpkinseed in a northern New York lake increased diurnal use of macrophytes in the presence of northern pike. Additionally, pumpkinseed migrated from the vegetation in low light conditions later in the day (Coleman and Wilson 1996). Further studies of predator avoidance behaviour on members of the *Lepomis* genus include Savino and Stein (1989) and He (1990). Savino and Stein (1989) examined anti-predator behaviour under different degrees of macrophyte structural complexity. Four different densities of macrophytes were examined: 0, 50, 250, and 1000 stems•m^{-1}. Prey fish that modified their behaviour in the presence of northern pike were compared to those that did not change their behaviour. In areas of high macrophyte density, sunfish (*Lepomis* sp.) were less likely to be consumed by northern pike (Savino and Stein 1989). He (1990) examined whole lake predation effects of northern pike on a prey fish assemblage. After a year of pre-manipulation study, northern pike were introduced into a small predator-free lake inhabited by bluegill sunfish. He (1990) estimated the direct and indirect predation effects of the northern pike introduction on sunfish populations. Observable indirect effects included increased use of aquatic vegetation in the presence of northern pike (He 1990).

Predator dynamics include prey acquisition and the regulation of preyfish abundance (Wolfert and Miller 1978, Savitz et al. 1983, Hanson and Leggett 1986, He 1990, Wahl and Stein 1991). Wolfert and Miller (1978) sampled northern pike from eastern Lake Ontario for two years to determine diet composition. While they concluded that the principal forage species was dependent on prey availability rather than prey type, yellow perch was the most common species in the northern pike diet (Wolfert and Miller 1978). Similarly, Wahl and Stein (1991) found that northern pike diets were dominated by pumpkinseed in late autumn and spring in areas where the two species overlapped. In areas where all three species occur, northern pike preferentially preyed on yellow perch rather than pumpkinseed (Wolfert and Miller 1978, Diana 1979).

Northern pike predation is an important mechanism for the regulation of forage fish abundance (Kempinger et al. 1978, Snow and Kendall 1978, Diehl and Ekloev 1995, Findlay et al. submitted 2000). Kempinger et al. (1978) investigated the effects of northern pike management on a yellow perch population. Yellow perch abundance declined when a minimum size limit was placed on northern pike angling (Kempinger et al. 1978). Kempinger concluded that an increase in predation by northern pike, due to less angling pressure, was the mechanism responsible for decreased yellow perch abundance (Kempinger et al. 1978).

Findlay et al. (submitted 2000) examined the lower level trophic effects of introducing northern pike to a yellow perch dominated lake in the ELA. Two years following the introduction of northern pike, the yellow perch abundance was greatly reduced. The decreases in yellow perch abundance and biomass were attributed directly to predation by northern pike (Findlay et al. Submitted 2000). Snow and Kendall (1978) found a similar relationship between northern pike and pumpkinseed. Northern pike regulated pumpkinseed populations when pumpkinseed abundance was initially low (Snow and Kendall 1978).

Population interactions between yellow perch and pumpkinseed, while historically less researched than northern pike and yellow perch, are fairly well understood (Hanson and Leggett 1986, Savitz et al. 1983). Hanson and Leggett (1986) concluded that yellow perch and pumpkinseed do not exhibit sufficient dietary overlap to stimulate competition. Additionally, Savitz et al. (1983) found that in areas of habitat overlap, yellow perch and pumpkinseed exhibit differential habitat utilization (i.e. time spent in individual habitat types). These two species also utilized different habitat for reproductive purposes (Kubecka and Svatora 1993, Flesch et al. 1994, Danylchuck and Fox 1994). Pumpkinseed are nest builders that spawn in sand and/or gravel substrate, and yellow perch are non-guarding spawners that broadcast eggs onto aquatic vegetation (Moyle and Cech 1996).

2.4 The Feeding Ecology of Northern Pike, Yellow Perch, And Pumpkinseed Sunfish

The species composition of northern pike diets has been researched extensively (Wolfert and Miller 1978, Mann 1982, Savitz et al. 1983, Hanson and Leggett 1986, Chapman and MacKay 1990, He 1990, Wahl and Stein 1991, Gres 1994, Morrow et al. 1997). Morrow et al. (1997) examined larval northern pike diets to determine preferred prey species. The commonly consumed taxa in larval diets after yolk absorption were copepods (Morrow et al. 1997). In a similar study by Gres (1994), larval northern pike diets were found to include Chaoboridae, Chironomidae, Diptera, and zooplankton. The shift to vertebrate prey items usually coincided with the onset of cannibalism, and varied from a total length of 60 mm to 100 mm. Further, cannibalism occurred in up to 66% of individuals > 60 mm (Bry et al. 1992).

Northern pike shift to an exclusively piscivorous diet starting at age one (Diana 1979, Mann 1982). Adult northern pike are euryphagous carnivores whose diet usually depends on the planktivorous fish species that are associated with their habitat (Moyle and Cech 1996). Mann (1982) investigated northern pike dietary preferences from the onset of larval exogenous feeding to individuals of age two. Northern pike older than age 0 were predominantly piscivorous. Cannibalism accounted for the majority of young northern pike mortality (Mann 1982).

Yellow perch populations experience size–dependant ontogenetic shifts in preferred prey items (Post and McQueen 1987, Paszkowski and Tonn 1994, Lott et al. 1996, Fisher and Willis 1997). Larval yellow perch start feeding exogenously at total lengths < 10mm. At this time the larval yellow perch diet is made up mostly of copepod nauplii. Yellow perch 10 – 50mm shift their diets to larger prey (i.e. adult copepods, small cladocerans, and daphnia) (Post and McQueen 1987, Fisher and Willis 1997). Juvenile yellow perch (TL > 50mm) and adults (TL > 150mm) feed on macro-invertebrates, large zooplankton, and amphipods (Lott et al. 1996, Paszkowski and Tonn

1994). Additionally, adult yellow perch cannibalize larval yellow perch and feed on other small fishes (Paszkowski and Tonn 1994).

Pumpkinseed sunfish exhibit an ontogenetic shift in diet similar to that of yellow perch (Keast 1978, Hanson and Qadri 1984, Godhino and Ferreira 1994). Exogenously feeding juvenile pumpkinseed select a mixed diet of zooplankton, cladocerans, copepods, chironomid larvae, and daphnids (Hanson and Qadri 1984, Godhino and Ferreira 1994). Adult fish are specialized gastropod carnivores. Pumpkinseed jaw morphology has evolved a specialized characteristic to crush gastropod shells. This characteristic does not become fully functional until pumpkinseed reach age 1 (Keast 1978).

2.5 The Management Implications of Macrophyte Removal

A comprehensive literature search was used to determine current management practices that relate to aquatic macrophytes. Most studies of macrophyte management focus on the control of eutrophication and invasion by nuisance exotic species of macrophytes. Macrophyte removal is used as a management tool to reduce the effects of nuisance macrophyte species. These effects include displacement of native macrophyte communities, fish stunting, reductions in water clarity, and reduced angler access (K. McClosky, pers. comm., Kansas Department of Wildlife and Parks, Wichita, Kansas 1997, Olsen et al. 1998, Wynne 1992).

Olson et al. (1998) examined the effectiveness of macrophyte removal to reverse population stunting of largemouth bass (*Micropterus salmoides*) and sunfish (*Lepomis* sp.) in four lakes that had extensive Eurasian watermilfoil (*Myriophyllum spicatum*). The removal of up to 50% of littoral zone macrophytes resulted in increased growth rates for age-3 bluegill (*Lepomis macrochirus*). However, the effects of macrophyte removal on total fish biomass and recruitment were not assessed. Therefore, it is unclear whether fish abundances were affected in a manner similar to that observed by Mills (in Jansen 2000). Perturbations such as this are considered short-term, and are assumed not to have an effect on fish production (Olson 1998).

Macrophyte removal is used to increase both water clarity and angler access in the United States (Wynne 1992). The stocking of triploid (sterile) grass carp (*Ctenopharyngodon idella*) is a popular and effective method to decrease aquatic vegetation (Wynne 1992, Bonar et al. 1993, K. McClosky, pers. comm., Kansas Department of Wildlife and Parks, Wichita, Kansas 1997). Grass carp are voracious herbivores that consume up to 150% of their total body weights in aquatic macrophytes per day (Singh 1995). Further, the introduction of grass carp has resulted in reductions of aquatic vegetation by up to 30% in reservoirs in Oregon (Bonar et al. 1993). Whether macrophyte reductions by grass carp have effects on native fish populations similar to those observed by Mills (in Jansen 2000) has not been well researched.

Aquatic systems can be negatively impacted by the introduction of grass carp (Thiery 1991, Rabasco unpub. data 1997, Hiney 1998). Thiery (1991), Rabasco (unpub. data 1997), and Hiney (1998) observed changes in native fish abundances similar to Mills (in Jansen 2000). Thiery (1991) observed ecosystem level effects of grass carp introduction to the Coachella Canal, California. These effects included the total elimination of all aquatic macrophytes, a reduction in the invertebrate population in the canal, and a reduction in largemouth bass abundance. Evidence from a small (15 ha) pond in Kansas indicates that largemouth bass recruitment declined for ten years after the introduction of grass carp (Rabasco unpub. data 1997). Fathead minnow (*Pimephales promelas*) abundance decreased from "plentiful" to "near zero" during the ten year span. The decrease in this prey species was attributed to the removal of reproductive substrate by grass carp (Rabasco unpub. data 1997). Hiney (1998) observed competitive displacement of native fish by grass carp in the Armand Bayou, Texas. The mechanism for displacement was the loss of reproductive habitat due to consumption of aquatic macrophytes by grass carp (Hiney 1998).

Many authors have addressed the effects of macrophyte removal on fish populations. These include Kendall and Nelson (1978), Swales (1982), Engel (1990), Maceina et al. (1991), Bettoli et al. (1992), Bryan and Scarnecchia (1992), Wilcox and Meeker (1992). Kendall and Nelson (1978) examined the effects of water level management on fish populations in Lake Oahe, Missouri. They observed changes similar to those observed by Mills (in Jansen 2000). Water level fluctuation and wave action reduced the amount of aquatic vegetation in the reservoir. The availability of northern pike and yellow perch spawning substrate declined and the abundance of both species was reduced.

Wilcox and Meeker (1992) also found similar results to Mills (in Jansen 2000) in regulated lakes in northern Minnesota. There was a positive correlation between the year-class strength and abundance of northern pike and the amount of near-shore vegetation (Wilcox and Meeker 1992). Drawdown of the lake led to reduced structural complexity in near-shore aquatic vegetation. Subsequently, there was a reduction in available spawning habitat for northern pike and yellow perch populations (Wilcox and Meeker 1992).

Swales (1982) investigated the effects of macrophyte removal on the River Perry in Shropshire, England. Again, the results of this study were similar to Mills (in Jansen 2000). Yellow perch, northern pike, and dace *(Leuciscus leuciscus)* dominated the fish community in this river. A 400 m length of the river was sub-divided into four 100 m sections. Each section differed according to macrophyte cutting regime: complete removal, partial removal, and two sections left undisturbed. Fish sampling by electrofishing was conducted in each section before and after macrophytes were removed. Removal methods (DeLury and Leslie methods) were used to determine fish densities in each experimental section. Northern pike densities (no. • m^2) in the fully denuded section dropped by a factor of four after macrophytes were removed.

Engel (1990) investigated the ecological impacts of mechanical macrophyte harvesting on Halverson Lake, Wisconsin. Of particular interest to this study was the direct effects of harvesting on young-of-the-year yellow perch and sunfish (*Lepomis* sp.). The surface area of the Halverson Lake was 70% covered by coontail (*Ceratophyllum demersum*), and pondweed (*Potamogeton* sp.). Fish sampling and abundance estimates (via electrofishing gear) were performed before and after macrophytes were harvested. In June and July of 1980 mechanical harvesters removed 70% of submersed macrophytes in 1.4 m swaths. Harvesting removed approximately 52, 000 fish fry during 1980 and 1981 (Engel 1990). Engel (1990) estimated that this number constituted approximately 25% of all the fish fry in the lake.

Bettoli et al. (1992) examined the effects of macrophyte removal on Lake Conroe (8,100 ha), southeast Texas. Stocked grass carp reduced littoral zone macrophytes from 44% to 0% in seven years. A seven-year monitoring program was initiated after the grass carp were stocked. First, water clarity decreased as a result of increased algae biomass. Second, two years after total macrophyte removal, zooplankton abundance decreased by 50%. Third, they observed changes in fish abundance similar to the Lake 191 experiment. Abundance of forage fishes (i.e. threadfin shad, *Dorosoma petenense*, bullhead minnow, *Pimephales vigilax*, and blacktail shiner, *Notropis venustus*, increased by four orders of magnitude (Bettoli et al. 1992). However, after all macrophytes were removed centrarchid (*Lepomis* sp.) abundance decreased.

In a separate but related study of Lake Conroe, Maceina et al. (1991) studied the effects of macrophyte removal by grass carp on black and white crappie (*Poxomis nigromaculatus* and *P. annularis*). Individuals were collected annually for seven years after littoral zone macrophyte cover was reduced to 0%. Both populations experienced decreases in abundance similar to the changes in northern pike abundance observed by Mills (in Jansen 2000). From 1980 to 1986 the number of fish/hectare of age one white and black crappie dropped from a mean value of 119 to a mean value of 0.4. Additionally, mean catch-per-unit-effort (CPUE) decreased from 1.4 prior to macrophyte removal to 0.6 after macrophyte density was reduced to 0%.

Bryan and Scarnecchia (1992) conducted a study to determine the differences in young-of-the-year fish abundance and species richness between disturbed and undisturbed sites in Spirit Lake, northwestern Iowa. The disturbed sites were developed shorelines that had littoral zone macrophytes removed. The study involved sampling thirty-four species of fish (including northern pike, yellow perch, and sunfish sp.). Young-of-the-year fish were sampled for two years from nine 100 m blocks from either a disturbed (i.e. residential development of shoreline) or natural site (i.e. no development). Catch-per-unit-effort (CPUE) was used to describe the relative abundance of fish species at different sampling sites. The researchers quantified the total numbers of different species caught at each site to determine species richness. Differences in fish abundance between developed and undeveloped sites were similar to the changes Mills (in Jansen 2000) observed after macrophytes were harvested from Lake 191. Natural sites contained both higher species richness and abundance of individual species than disturbed sites (Bryan and Scarnecchia 1992).

2.6 Summary

It is well established that aquatic macrophytes are important components of fish habitats. Northern pike frequently associate with macrophytes (Franklin and Smith 1963, Diana 1977 and 1979, Dube and Gravel 1980, Chapman and MacKay 1984, Osterberg 1985, Cook and Bergersen 1988, Savino and Stein 1989, Headrick and Carline 1993, Moyle and Cech 1996, Farrell and Werner 1996). Northern pike spawning success is dependent on a high proportion of vegetated littoral zone habitat (Dube and Gravel 1980, Moyle and Cech 1996). Further, northern pike associate with macrophytes for the acquisition of prey (Diana 1979, Savino and Stein 1989, Moyle and Cech 1996).

Yellow perch and pumpkinseed also utilize littoral zone macrophytes (He 1990, Dionne and Folt 1991, Wilcox and Meeker 1992, Kubecka and Svatora 1993, Flesch et al. 1994, Osenberg et al. 1994, Coleman and Wilson 1996, Fisher and Willis 1997, Cobb and Watzin 1998). Yellow perch use littoral zone macrophytes for reproduction, refuge from predation, and acquiring prey (He 1990, Dionne and Folt 1991). Pumpkinseed utilize macrophytes for predator avoidance and prey acquisition (Dionne and Folt 1991, Osenberg et al. 1994, Coleman and Wilson 1996)

In areas where northern pike occur with yellow perch and/or pumpkinseed, the interactions between these species are characterized as predator-prey relationships (Wolfert and Miller 1978, Snow and Kendall 1978). Northern pike predation is an important mechanism for the regulation of yellow perch and pumpkinseed populations (Kempinger et al. 1978, Snow and Kendall 1978, Diehl and Ekloev 1995, Findlay et al. submitted 2000). Additionally, yellow perch and pumpkinseed increase their use of macrophytes in the presence of northern pike (Coleman and Wilson 1996, Weaver et al. 1997, Jacobsen and Perrow 1998).

Northern pike, yellow perch, and pumpkinseed all exhibit size-dependent ontogenetic shifts in diet (Keast 1978, Wolfert and Miller 1978, Mann 1982, Savitz et al. 1983, Hanson and Qadri 1984, Hanson and Leggett 1986, Post and McQueen 1987, Chapman and MacKay 1990, He 1990, Wahl and Stein 1991, Godhaino and Ferreira 1994, Gres 1994, Paszkowski and Tonn 1994, Lott et al. 1996, Fisher and Willis 1997, Morrow et al. 1997). Larval northern pike consume mostly benthic invertebrates and zooplankton (Gres 1994). The first vertebrate prey items that northern pike eat are usually other small northern pike (Gres 1994). Further, northern pike cannibalism continues throughout adult stages (Wolfert and Miller 1978).

Larval yellow perch consume small zooplankton and benthic invertebrates (Post and McQueen 1987). Juvenile and adult yellow perch eat zooplankton, benthic invertebrates and small fish including yellow perch (Fisher and Willis 1997). The diet of larval and juvenile pumpkinseed is similar to yellow perch (Hanson and Qadri 1984). Adult pumpkinseed are specialized gastropod carnivores (Keast 1978).

Macrophyte removal is used as a management tool to reduce the effects of eutrophication and nuisance macrophyte species (Newman et al. 1996). Additionally, macrophytes are removed to increase water clarity and angler access (Wynne 1992). Removing littoral zone macrophytes has a variety of effects on resident fish populations. These effects include reduced recruitment, reduced population density, removal of fish fry by harvesting equipment, and reductions in fish abundance similar to those observed by Mills (in Jansen 2000, Kendall and Nelson 1978, Swales 1982, Engel 1990, Maceina et al. 1991, Bettoli et al. 1992, Bryan and Scarnecchia 1992, Wilcox and Meeker 1992).

Understanding the results of other studies on the importance of macrophytes to fish populations and the effects of macrophyte removal on fish populations was essential to this study for both the formation of hypotheses and the interpretation of results. Additionally, it was important to understand the reasons that resource agencies implement macrophyte harvesting programs and allow landowners to remove macrophytes.

3. METHODOLOGY

3.1 Field Sampling of Fish

The sampling periods were chosen based on what was already known about fish growth in Lake 191. Most growth for the fishes in Lake 191 takes place during the period from late May to early September (K. Mills, pers. comm., Freshwater Institute, Winnipeg, Manitoba 1999). Items found in the stomachs of fishes during this period are important for overall fish production in Lake 191. Thus, sampling during this period provided links to the changes in fish abundance observed by Mills (in Jansen 2000).

Field sampling was conducted during three periods in the summer of 1999: June 1st – June 28th, July 16th – August 10th, and August 29th – September 10th. Yellow perch and pumpkinseed were sampled during all three periods. Northern pike were sampled only during the second period for two reasons. First, macrophyte removal had reduced northern pike abundance by more than 50% of the original pre-manipulation estimates. Removing more individuals could have confounded interpretation of the experiment due to over-exploitation. Second, mid-summer is the period of maximum growth for northern pike in Lake 191 (K. Mills, pers. comm., Freshwater Institute, Winnipeg, Manitoba 1999). Because yellow perch and pumpkinseed were very abundant in Lake 191, the total number removed during the sampling periods was likely less than 1% of each population.

3.2 Sampling Schedule

June 1999: The first sampling period began June 1st at Lake 191 in the ELA. Yellow perch were sampled from June 1st to June 16th. Pumpkinseed were sampled from June 8th to June 28th.

July – August 1999: The second sampling period began July 16th and concluded August 10th. Yellow perch and pumpkinseed were sampled from July 16th to July 26th. Northern pike were sampled from July 24th to August 10th.

August – September 1999: The final sampling period was conducted from August 29th to September 10th. Yellow perch and pumpkinseed were sampled from August 29th to September 10th.

Three separate samples of the Lake 191 yellow perch and pumpkinseed populations were collected during the 1999 field season. The first three days of a sampling week were spent capturing targeted species. The next three days were spent processing the samples (see below for processing details).

Sampling consisted of two different methods and gear types. Preyfish and juvenile northern pike (< 300mm) were sampled with a 50 m beach seine using methods described by Hayes (1983) and angling was conducted using small lures. Adult northern pike were sampled via angling using spincasting tackle and barbless lures. Seining took place in vegetated and denuded areas in the littoral zone. A two-person team using a small motor boat operated the seine. Sampling consisted of a four-step process. First, the towline of one of the wings of the seine was anchored to the shore. Second, the opposite wing was attached to the stern of a small motor boat and the net was piled in the boat. Third, the seine was set in a semi-circle as the boat moved around and through the target area and the wing attached to the boat was brought to shore. Finally, the wings and bag were pulled onto shore and the catch was removed. The catch was sorted according to species, and species were pooled according to the day of capture. Individual fish were measured using a standard measuring board (FL ± 1mm), and this information was used to generate length-frequency distributions. Fish were frozen directly after capture to slow digestion of stomach contents, and brought to the lab for processing (Murphy and Willis 1996).

3.3 Fish Stomach Content Analysis

Frozen fish were thawed and dissected to analyze stomach contents. Stomachs were first removed starting from the juncture of the stomach and esophagus to the juncture of the stomach and the duodenum. After removal, stomachs were slit longitudinally and the contents flushed with 70% ethyl alcohol onto a glass petri dish. Stomach contents were sorted, counted, and identified to species level using a dissecting microscope (500X). For items that were in the advanced stages of digestion, primarily fishes, identification was achieved through the use of reference fish species and body parts (i.e. otoliths and preopercles) (Ogle et al. 1996). Invertebrate prey items were identified to family and/or species when possible.

Stomach contents were weighed using a standard electronic laboratory scale (± 1 mg). Stomach content weight was determined as the difference between the weight of full and empty stomachs (Bagenal 1978). Diet composition for each fish was determined by calculating the percent composition by number of each prey category. Diet composition was then pooled for each species of fish.

Northern pike scales found in fish stomachs were used to estimate the fork lengths of the fish that were consumed. Analyses were performed according to the method established by Frost and Kipling (1959). This method uses a body – scale relationship to estimate the total lengths of fish. The body – scale relationship is:

$\log L = 0.836 + 0.749 \log S$ in which: L = total length of the fish,

S = length of the scale.

For northern pike stomachs that contained several scales an average scale length was used in the body – scale equation. Total length estimates were converted to fork length estimates using the method established by Carlander (1969). The conversion equation is:

$FL = TL \bullet 0.937$ in which: FL = fork length, and

TL = total length.

These fork lengths were then used to generate a length frequency distribution for the northern pike that were eaten. This length frequency distribution was then compared to the gut content analysis (GCA) and whole lake (WL) length frequency distributions of sampled fish.

3.4 Analyses of Stomach Content Data

Three methods were used to summarize the stomach content data. First, the percent composition by number of dietary items in all of the stomachs combined for a species for each sample was determined (Bagenal 1978). Second, the relative importance of prey taxa was determined for all of the stomachs of a species combined for each sample period. Third, the percent composition by number of diet items in all of the stomachs combined for size classes of a species for each sampling period was determined.

The percent composition by number of dietary items was conducted in three steps. First, the prey items in each individual fish stomach were identified. Second, the individual prey items were grouped into 'gut content categories' (i.e. Benthic Invertebrates, Fish Items, and Zooplankton). Third, the percent composition by number of each content category was calculated for each species for each sample period.

The relative importance of prey taxa was estimated using the Relative Importance Index (RI) established by George and Hadley (1979). This index is a mean of percent frequency of occurrence, percent composition by number, and percent composition by mass, for all prey taxa. The RI Index is used to reduce bias that occurs from using any one of the three aforementioned measures individually (Wallace 1981). For a given fish species the RI_i of a prey taxon is calculated as follows:

$$RI_i = 100\ AI_i / \Sigma^n{}_{i=1}\ AI_i$$

in which:

AI_i = percent frequency of occurrence of prey taxon i + percent total numbers of prey taxon i + percent total mass of the prey taxon i,

n = number of different prey types,

% frequency of occurrence = percentage of all stomachs containing food in which prey taxon i occurred,

% total numbers = percentage that items of prey taxon i contributed to the total number of food items in all stomachs, and

% total mass = percentage that the mass of prey taxon i contributed to the total mass of food in all stomachs.

The RI values for individual prey taxa were combined to form amalgamate RI values for the gut content categories. Additionally, RI values were calculated for individual zooplankton species that occurred in yellow perch and pumpkinseed diet. Partially digested fish items that were identified by hard structures (i.e. vertebral columns, scales, etc.) were omitted from the RI calculations, because they underestimate the mass component of the calculation (Little et. al. 1998). The majority of food found in northern pike stomachs was partially digested fish items. Therefore, the RI was not applied to the northern pike samples. These data were then organised according to sample period. This information provides insight into the relative importance of diet items over time.

The diet composition of yellow perch, pumpkinseed, and northern pike is often a function of the size class of the individual fish (Keast 1978, Post and McQueen 1987). Therefore, analyzing the diet composition of the fishes sampled from Lake 191 as a function of their size class may reveal important causation for changes observed by Mills (in Jansen 2000) occurred. The diet composition information was broken down by predator size class using two steps. First, the percent composition by number of diet items in individual fish stomachs was determined for each species in each sample period. Second, the average percent composition by number of a diet item was calculated for 10mm size classes of each fish species for each sample period. This analysis highlights the importance of the size selectivity of fish feeding behaviour.

4. RESULTS

4.1 Length Frequency Distributions of Fish Populations and the Subset Used for Gut Content Analysis

Length frequency distributions of the fish populations in Lake 191 have been generated from complete population censusing in fall 1999 and these were compared to the subset for each species used for stomach analysis (Figs. 6 - 8). These complete census distributions have been used to monitor the effects of macrophyte removal on the fish populations in Lake 191 (Jansen 2000). Data resulting from the gut content analysis samples in 1999 were also used to generate length frequency distributions (GCA, N = 90 for yellow perch and pumpkinseed, and N = 20 for northern pike) (Figs. 6 - 8). These distributions were used to determine the representativeness of the GCA samples (Figs. 6 – 8).

The northern pike GCA samples covered most of the middle range of the frequency distributions generated previously by Mills (in Jansen 2000). Fish missing from the northern pike GCA samples included YOY northern pike and fish from the largest size classes (Fig. 6). The size classes of northern pike in the 'GCA' length-frequency distributions ranged from 231 mm to > 420 mm (Fig. 6). The size classes in the GCA northern pike samples had nearly equal numbers of fish in each. The majority of northern pike in the WL distributions were in the 301 mm to > 420 mm size classes (Jansen 2000) (Fig. 6).

The yellow perch and pumpkinseed GCA samples spanned almost the entire range of the WL samples, although the largest yellow perch and pumpkinseed were not sampled for gut content analysis (Figs. 6 & 7). The size classes in the GCA yellow perch

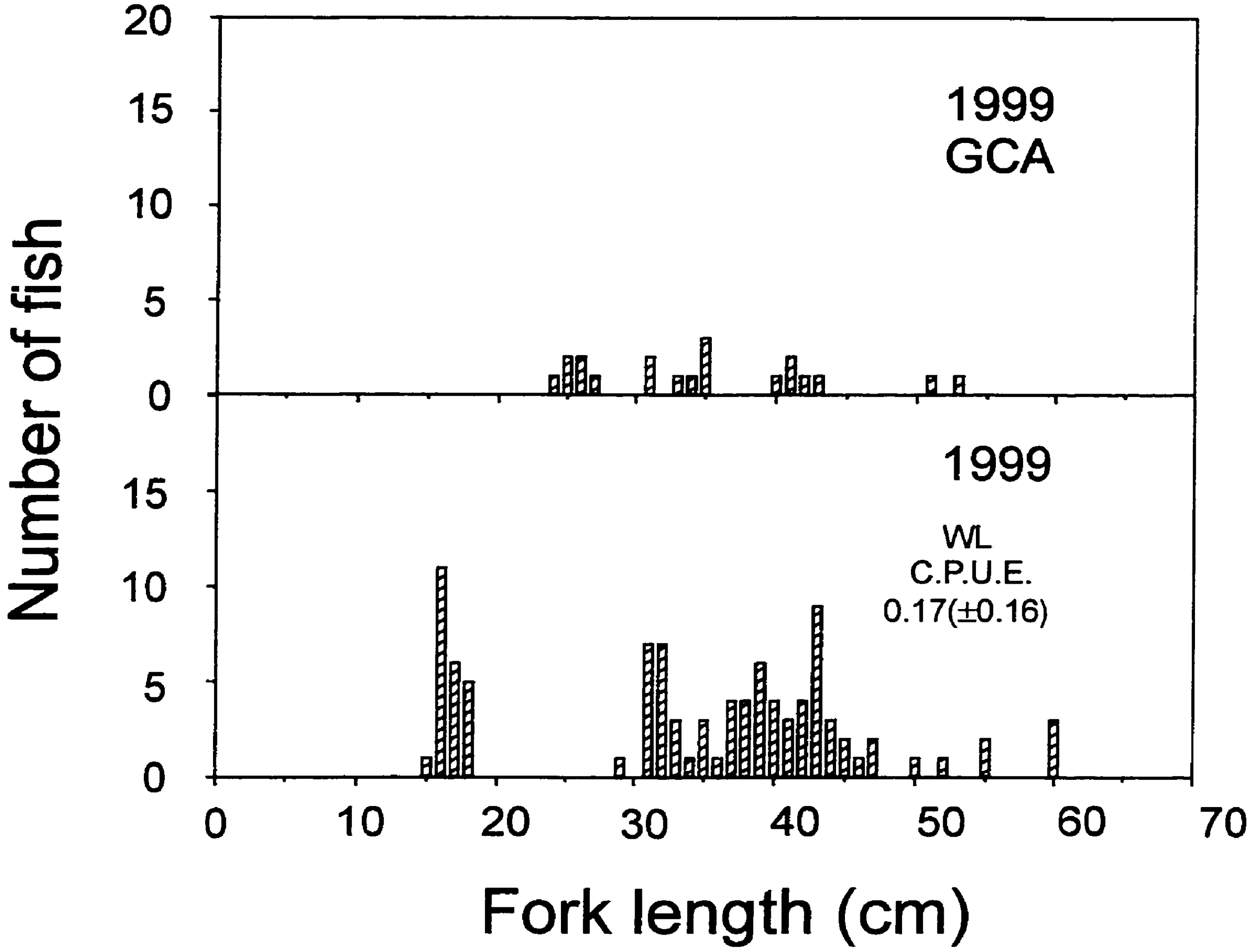


Figure 6: Length frequency distributions for northern pike sampled for gut content analysis (GCA) and whole lake analysis (WL) in ELA Lake 191 in 1999. Mean Catch-Per-Unit-Effort (C.P.U.E) and 95% confidence intervals are included for WL.

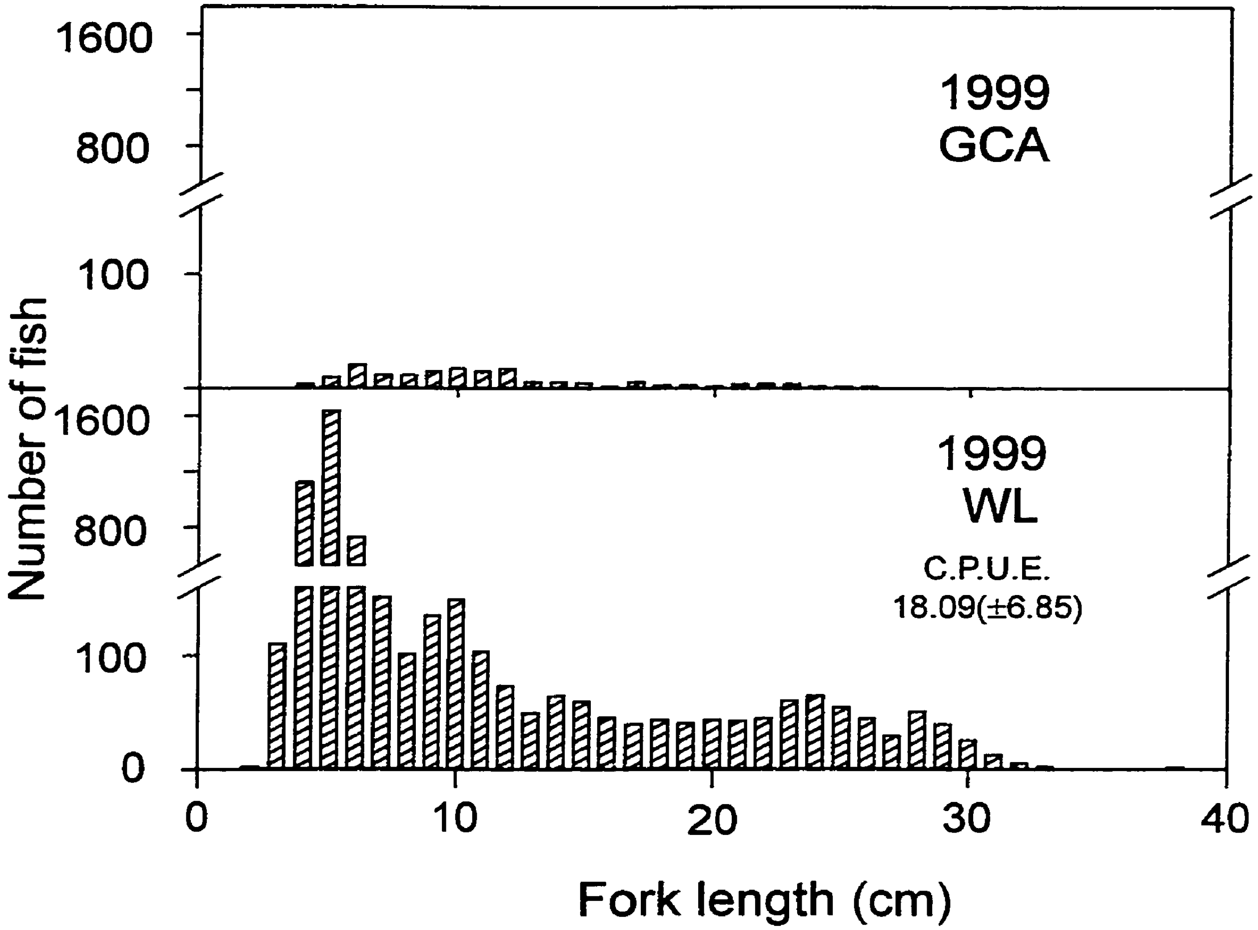


Figure 7 : Length frequency distributions for yellow perch sampled for gut content analysis (GCA) and whole lake analysis (WL) in ELA Lake 191 in 1999. Mean Catch-Per-Unit-Effort (C.P.U.E) and 95% confidence intervals are included for WL.

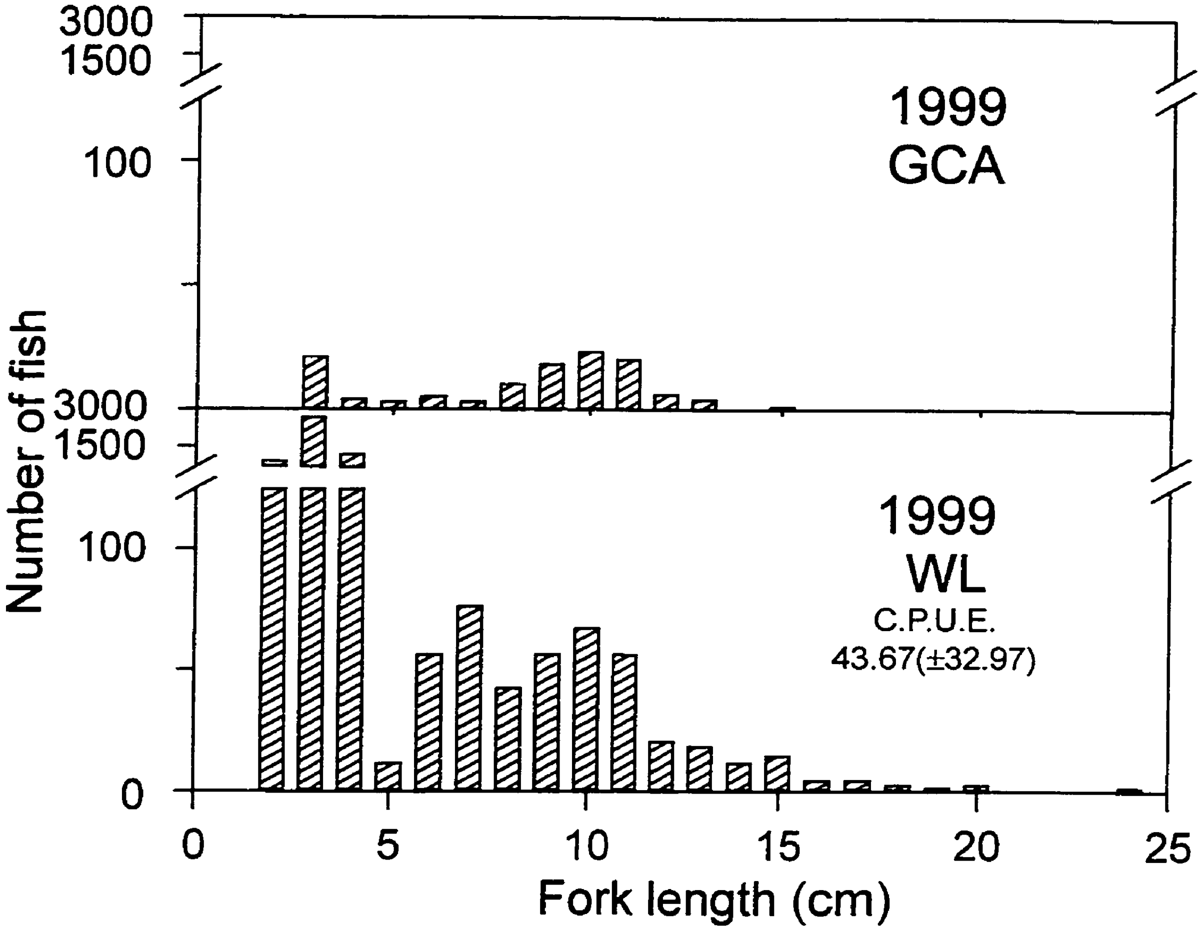


Figure 8: Length frequency distributions for pumpkinseed sampled for gut content analysis (GCA) and whole lake analysis (WL) in ELA Lake 191 in 1999. Mean Catch-Per-Unit-Effort (C.P.U.E) and 95% confidence intervals are included for WL.

frequency distribution ranged from 51 – 230 mm while the WL distribution ranged from 31 to 380 mm (Fig. 7). Few individuals in the population were > 300mm. The size classes in the GCA pumpkinseed frequency distribution ranged from 20 – 140 mm while the WL distribution ranged from 10 – 200 mm. Few individuals in the population were > 150 mm.

4.2 Gut Content Analysis

Results from the gut content analysis are presented in three formats for each species: percent composition by number of diet items in stomachs, the relative importance of diet items in stomachs using the Relative Importance Index (George and Hadley 1979), and percent composition by number of diet items in each size class of fish for each species.

4.2.1 Percent Composition by Number of Diet Items in Fish Stomachs

Zooplankton and benthic invertebrates were the primary components of yellow perch diet. Zooplankton species included *Bosmina longirostiris*, *Chaoborus* sp., *Leptodora kinditii*, *Daphnia pulex*, and *D. galeata mendota*. Copepod naupli were also present. Benthic invertebrates found in yellow perch stomachs included chironomid larvae, trichopteran larvae, Ephemerellidae nymphs, Lestidae nymphs, Macromiidae and Gomphidae nymphs, *Hyalella azteca*, clams of the family Sphaeridae, aquatic mites, and crayfish. The average percent composition by number of zooplankton and benthic invertebrates for all sampling periods was 45% and 51%, respectively (Fig. 9).

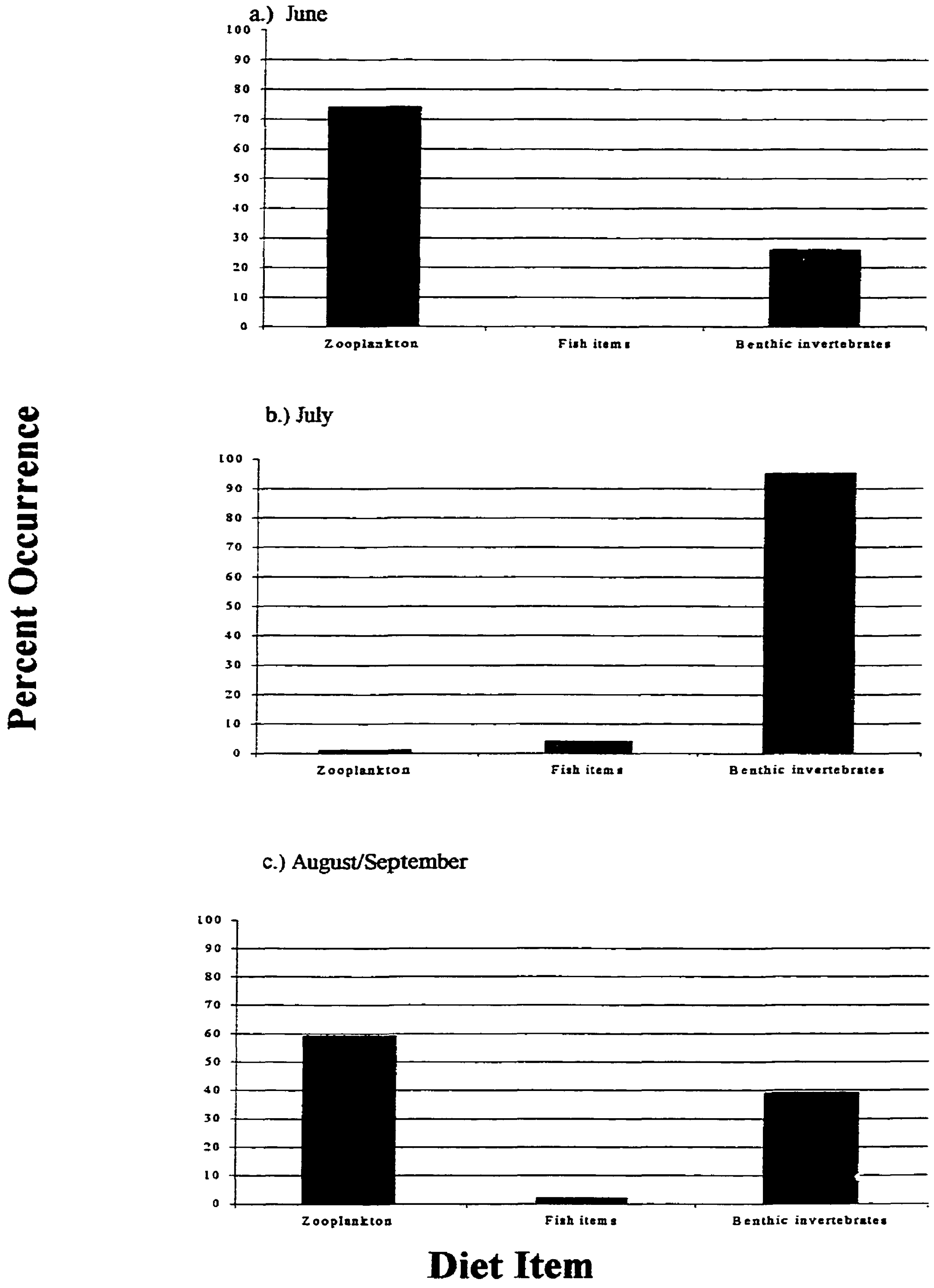
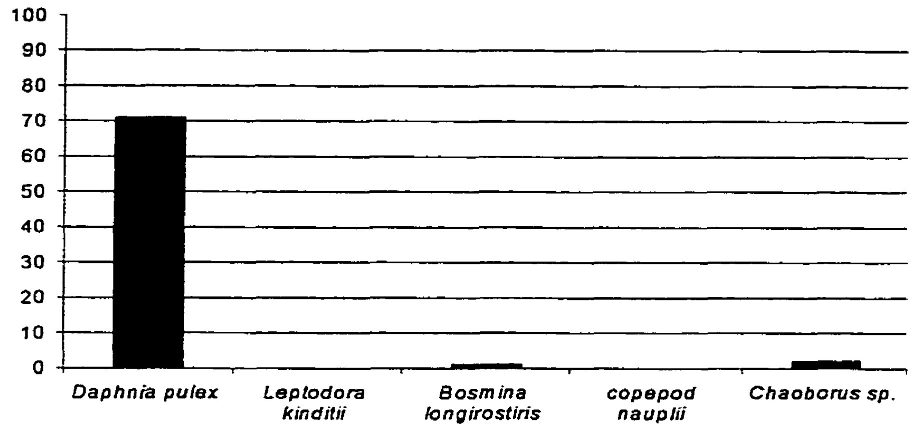


Figure 9 a.) – c.): Diet of yellow perch (expressed as percent total numbers of items found in yellow perch stomachs) (N = 90, with 30 fish sampled in each period) in ELA Lake 191: 1999.

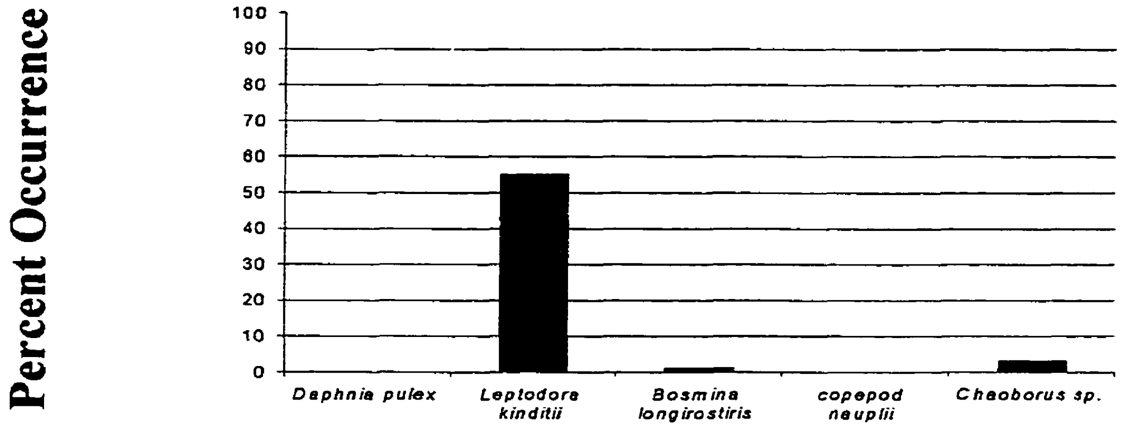
Consumption of zooplankton by yellow perch changed dramatically from one period to another. Yellow perch ate mostly zooplankton in the first (74%) and third (59%) periods (Fig. 9). Further, *D. pulex* made up 71% of yellow perch diet in the first sampling period, and *L. kinditii* made up 55% of yellow perch diet in the third sampling period (Fig. 10). Yellow perch consumed few zooplankton (1%) in the second sampling period (Fig. 9).

Yellow perch consumption of benthic invertebrates and fish also differed according to sampling period (Fig. 9). Benthic invertebrates did not account for a majority of yellow perch diet in the first (26%) and third (39%) sampling periods. However, the majority of yellow perch diet in the second sampling period was benthic invertebrates (95%). No fish were found in yellow perch stomachs in the first sampling period. Fish made up 4% and 2% of yellow perch diet in the second and third sample periods, respectively. Yellow perch consumed northern pike, pumpkinseed and other yellow perch. The total percentage of empty yellow perch stomachs for all three sampling periods was 9%. There were no yellow perch in sample period one with empty stomachs. Sample periods two and three had an almost equal number of yellow perch with empty stomachs (four and six respectively).

Benthic invertebrates and zooplankton were the most frequent components of pumpkinseed diet (Fig. 11). Benthic invertebrates included larvae of the groups Chironomidae, Trichoptera, Coleoptera; nymphs of the families Ephemerellidae, Lestidae, Gomphidae, Macromiidae, Liellullidae and/or Cordullidae; and Sisyridae; clams of the family Sphaeriidae; aquatic mites; gastropods; and *H. azteca*. The species composition of zooplankton food items eaten by pumpkinseed were similar to those eaten a.) June



b.) July



c.) August/September

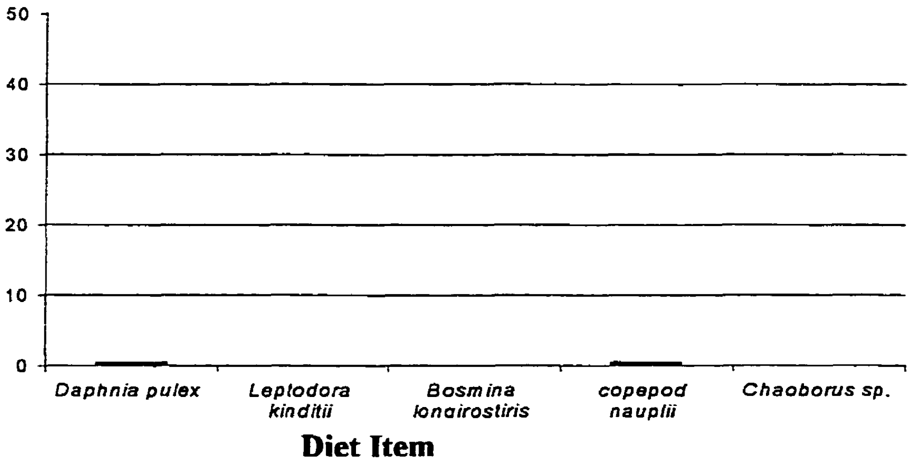
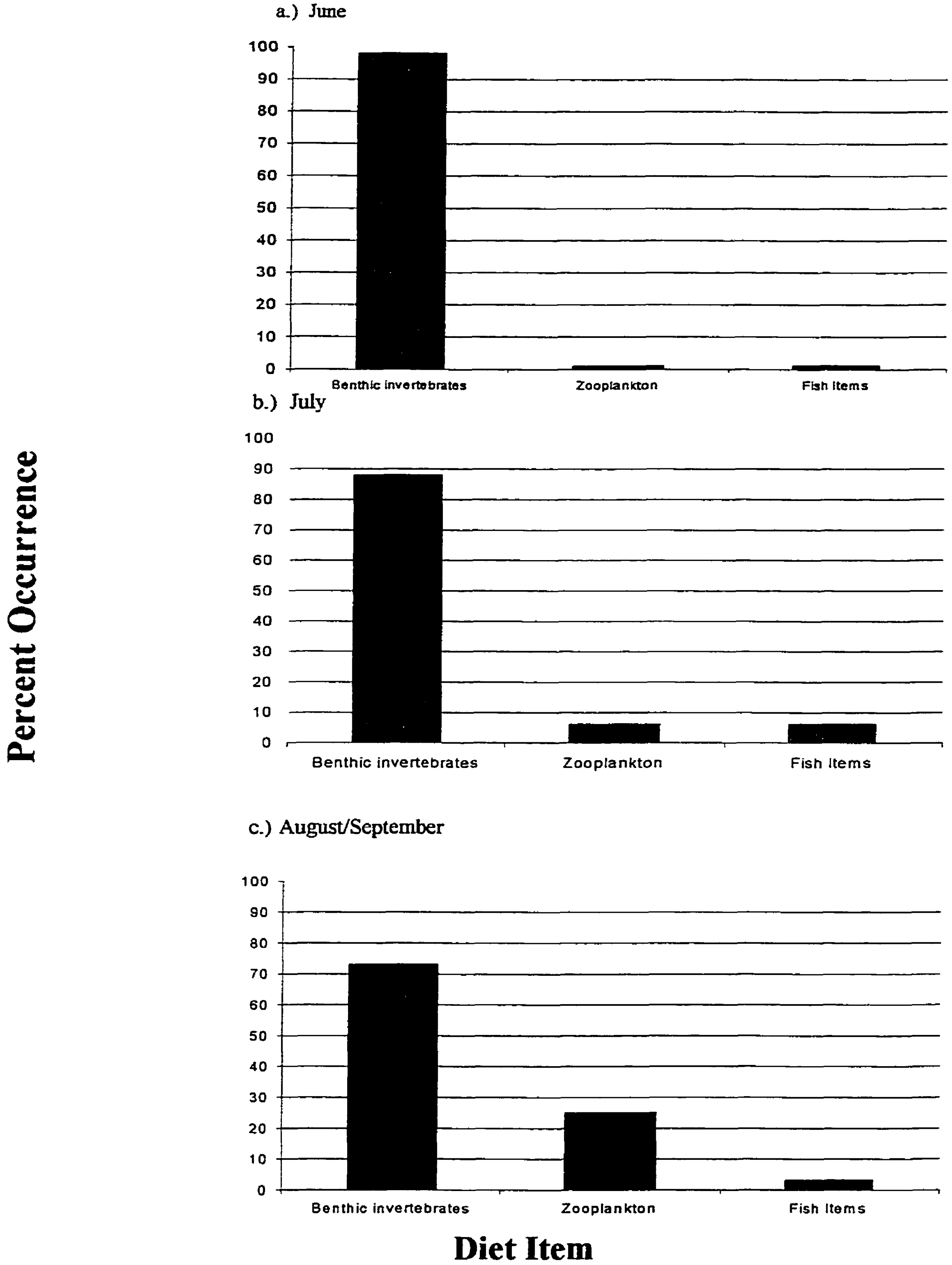


Figure 10 a – c: Yellow perch consumption of zooplankton (N = 90, with 30 fish in each period) in ELA Lake 191: 1999.



a.) June

b.) July

c.) August/September

Figure 11 a – c: Pumpkinseed diet (expressed as a percent of total numbers of items found in pumpkinseed stomachs (N = 90, with 30 fish in each period) in ELA Lake 191: 1999.

by yellow perch, but differed in the exclusion of *D. galeata mendota* and the inclusion of both *Acanthocyclops vernalis* and *Diaptomus minutus*. *B. longirostiris* and *Choaborus* sp. were the most frequent zooplankton species (Fig. 12).

Benthic invertebrates always comprised the overwhelming majority of food items found in the stomachs of pumpkinseed, although this importance seemed to decrease somewhat over the course of the summer. The percent composition by number of benthic invertebrates in pumpkinseed stomachs was 98%, 88%, and 73% in sample periods one, two, and three respectively (Fig. 11). Zooplankton comprised a smaller percentage of pumpkinseed diet than benthic invertebrates, although this percentage seemed to increase over the course of the summer. The percent composition by number of zooplankton in pumpkinseed stomachs was 1%, 6%, and 25% in sample periods one, two, and three, respectively (Fig. 11). The most commonly consumed zooplankton species and/or species associated with plankton were *B. longirostiris* and *Choaborus* sp. (Fig. 12).

Fish items did not comprise a large percentage of pumpkinseed diet. The percent composition by number of fish items in pumpkinseed stomachs was 1%, 6%, and 3% in sample periods one, two, and three respectively (Fig. 11). Pumpkinseed consumed northern pike, yellow perch, and other pumpkinseed. The total percentage of empty pumpkinseed stomachs for all three sampling periods was 18%. There were no pumpkinseed in sample period one with empty stomachs. Sample period three had the highest percentage of empty stomachs (43%).

The diet of northern pike differed considerably from the diets of yellow perch and pumpkinseed sampled from Lake 191 (Fig. 13). Of the stomachs that contained food, 67% (six of nine) contained northern pike morphological structures. These included

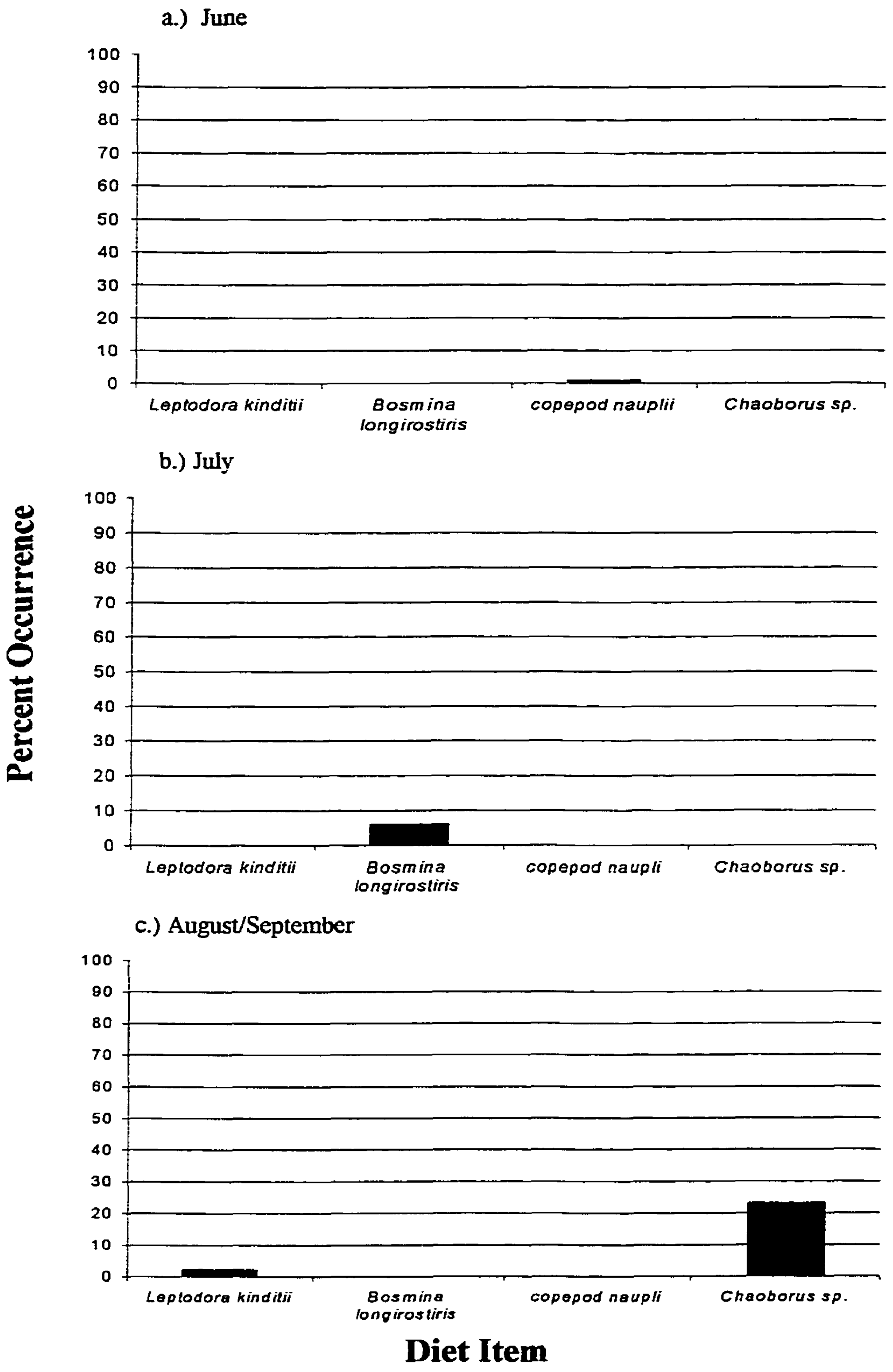


Figure 12 a – c: Pumpkinseed consumption of zooplankton (N = 90, with 30 fish in each period) in ELA Lake 191: 1999.

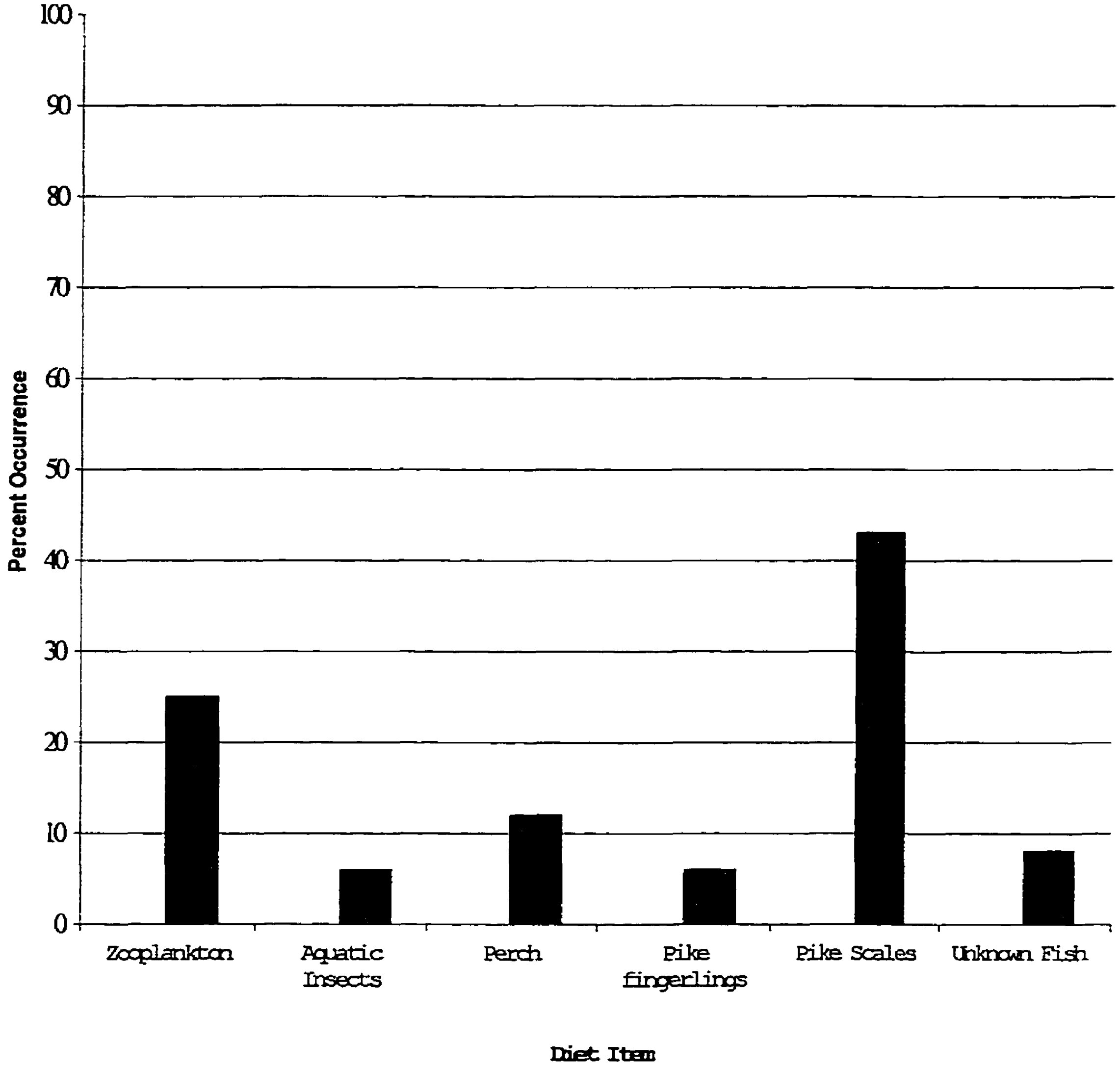


Figure 13: Northern pike diet (expressed as percent total numbers of items found in northern pike stomachs) (N = 20, with 9 empty stomachs) in ELA Lake 191: 1999.

scales, fish vertebral columns accompanied by scales, and fully intact northern pike fingerlings. The size classes of northern pike that were eaten by fish ranged from 30 mm to 210 mm. The majority of northern pike eaten by fish were less than 110 mm (Fig. 14). The second most common item found in northern pike stomachs was zooplankton (25%). Yellow perch constituted 12% of the total diet of northern pike (Fig. 13). Nearly half of all northern pike sampled (45%) had empty stomachs.

4.2.2 Relative Importance of Diet Items in Yellow Perch Stomachs

Seasonal variation in yellow perch and pumpkinseed diet was assessed using the Relative Importance Index (RI) (Figs. 15 & 16). In the first sample period, zooplankton and benthic invertebrates were equally important in yellow perch diet (RI = 47% and 53%, respectively). In the second sample period, benthic invertebrates made up the majority of yellow perch diet (RI = 98%). In the final sample period, benthic invertebrates were more than twice as important as zooplankton in yellow perch diet (RI = 71% and 29%, respectively. The two zooplankton species with the greatest RI were *D. pulex* and *L. kinditii* (Fig. 16). In the first sample period, benthic invertebrates accounted for the majority of pumpkinseed diet (RI = 94%). In the second sample period, benthic invertebrates were nearly seven times more important than zooplankton in pumpkinseed diets (RI = 87 and 13%, respectively). In the final sample period, benthic invertebrates were three times more important than zooplankton in pumpkinseed diet (RI = 765 and 24%, respectively) (Fig. 15). The two zooplankton species with the greatest RI were *B. longirostiris* and *Choaborus* sp. (Fig. 16).

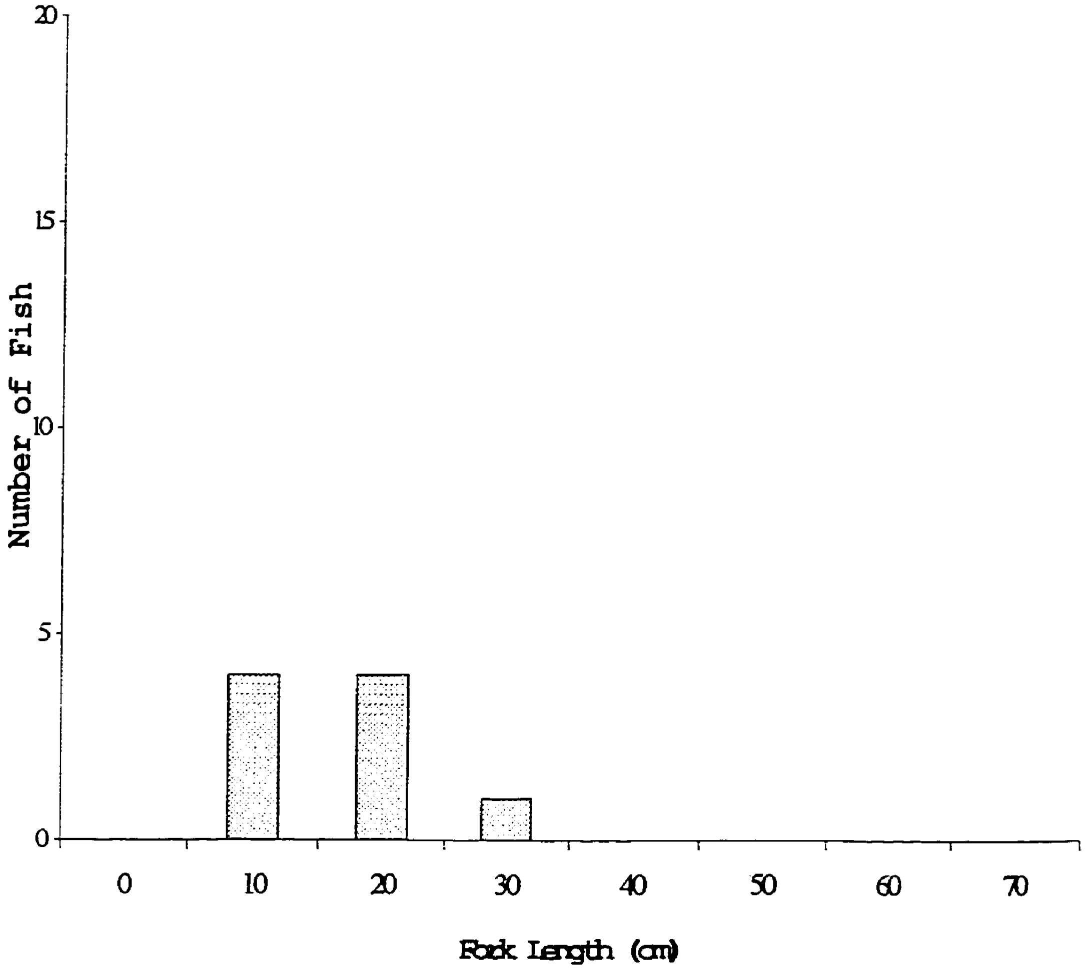


Figure 14: Estimated sizes of northern pike consumed by northern pike, yellow perch, and pumpkinseed (N = 9) in ELA Lake 191: 1999 [Numbers on the X axis indicate the upper limit of size classes (e.g. 10 indicates the 0 to 10cm size class)].

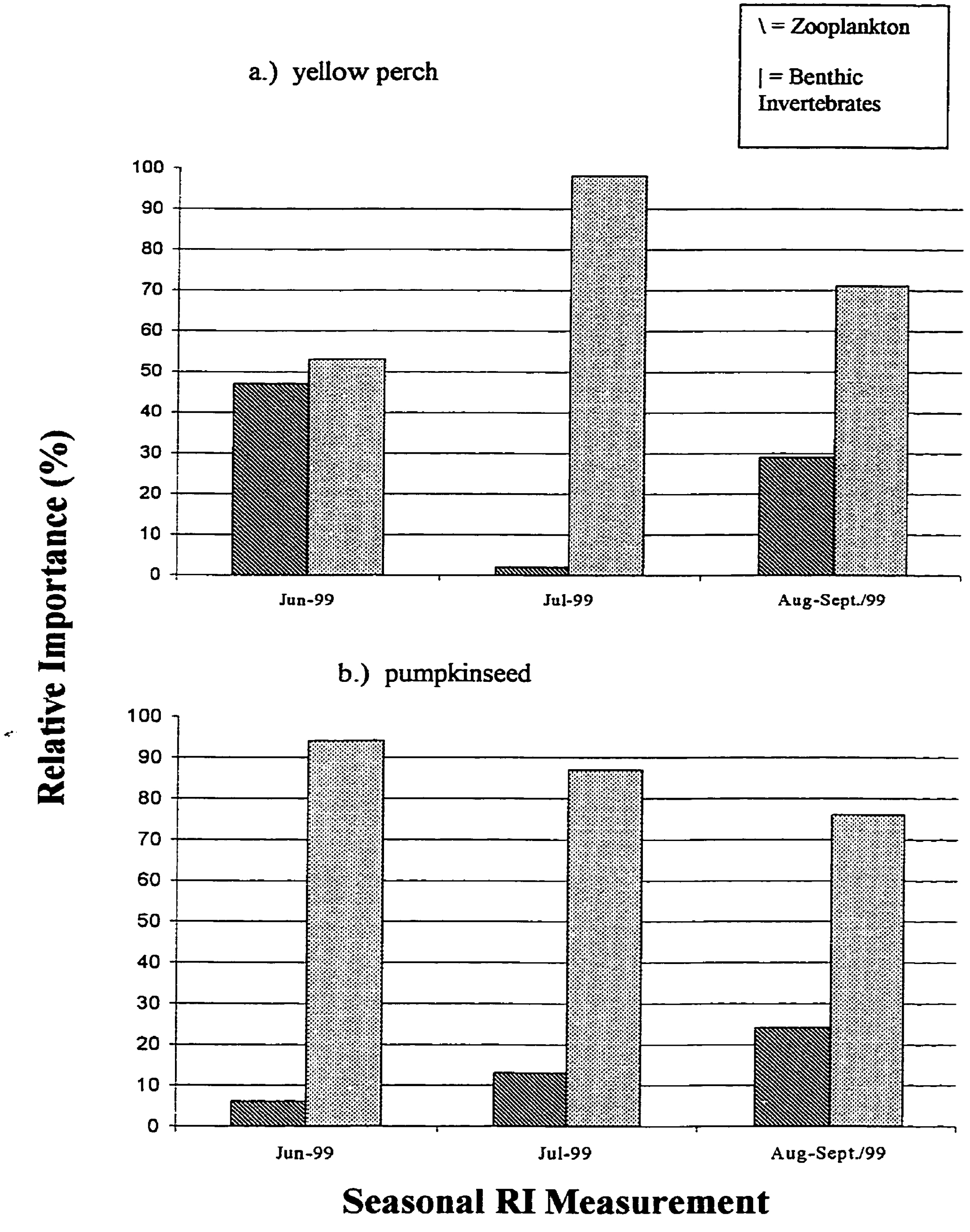


Figure 15: Seasonal variation in the diet of a.) yellow perch and b.) pumpkinseed based on the Relative Importance (RI) index of two categories of prey (For all sampling periods N = 30) in ELA Lake 191: 1999.

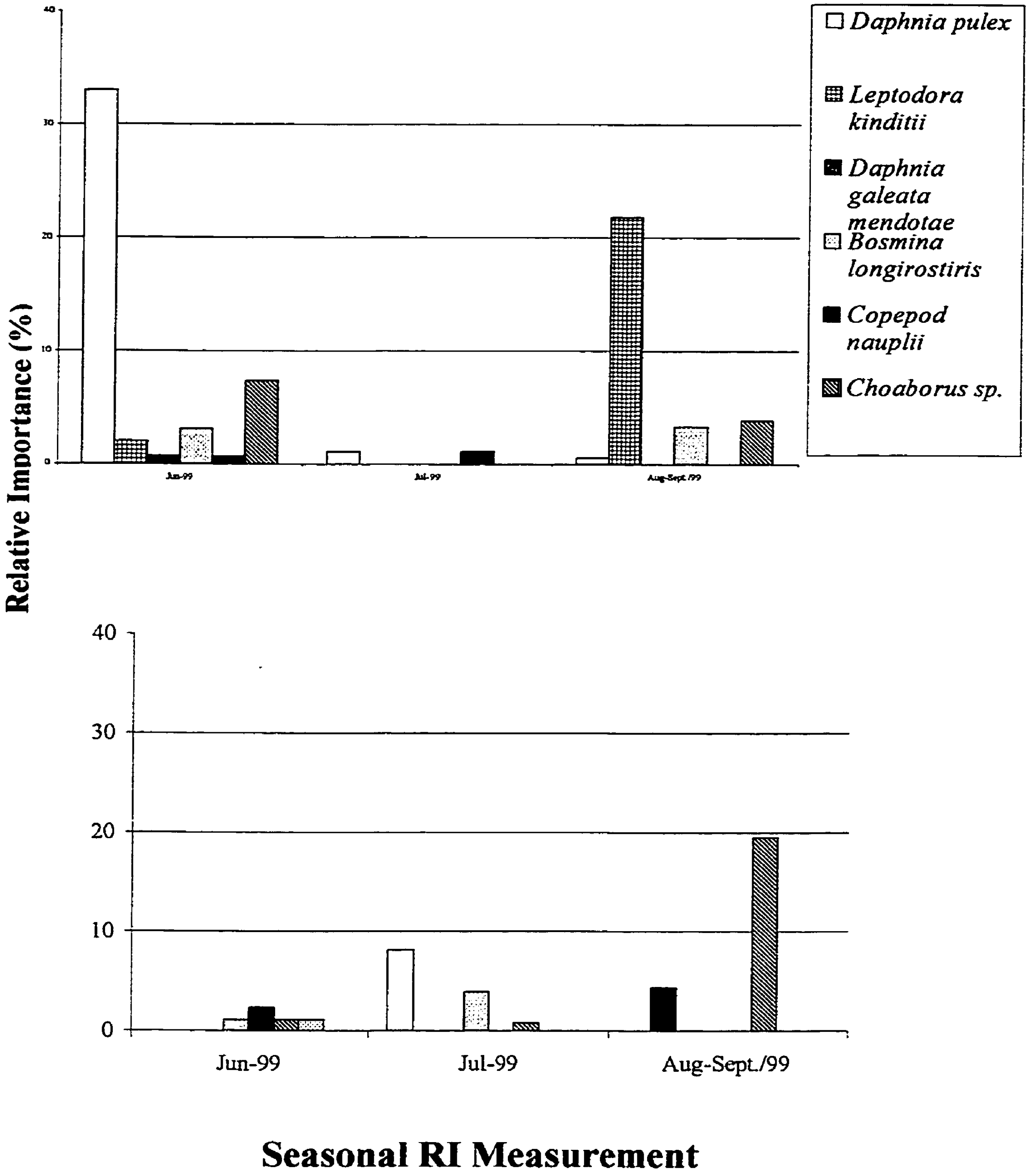


Figure 16: Seasonal variation in the diet of a.) yellow perch and b.) pumpkinseed based on the Relative Importance (RI) index of zooplankton (For all sampling periods N = 30) in ELA Lake 191: 1999.

4.2.3 Diet as a Function of Predator Size Class

The sizes of yellow perch clearly influenced their diets. Smaller yellow perch (< 130 mm) ate a combination of zooplankton and benthic invertebrates, while larger individuals ate benthic invertebrates (Figs. 17 & 18). Fishes did not occur in yellow perch diet until the second and third sampling periods (Fig. 19). Smaller yellow perch consumed fish during the second sampling period, while larger individuals consumed fish in the third sample period. Other yellow perch were the most frequent fish found in yellow perch stomachs, although small northern pike also occurred.

Benthic invertebrates were the most important component of diets of pumpkinseed in Lake 191. Unlike yellow perch, small pumpkinseed in sampling period three consumed a combination of zooplankton and benthic invertebrates. Larger pumpkinseed (> 60 mm) ate benthic invertebrates almost exclusively in sampling periods one and two, and a combination of zooplankton and benthic invertebrates in sampling period three (Figs. 20 & 21). Fish items were found occasionally in pumpkinseed stomachs, and these occurred only in larger individuals (Fig. 22). The fish were primarily smaller yellow perch and pumpkinseed, but pumpkinseed eggs and northern pike (n = 1) also occurred.

There were surprising results for northern pike when their diets were analysed by size groups (Fig. 23). Zooplankton and benthic invertebrates occurred in the stomachs of large as well as small northern pike. Northern pike preyed on smaller northern pike, indicated directly by occurrence of individuals, and indirectly by inferred lengths of scales. Age 0 northern pike were consumed by all sizes of larger northern pike.

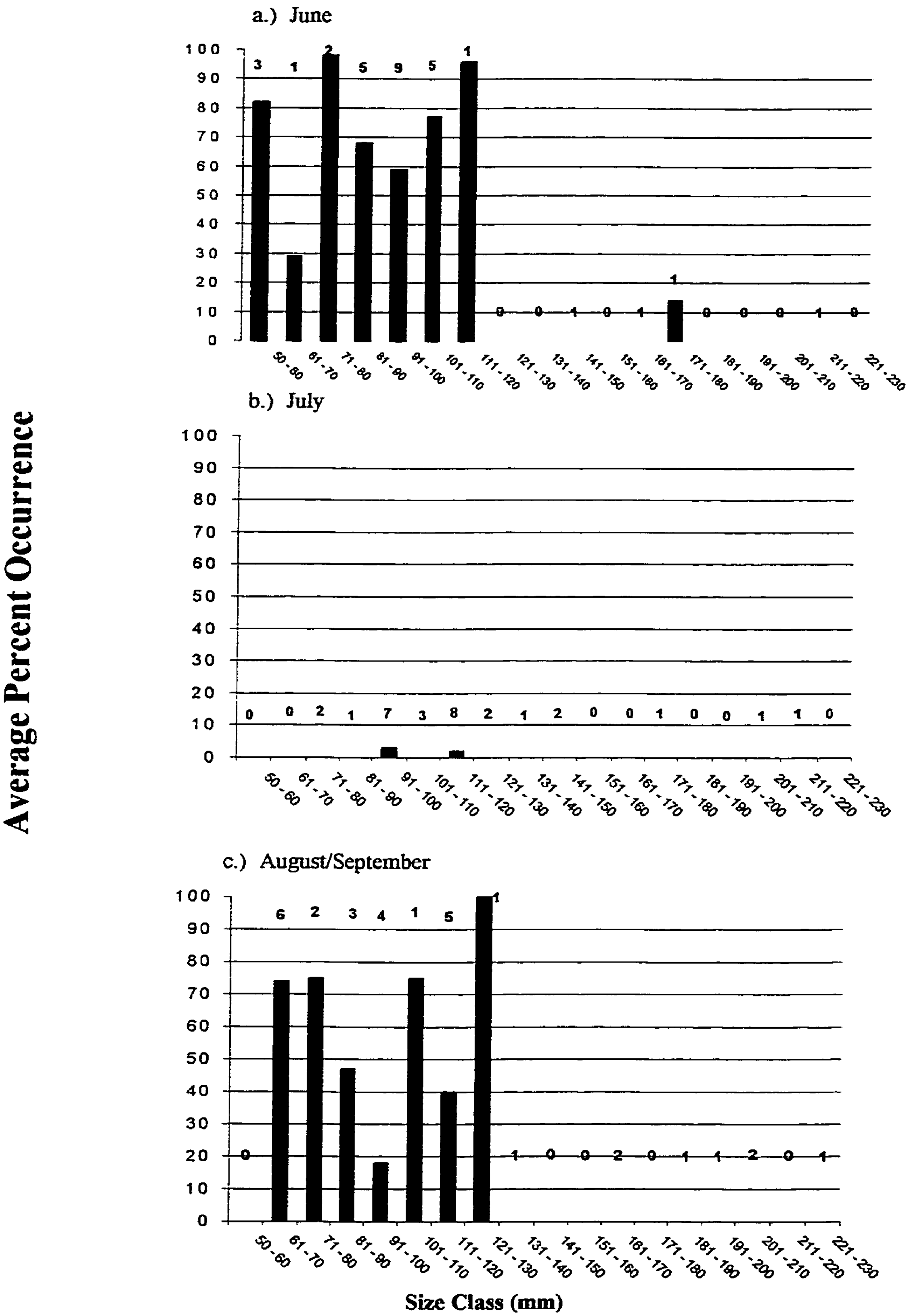


Figure 17 a.) – c.): Consumption of zooplankton as a function of yellow perch size (N = 90, with 30 fish sampled in each period): in ELA Lake 191: 1999. Numbers above columns indicate the number of fish sampled in each size class.

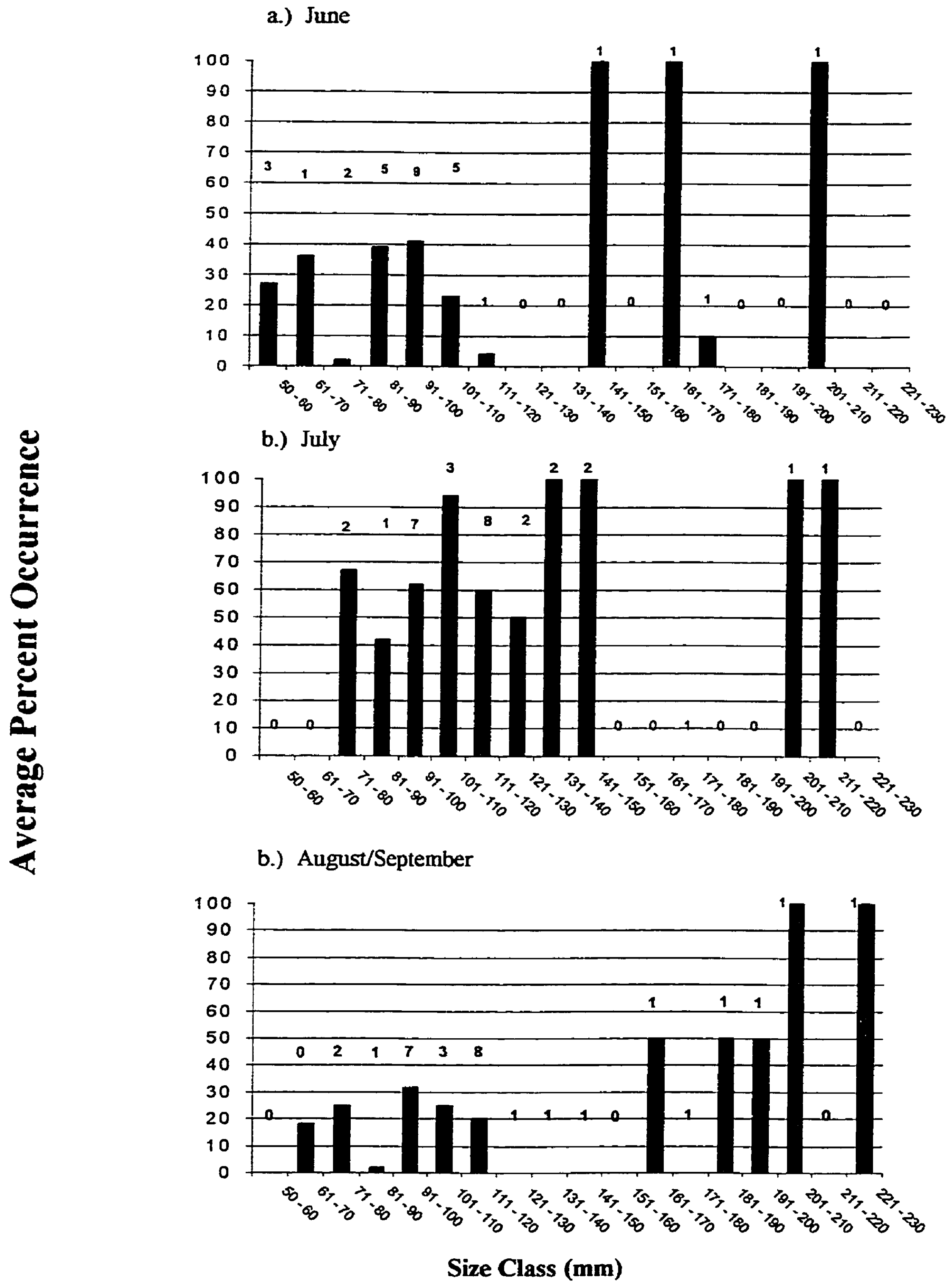


Figure 18 a.) – c.): Consumption of benthic invertebrates as a function of yellow perch size (N = 90, with 30 fish sampled in each period): in ELA Lake 191: 1999. Numbers above columns indicate the number of fish sampled in each size class.

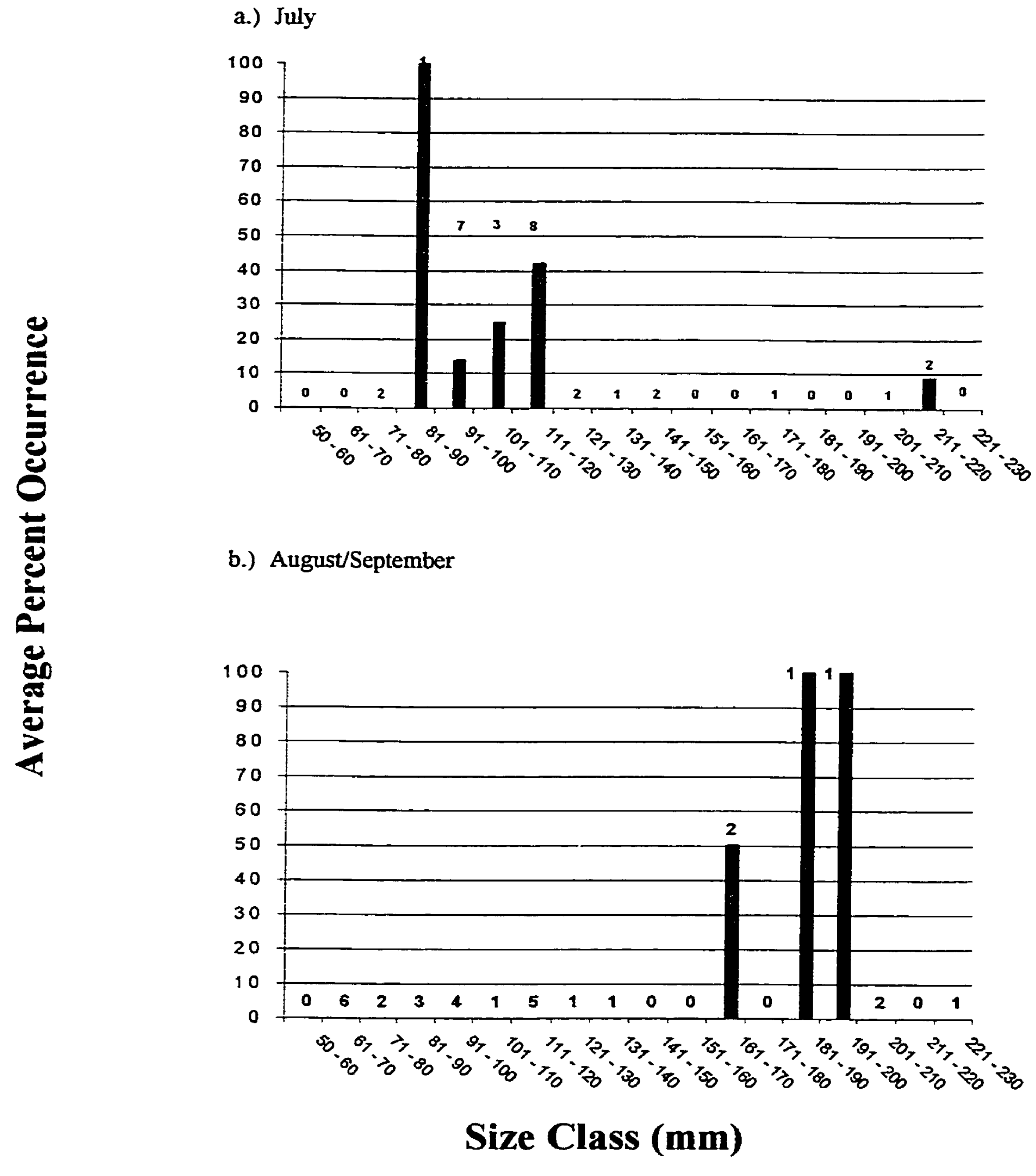


Figure 19 a.) – b.): Consumption of fish items as a function of yellow perch size (N = 90, with 30 fish sampled in each period) in ELA Lake 191: 1999. Numbers above columns indicate the number of fish sampled in each size class.

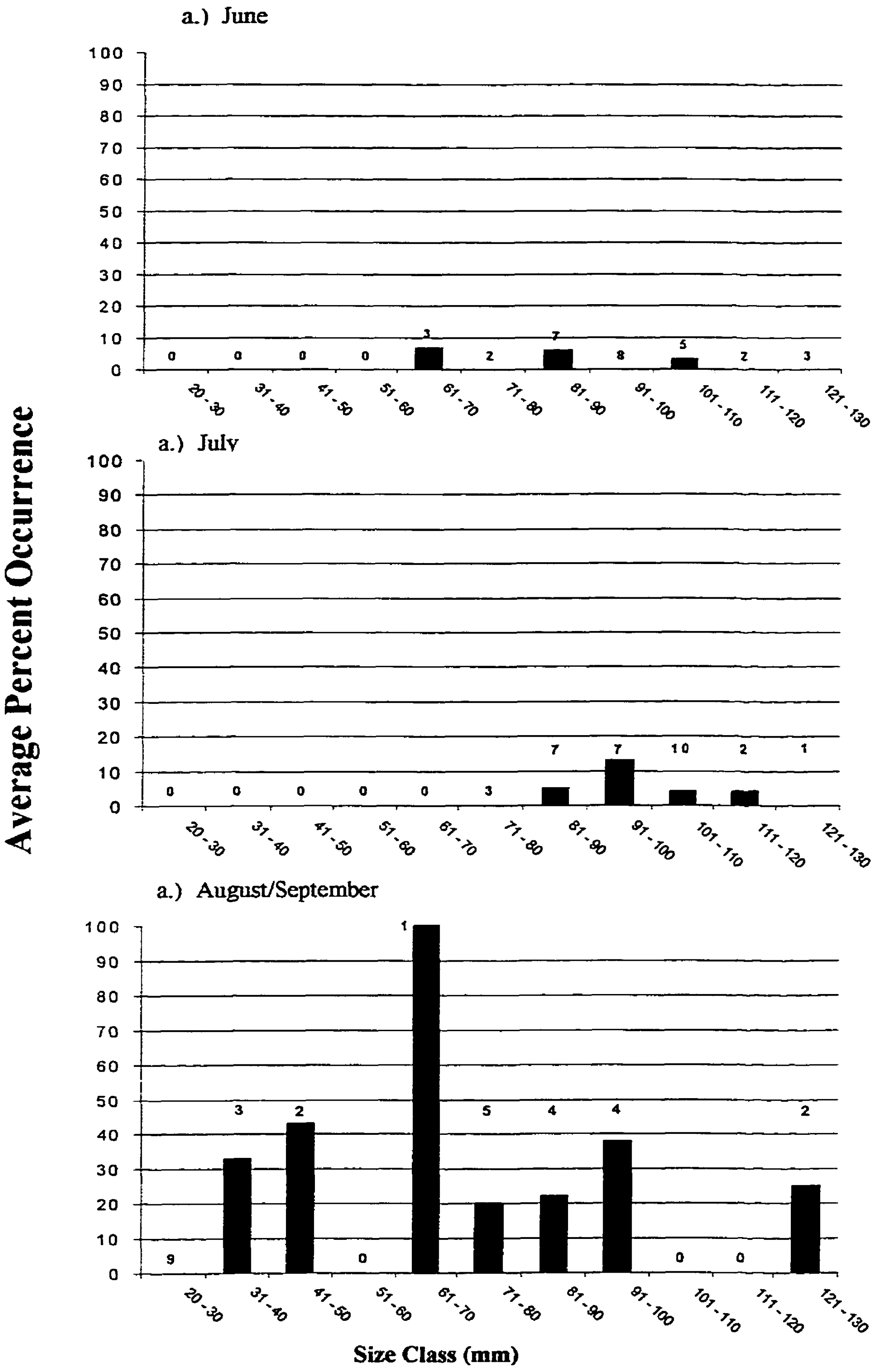


Figure 20 a.) – c.): Consumption of zooplankton as a function of pumpkinseed size (N = 90, with 30 fish sampled in each period) in ELA Lake 191: 1999. Numbers above columns indicate the number of fish sampled in each size class.

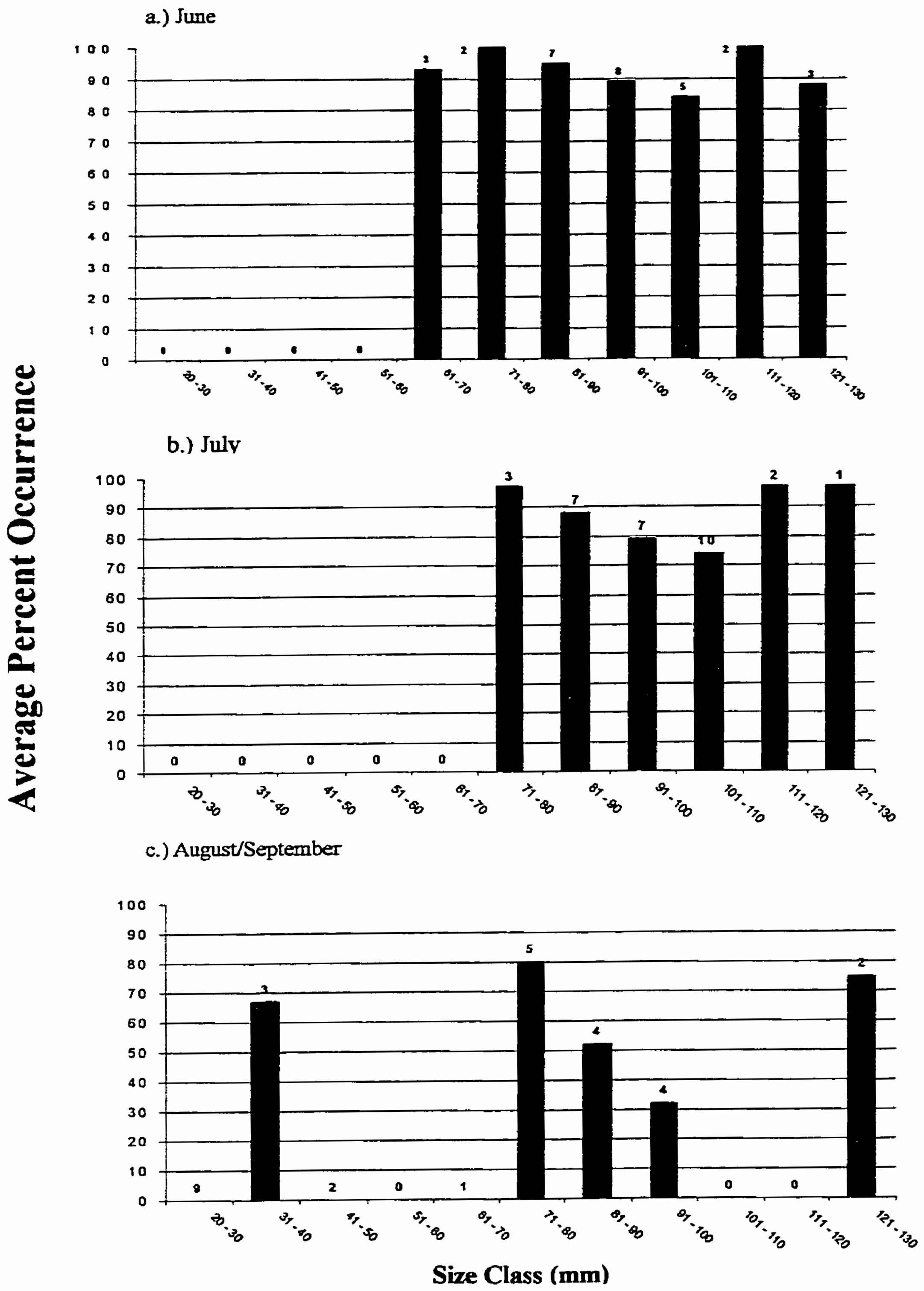
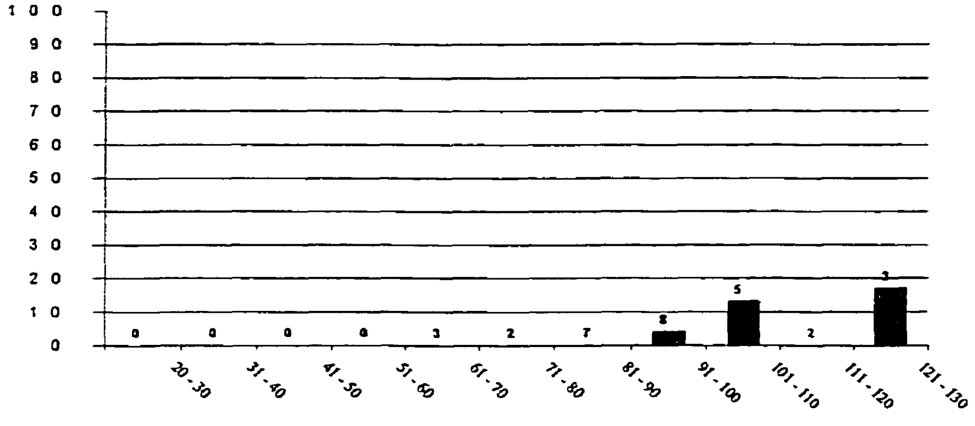
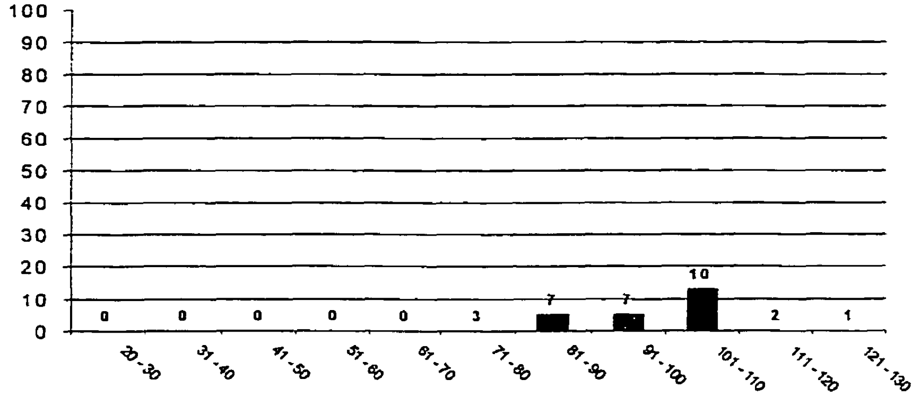


Figure 21 a.) – c.): Consumption of benthic invertebrates as a function of pumpkinseed size (N = 90, with 30 fish sampled in each period): Lake 191:ELA: 1999. Numbers above columns indicate the number of fish sampled in each size class.

a.) June



b.) July



c.) August/September

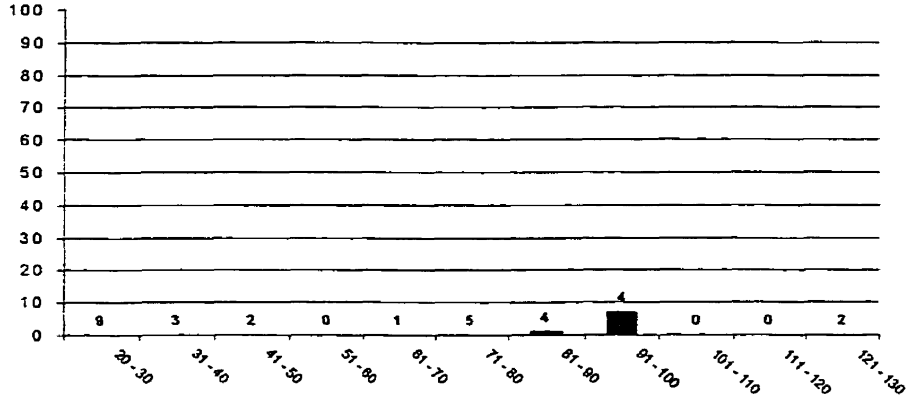
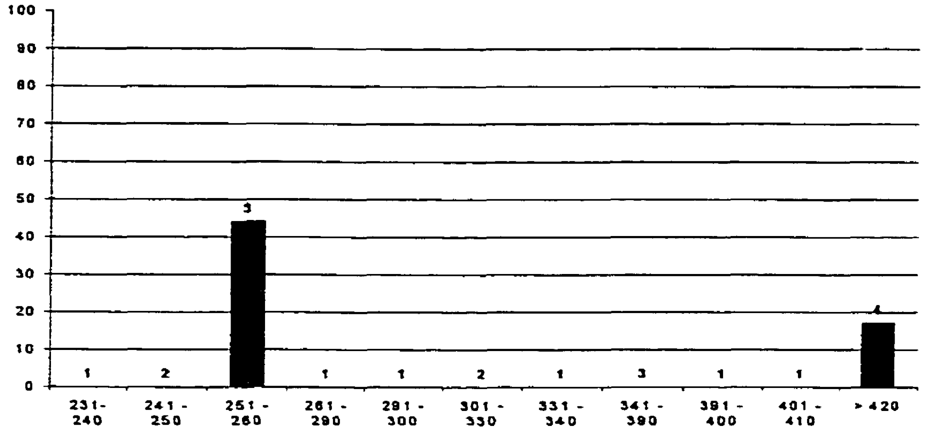
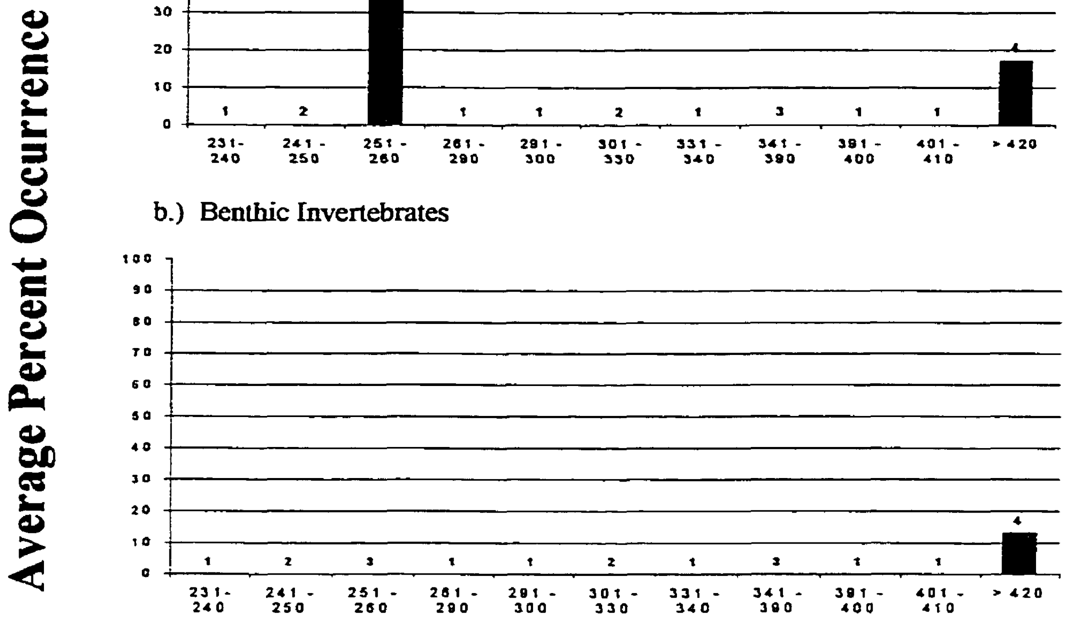


Figure 22 a.) – c.): Consumption of fish as a function of pumpkinseed size (N = 90, with 30 fish sampled in each period) in ELA Lake 191: 1999. Numbers above columns indicate the number of fish sampled in each size class.

a.) Zooplankton



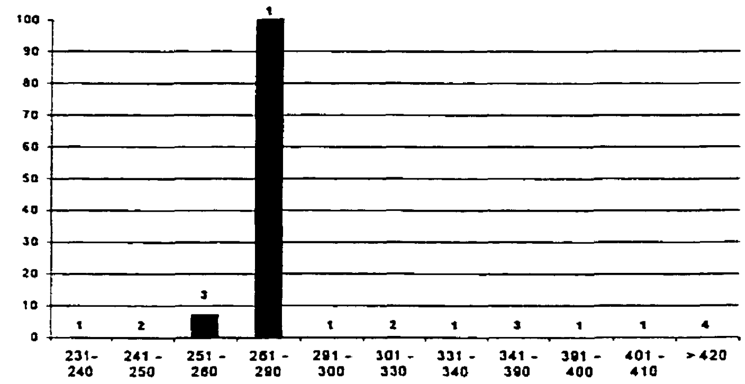
b.) Benthic Invertebrates



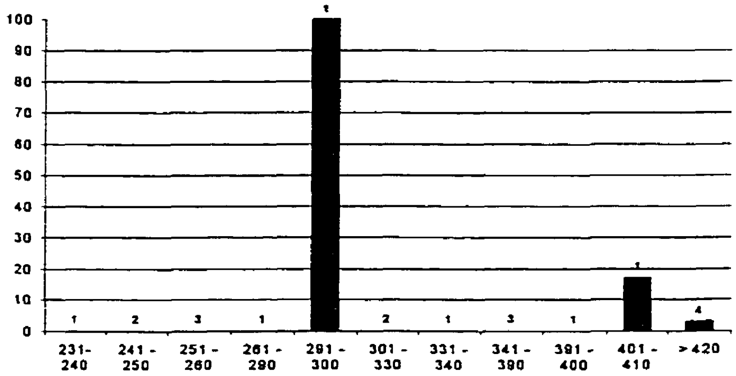
c.) Occurrence of empty northern pike stomachs

Figure 23 a.) – c.): Consumption of prey taxa as a function of northern pike size (N = 20, with nine empty stomachs) in ELA Lake 191: 1999. Numbers above columns indicate the number of northern pike sampled in each size class.

d.) Northern pike scales found in northern pike stomachs (as evidence of cannibalism)



e.) Northern pike



f.) Yellow perch

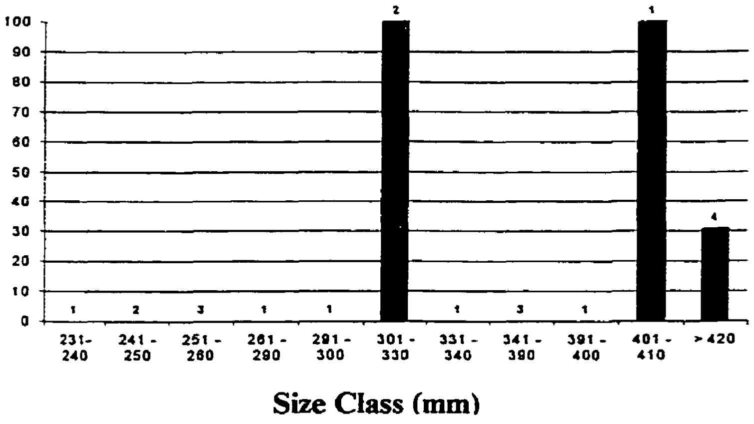


Figure 23 d.) – f.) (continued): Consumption of prey taxa as a function of northern pike size (N = 20, with nine empty stomachs) in ELA Lake 191: 1999. Superscript numbers indicate the number of northern pike sampled in each size class.

Yellow perch were consumed primarily by larger northern pike and pumpkinseed were not present in any northern pike stomachs.

5. DISCUSSION

5.1 The Effects of Macrophyte Removal on Lake 191

Removing macrophytes from Lake 191 resulted in several changes in the trophic levels of the lake. First, northern pike abundance decreased by over 50% in the five years that macrophytes were harvested. Second, there was a marked decrease in age-0 northern pike in cut and uncut areas. Third, the abundance of smaller size classes (> 60 mm) of yellow perch and pumpkinseed and recruitment of these two populations has increased markedly (Jansen 2000). Fourth, zooplankton abundance in Lake 191 has changed as a result of macrophyte harvesting (Salki Freshwater Institute, pers. comm., Winnipeg, Manitoba 1999). The zooplankton community has shifted from a normal distribution of cladocerans, copepods, and cyclopoids to a population made up mostly of copepod nauplii, small cyclopoids, and *Holopedium gibberum* (Salki in prep. 2000). The feeding relationships between fish and zooplankton help explain the changes observed by Mills (in Jansen 2000) and Salki (in prep. 2000).

5.2 Feeding Relationships Between Trophic Levels in Lake 191

The fish sampled in Lake 191 had very different diet compositions. Yellow perch ate mostly large zooplankton and benthic invertebrates, switching prey based on seasonal availability. Additionally, a small percentage of yellow perch (2% – 4%) ate either yellow perch or northern pike. Pumpkinseed ate mostly benthic invertebrate. When pumpkinseed consumed zooplankton they ate mostly large species. Additionally, a small percentage (3% – 6%) of pumpkinseed ate either pumpkinseed or northern pike. Most (67%) of the northern pike sampled exhibited cannibalism. A smaller percentage (25%) of northern pike ate yellow perch.

5.3 The Implications of Fish Diet Compositions

Macrophyte harvesting in Lake 191 led to a decrease in the abundance of northern pike, increases in abundance of yellow perch and pumpkinseed, and changes in the relative abundance of zooplankton species. The feeding relationships between trophic levels in Lake 191 were analysed to help explain some of the underlying reasons for these changes. Northern pike diet was analysed in reference to the effects of loss of macrophytic refuge on small northern pike. Yellow perch and pumpkinseed diets were analysed in relation to the changes in zooplankton community structure observed by Salki (in prep. 2000), and the increases in yellow perch and pumpkinseed abundance observed by Mills (in Jansen 2000). Preyfish preference for large zooplankton is forwarded as one of the reasons the abundance of large zooplankton decreased in Lake 191 in 1999. Additionally, high rates of consumption of benthic invertebrates by yellow perch and pumpkinseed was partially responsible for the increase in abundance of these fish species.

The occurrence of cannibalism in Lake 191 northern pike was higher than that reported by previous studies on northern pike diet (Frost 1954, Lawler 1965, Diana 1979). In most cases, the occurrence of cannibalism in northern pike is directly related to two factors: prey availability and northern pike density (Craig 1996). Cannibalism in northern pike is usually inversely proportional to the density of alternative prey species (Craig 1996). However, northern pike cannibalism in Lake 191 was high at the same time that the yellow perch and pumpkinseed abundances were increasing. This may be partially explained by differences in habitat selection between YOY northern pike and YOY yellow perch and pumpkinseed. Yellow perch and pumpkinseed YOY associate with the pelagic zone of lakes (Bryan and Scarnecchia 1992). Northern pike YOY are often found associated with the macrophytes of lake littoral zones (Bryan and Scarnecchia 1992), and adult and juvenile northern pike spend a majority of their time searching for prey in these areas (Diana 1979, Savino and Stein 1989, Moyle and Cech 1996). Further, the differences in fin morphology between small northern pike and yellow perch and pumpkinseed were forwarded as an explanation for the high rates of cannibalism amongst Lake 191 northern pike.

The removal of 50% of the macrophytes in Lake 191 has decreased the amount of refuge area available to YOY northern pike. Savino and Stein (1989) found that the physical complexity and density of aquatic macrophytes related inversely to the probability that preyfish were caught by predators. A decrease in the amount of refuge available to young northern pike may increase the chance that they are eaten by adult fish. The removal of vegetation should affect yellow perch and pumpkinseed in much the same way. However, YOY northern pike were more important in the diets of northern pike in Lake 191 than either yellow perch or pumpkinseed.

Northern pike in Lake 191 did not consume yellow perch at a rate similar to other populations (Frost 1954, Lawler 1965). The percentage of northern pike found in Lake 191 northern pike stomachs was more than four times the percentage of yellow perch, while in other studies northern pike usually consume more yellow perch than northern pike (Frost 1954, Lawler 1965). Surprisingly, yellow perch occurrence in northern pike stomachs was lower than zooplankton occurrence. Northern pike in Lake 191 preyed on YOY northern pike rather than the more abundant YOY yellow perch and pumpkinseed.

The preyfish (i.e. yellow perch and pumpkinseed) that inhabit the littoral zone of Lake 191 have spiny-rayed fins, while YOY northern pike have relatively soft-rayed fins. Differences in fin rays between spiny-rayed and soft-rayed preyfish can affect predator preference (Eklov and Hamrin 1989), and may be partially responsible for the high rates of cannibalism in Lake 191 northern pike. Loss of macrophytic refuge coupled with differences in fin morphology between YOY northern pike and YOY yellow perch and pumpkinseed may explain both the decrease in YOY northern pike abundance and the increase in preyfish abundance observed by Mills (in Jansen 2000) between 1995 and 1999 in Lake 191. If adult northern pike selected YOY northern pike based on the absence of spiny-ray fins, and the loss of macrophytic cover made YOY northern pike more vulnerable to predation, then cannibalism may help to explain the decrease in northern pike abundance. Additionally, adult northern pike preference for conspecifics may have led to a decrease in predation of yellow perch and pumpkinseed. This decrease may be one of the reasons that yellow perch and pumpkinseed abundance increased.

Yellow perch diet reflected the changes in zooplankton community structure observed by Salki (in prep. 2000). Zooplankton abundance usually peaks in the spring and again in the fall (A. Salki, pers. comm., Freshwater Institute, Winnipeg, Manitoba 1999). During times of low zooplankton abundance, yellow perch switch to more abundant larvae of aquatic insects. Therefore, it is not surprising that zooplankton were more important in yellow perch diet in the first and third sampling periods while aquatic insects were more important in the second sampling period. This indicates that the yellow perch in Lake 191 are not obligate planktivores or benthivores. They likely switch prey depending on their availability. Although zooplankton made up a majority of items in yellow perch stomachs in the first and third sampling periods, the species diversity of zooplankton prey was low relative to the species diversity of zooplankton in Lake 191 (A. Salki, pers. comm., Freshwater Institute, Winnipeg, Mb. 2000). The primary zooplankton in yellow perch diet were *D. pulex* in the first sampling period and *L. kinditii* in the third sampling period. These two species were the largest zooplankton species in Lake 191 in 1999 (Salki in prep. 2000). Although these two species were the largest, they were much less abundant than other zooplankton species. Fishes normally consume the largest food item they are able to swallow (Frost 1954, Lawler 1965). This explains the yellow perch preference for *D. pulex* and *L. kinditii* that was evident in the 1999 samples. Despite its size, the relatively large zooplankton species *Holopedium gibberum* was not found in any of the yellow perch or pumpkinseed stomachs that were analyzed. This was not surprising considering that *H. gibberum* is covered with a gelatinous sheath that usually dissuades fish from consuming them (Wahlstrom et al. 2000).

The increase in yellow perch abundance, coupled with their apparent preference for large species of zooplankton may be responsible for the shift in the zooplankton community that was observed by Salki for Lake 191 (in prep. 2000). Large numbers of small yellow perch may have consumed enough of the larger zooplankton to shift the community towards an increased abundance of small zooplankton species. This would help to explain why *D. pulex* abundance decreased in 1999 at the same time that the total abundance of littoral zone crustaceans increased (Salki, in prep. 2000). If the observed increase in yellow perch abundance is a direct result of macrophyte harvesting, then it could be argued that subsequent changes in the zooplankton community are an indirect result of macrophyte harvesting.

Yellow perch consumed a larger diversity of both species and sizes of benthic invertebrates than zooplankton. Yellow perch consumed five species of zooplankton including *B. longirostiris*, *Choaborus* sp., *Leptodora kinditii*, *D. pulex*, and *D. galeata mendota*. There were ten species of benthic invertebrates in yellow perch diet including chironomid larvae, trichopteran larvae, Ephemerellidae nymphs, Lestidae nymphs, Macromiidae and Gomphidae nymphs, *Hyalella azteca*, clams of the family Sphaeridae, aquatic mites, and crayfish. Thus, relative to benthic invertebrates, zooplankton may be of secondary importance in yellow perch diet.

The difference in importance between benthic invertebrates and zooplankton in the diet of Lake 191 yellow perch diet may help explain how macrophyte harvesting led to an increase in yellow perch abundance. Monohan and Caffrey (1996) found that cutting macrophytes in definable lanes allowed planktivorous fish access to benthic invertebrates that would otherwise be non-accessible because of high macrophyte densities in this lake. Increased access to benthic invertebrates might explain why they dominated yellow perch and pumpkinseed diets in Lake 191. Benthic invertebrates are normally larger and more calorically dense than zooplankton (Driver 1981, Karamushko 1996). Macrophyte cutting in Lake 191 may have allowed the planktivorous fish populations increased access to this high quality food source. If this is the case, then high levels of benthic invertebrates in planktivorous fish diets may have contributed to the increases in these populations that were observed by Mills (in Jansen 2000). The reason that increased access to benthic invertebrates did not increase YOY northern pike abundance in the same manner may be because of cannibalism by adult northern pike. The benefits to YOY northern pike from greater access to benthic invertebrates may be negated by greater cannibalism in these open areas by larger northern pike.

Yellow perch ate both northern pike and yellow perch. Although feeding on fish by yellow perch did not exceed 5% in any of the three sampling periods, it is still important because the abundance of yellow perch of all sizes increased more than 18-fold (0.6 to 18.1 CPUE) during the study. Therefore, although fish were a small percentage of yellow perch diet, the overall impact on northern pike could have been very great.

The occurrence of northern pike in the diet of yellow perch is not unusual (Lott et al. 1996). However, the size of the yellow perch in the GCA sample that ate northern pike fry seems smaller than normal for piscivory in yellow perch populations (Lott et al. 1996). When this extreme example is coupled with the high occurrence of cannibalism in the GCA northern pike samples, it indicates that small northern pike are extremely vulnerable to predation. Macrophyte removal may not have had as profound an effect on small yellow perch and pumpkinseed as it did on young northern pike. This difference may be due to the differences in habitat selection between young northern pike and young yellow perch and pumpkinseed discussed previously.

The analysis of pumpkinseed diet also had implications for the effects of macrophyte removal on trophic levels in Lake 191. Pumpkinseed diet changed according to season. Zooplankton occurrence in pumpkinseed diets increased as the year progressed. By the third sampling period, zooplankton made up 25% of pumpkinseed diet. Analysis of pumpkinseed diet supported the conclusions made earlier about both the effects of yellow perch on the size/species composition of the zooplankton community, and the indirect effects of macrophyte harvesting on the zooplankton community. As the abundance of small pumpkinseed increased, their preference for larger zooplankton species may have shifted the zooplankton community in favour of large numbers of small zooplankton species. Again, macrophyte harvesting may be responsible for the increased abundance of pumpkinseed observed by Mills (in Jansen 2000). Thus, macrophyte harvesting may be indirectly responsible for the changes in the zooplankton community that were observed by Salki (in prep. 2000).

Benthic invertebrates were the most important components in the diets of pumpkinseed throughout the summer. High levels of benthic invertebrates are not unusual in pumpkinseed diets (Keast 1978). However, the percentage of benthic invertebrates observed in pumpkinseed diets in Lake 191 is more than 15% higher than the results of comparable studies (Keast 1978, Hanson and Qadri 1984). The relatively high occurrence of benthic invertebrates in pumpkinseed diets (as compared to similar studies) may be related to the effects of macrophyte harvesting observed by Mills (in Jansen 2000). The reasoning behind this is the same as that which was stated previously for yellow perch in Lake 191. Removing macrophytes in definable lanes may increase pumpkinseed access to benthic invertebrates. This allows pumpkinseed to exploit a calorically dense prey item, and thus may have contributed to the increases in pumpkinseed abundance observed by Mills (in Jansen 2000).

The low occurrence of fish items in pumpkinseed stomachs is consistent with other studies (Hanson and Qadri 1984, Godhino and Ferreira 1994), but it is never-the-less surprising that fish items occurred in pumpkinseed diet. Pumpkinseed are not usually viewed as piscivores (Keast 1978, Hanson and Qadri 1984, Godhino and Ferreira 1994). Yellow perch and pumpkinseed scales were found in the stomachs of smaller-sized pumpkinseed (fork lengths between 86 and 105 mm). Included in this group was an 87 mm pumpkinseed with many northern pike scales in its stomach. The estimated fork length of this northern pike fry was 40 mm. When the mouth size and morphometry of pumpkinseed in that size class are considered, it seems unusual to find evidence of cannibalism and piscivory (Keast 1978). Again, the occurrence of northern pike fry in the stomachs of small fish may hint at their vulnerability to predation in Lake 191 due to decreased cover afforded by macrophytes.

5.4 Comparison of Relative Importance and Percent Composition by Number Analyses

The Relative Importance Index (RI) was used to reduce bias that may have occurred from using the percent composition by number analysis (Wallace 1981). The RI analysis takes into consideration the weights of individual prey items. Thus, the RI index may be a more accurate representation of the importance of prey items to fish diets (Wallace 1981). The results generated from the percent composition by number and the RI analysis were generally similar for both yellow perch and pumpkinseed. Seasonal changes in the occurrence of diet items were the same for both analyses for yellow perch and pumpkinseed. Thus, the RI index supported most of the conclusions formulated when using the percent composition by number analysis.

However, there were some differences between the results generated from the two methods. The contribution of benthic invertebrates to yellow perch diet was higher in all three sampling periods for the RI analysis. In both the first and third sampling periods the RI of benthic invertebrates was nearly double that of the percent composition by number. The RI index indicates that benthic invertebrates were more important to yellow perch diet than the percent composition by numbers method. Benthic invertebrates are generally larger, weigh more, and are more calorically dense than zooplankton (Driver 1981, Karamushko 1996).

The results of the RI index for pumpkinseed were very similar to the results of the percent composition by number. The RI values did not differ from the earlier analysis by more than 7%. Harvesting macrophytes may have allowed small pumpkinseed to penetrate deeper into littoral zone areas. This in turn would allow pumpkinseed to exploit large calorically dense macroinvertebrates. The exploitation of this food source may have played a part in the increases in pumpkinseed abundance observed by Mills (in Jansen 2000). Also, the RI analysis indicated that when pumpkinseed consumed zooplankton they selected mostly larger species. This seems to support the conclusions made earlier on both the direct effects of pumpkinseed on the zooplankton community, and the indirect effects of macrophyte harvesting on the zooplankton community.

5.5 Diet as a Function of Predator Size Class

The percentage of large northern pike stomachs that contained zooplankton (27%) and benthic invertebrates (18%) was surprising for two reasons. First, the northern pike that consumed these items were relatively large individuals (251 – 260 mm, and > 420 mm). Northern pike normally consume the largest food item that they encounter or are conditioned to consuming, and there is usually a direct correlation between predator and prey size (Frost 1954, Lawler 1965). Zooplankton and benthic invertebrates are small food items relative to yellow perch and pumpkinseed. Given the opportunity, large northern pike usually select small preyfish rather than zooplankton and/or benthic invertebrates (Frost 1954, Lawler 1965). Large northern pike consumed zooplankton and benthic invertebrates during a period when preyfish abundance increased (Jansen 2000). Macrophyte harvesting may have had an impact on northern pike prey selection. Savino and Stein (1989) found that northern pike capture rates of small prey, relative to larger prey, increased when stem densities of associated vegetation decreased from high to moderate levels. At lower stem densities of macrophytes, larger prey items (i.e. *L. macrochirus*) exhibited more effective predator avoidance behaviours (i.e. shoaling) than smaller prey items (i.e. *P. promelas*). Removing macrophytes from the littoral zone may give larger prey items an advantage in terms of avoidance of capture (Savino and Stein 1989). This may help to explain the incidence of small prey items (i.e. zooplankton and benthic invertebrates) in the stomachs of large northern pike in Lake 191. Macrophyte harvesting may have given yellow perch and pumpkinseed an opportunity for increased use of predator avoidance behaviours. Thus, northern pike may be selecting smaller prey based on increased probability of capture.

The incidence of cannibalism in small size classes of northern pike (251 – 300 mm) in Lake 191was higher than documented in previous studies on northern pike diet (Frost 1954, Lawler 1965). There is normally a positive correlation between northern pike size and age (Craig 1996). Thus, the northern pike that exhibited high incidences of cannibalism were younger than the less piscivorous larger northern pike (> 400 mm). There is no diet data for any of the fish populations in Lake 191 prior to 1999. However, the food preferences of fish that inhabited the lake prior to macrophyte removal may give some indication of northern pike diet before the habitat was modified. Previous studies on predator feeding preferences indicated that selectivity is influenced by previous feeding experiences (Bryan and Larkin 1972). It is possible that the more cannibalistic size classes of northern pike have been conditioned to this feeding preference. Larger northern pike (i.e. older northern pike) consumed more yellow perch than the smaller northern pike. Again, the larger northern pike may be conditioned to pursuing and attacking yellow perch. The differences in prey selection between the small and large adult northern pike may be the result of differences in dietary conditioning between these groups. Larger northern pike were present in Lake 191 prior to macrophyte harvesting, and their prey preferences could have continued from this period into the years of macrophyte harvesting. Smaller northern pike did not have similar pre-harvesting preferences because few were present prior to macrophyte harvesting.

Juvenile yellow perch (FL > 100 mm) consumed a larger variety of prey types than adult yellow perch, and this difference may partially explain the increases in abundance of small yellow perch observed by Mills (in Jansen 2000). Additionally, smaller yellow perch exhibited greater seasonal flexibility in diet than larger yellow perch. This is most evident in the fluctuations of zooplankton and benthic invertebrates exhibited by small yellow perch between June and September, and the high consumption of fish by small yellow perch in August. The ability to exploit resources when they are relatively abundant leads to a competitive advantage in terms of nutrient procurement (Mills et al. 1987). The differences in diet breadth between small and large yellow perch may have given the smaller yellow perch an advantage. This advantage may be one of the reasons that the abundance of small yellow perch increased so rapidly. If small yellow perch took advantage of this change more so than large yellow perch, then macrophyte harvesting may be responsible for the changes in yellow perch abundance observed by Mills (in Jansen 2000).

Distinct size classes of pumpkinseed in Lake 191 consumed different food items. Adult pumpkinseed diet did not vary as much as juvenile pumpkinseed diet. Similar to yellow perch, small pumpkinseed may hold a competitive advantage over large individuals in feeding. This advantage may be the result of increased access to a greater diversity of prey resulting from macrophyte harvesting. Thus, greater prey availability may be responsible for the increase in pumpkinseed abundance observed by Mills (in Jansen 2000).

5.6 Limitations to the Conclusions

There were several differences between the GCA and WL length-frequency distributions for fish populations in Lake 191. The smaller size classes absent in the GCA samples were the smallest young-of-the-year (YOY) yellow perch in Lake 191. The larger size classes were the largest adult yellow perch in Lake 191. Therefore, conclusions regarding the diet composition of these unsampled size classes of the Lake 191 yellow perch population cannot be drawn from the GCA samples. However, enough YOY (10) and larger adults (6) were sampled to draw conclusion regarding the overall diet composition of these groups of yellow perch.

A striking feature of the length frequency distributions of pumpkinseed was the absence of small individuals in the first and second sampling periods. A wide range of pumpkinseed size ranges occurred only in the third sampling period. This is not surprising because there is a large over-wintering mortality of age 0 pumpkinseed in Lake 191 each year (K. Mills, pers. comm., Freshwater Institute, Winnipeg, Mb. 1998). It is unusual to capture many small pumpkinseed (< 50 mm) in May and June of each year.

Conclusions regarding the diet composition of YOY northern pike cannot be drawn from the GCA samples. However, the two factors that are important to this study are the contribution to overall northern pike diet by piscivory and cannibalism. Because the juveniles and adults captured for the GCA samples are well within the size ranges for these two factors, then conclusions about overall northern pike diet can be drawn from these samples.

5.7 Summary

Macrophyte harvesting in Lake 191 has had a number of trophic level effects. Mills (in Jansen 2000) and Salki (in prep. 2000) observed changes in resident fish and zooplankton communities resulting from macrophyte harvesting. Between 1995 and 1999 Mills (in Jansen 2000) observed a decrease in northern pike abundance, coupled with an increase in abundance of both yellow perch and pumpkinseed. Salki (in prep. 2000) observed both an increase in overall zooplankton abundance and a decrease in the abundance large zooplankton species and size classes. Examining the feeding relationships between trophic levels of Lake 191 has implications on the effects of macrophyte harvesting observed by Mills (in Jansen 2000) and Salki (in prep. 2000).

Most of the northern pike sampled in 1999 ate northern pike. This was unexpected because yellow perch and pumpkinseed abundance increased since the beginning of harvesting in 1996. Northern pike preference for conspecifics may be partially responsible for the decrease in northern pike abundance and associated increases in yellow perch and pumpkinseed abundance observed by Mills (in Jansen 2000). The decrease in northern pike abundance coupled with their apparent preference for conspecifics may be partially responsible for the increases in yellow perch and pumpkinseed in Lake 191. The factors that have been proposed as responsible for northern pike preference for cannibalism are differences in habitat selection, predator avoidance behaviour, and fin morphology between YOY northern pike and yellow perch and pumpkinseed.

Yellow perch and pumpkinseed ate mostly benthic invertebrates and zooplankton.

Further, RI analysis indicated that benthic invertebrates are a slightly more important component of preyfish diet in Lake 191. Macrophyte harvesting may have increased preyfish access to benthic invertebrates, and thus may be partially responsible for the increases in preyfish abundance in Lake 191. The fish sampled exhibited a preference for large species of zooplankton. This preference coupled with the increase in preyfish abundance may be responsible for the changes in zooplankton community structure in Lake 191. The changes in preyfish abundance have been attributed to macrophyte harvesting. Thus macrophyte harvesting may have indirectly led to the changes in zooplankton community structure.

6. REVIEW OF RELEVANT POLICY

6.1 Introduction

The purpose of this chapter is to review the policies of several provinces and states for the control and/or removal of aquatic macrophytes. The issues that led to widespread macrophyte control programs in the United States will be presented first. Next, the intent of macrophyte control regulations and their relevance to habitat protection will be examined. Finally, a critique of the existing regulations will be conducted including their advantages and disadvantages.

6.2 Macrophyte Control Issues in the United States and Southern Ontario

Macrophyte populations in North American lakes have changed considerably in recent decades (Nicholson 1981). These changes include loss of species richness, changes in species due to eutrophication, and increased macrophyte biomass in littoral zones (Nicholson 1981). Habitat managers and research scientists have ascribed these alterations partially to the invasion of aquatic systems by exotic macrophyte species (Nicholson 1981). The primary exotic invader is Eurasian watermifoil (*Myriophyllum spicatum*) (Newman et al. 1996). Eurasian watermilfoil was first observed in North American lakes in the 1940's, and has since spread in distribution from California to British Columbia in the West, and from Florida to Southern Ontario in the East (Madsen et al. 1991, McKee et al. 1986).

All of the states reviewed in this paper have extensive nuisance control programs to stop the spread of Eurasian watermilfoil. The current estimates for the number of lakes in each state that are infested are: 100 for Minnesota, 75 for Wisconsin, and more than 75 for Michigan (Minnesota Department of Natural Resources 2000, Wisconsin Department of Natural Resources 2000, Michigan Department of Natural Resources 2000). Additionally, McKee et al. (1986) indicated that eutrophication and aquatic weed proliferation, including exotics, were a problem in over 80% of southern Ontario reservoirs. Eurasian watermilfoil has not yet been reported in Manitoba, but due to the amount of boat traffic between the province and adjacent states with infestations, the problem remains a concern of local habitat managers (Manitoba Department of Conservation 2000).

Changes in the macrophyte communities of lakes caused by exotics can lead to changes in fish populations (Olsen et al. 1998). These effects include shifts in length-frequency distributions towards large populations of small gamefish and reduced foraging efficiency of piscivores (Olsen et al. 1998). Many of the macrophyte control programs in the United States and Canada have been formulated to control the spread of and/or mitigate the effects of invasion by exotic species (Newman et al. 1996). Thus, the primary goal of regulations governing macrophytes in the United States and Canada has been macrophyte control.

6.3 Aquatic Macrophyte Regulations

This section is organised into three sub-sections according to macrophyte control method (i.e. physical, chemical, and biological). Each sub-section examines the similarities and differences between the systems of regulations employed by Ontario, Manitoba, Minnesota, Wisconsin, and Michigan. The regulations are summarised in Table 2.

The Canada Federal Fisheries Act, sections 35(1) and (2) addresses all activities that relate to the destruction and/or loss of fish habitat (Table 2). Section 35(1) of the Federal Fisheries Act prohibits the "harmful alteration, disruption, and/or destruction (HADD) of fisheries habitat". Section 35(2) provides the minister of DFO with the ability to authorise HADD (DFO 1986). The Department of Fisheries and Oceans Canada (DFO) is responsible for the administration of the Fisheries Act (DFO 1986). Thus, the Federal Fisheries Act is the operational regulation that governs macrophyte control in Canada.

The DFO adopted the No Net Loss Policy (NNLP) for the management of fish habitat in 1986. The NNLP guides DFO in the administration of the Federal Fisheries Act (DFO 1986). The overall objective of the NNLP is to ensure that the productive capacity of fish habitat is sustained or enhanced in the provinces and territories of Canada (DFO 1986). This is accomplished through the dual mechanisms of mitigation and compensation. The operational definition of mitigation that is used by DFO in the administration of the NNLP is "actions taken during the planning, design, construction and operation of works and undertakings to alleviate potential adverse effects" (DFO 1986). DFO defines compensation as "replacement of natural habitat, or an increase in the productivity of natural habitat where mitigation techniques and other measures are not adequate" (DFO 1986).

The United States Federal government does not take a regulatory role in the modification of fish habitat. Instead, regulations that relate to the modification of fish habitat are formulated and enforced by individual state agencies (Minnesota Department of Natural Resources 2000, Wisconsin Department of Natural Resources 2000, Michigan Department of Natural Resources 2000).

6.3.1 Physical Control Regulations

There are a number of similarities and differences between the states and provinces in the way physical control of macrophytes is regulated. Ontario, Manitoba, Wisconsin, and Michigan do not directly regulate non-mechanical harvest of aquatic macrophytes (i.e. hand cutting, hand pulling, and/or raking) (K. Fisher, pers. comm., Freshwater Institute, Winnipeg, Mb. 1999, Wisconsin Department of Natural Resources 2000, L. Esman, pers. comm., Department of Environmental Quality, Lansing, Michigan 1999). Ontario and Manitoba indirectly regulate non-mechanical harvest of macrophytes through the use of Sections 35 (1) and (2) of the HADD provisions of the Federal Fisheries Act (DFO 1986). Wisconsin and Michigan do not indirectly regulate non-mechanical harvest of macrophytes (L. Esman, pers. comm., Department of Environmental Quality, Lansing, Michigan 1999, Wisconsin Department of Natural Resources 2000). Instead, non-mechanical removal of macrophytes is performed at the discretion of the landowner.

Table 2. Aquatic Macrophyte Regulations in Canada and the United States by jurisdiction

CONTROL METHOD/ JURISDICTION	ONTARIO	MANITOBA	MINNESOTA	WISCONSIN	MICHIGAN
NON – MECHANICAL HARVEST	Canada Federal Fisheries Act (HADD Provisions)	Canada Federal Fisheries Act (HADD Provisions)	Minnesota Rules – Chapter 6280	Not Regulated	Not Regulated
MECHANICAL HARVEST	Canada Federal Fisheries Act Section 35 (1) and (2) (HADD Provisions)	Canada Federal Fisheries Act Section 35 (1) and (2) (HADD Provisions)	Minnesota Rules – Chapter 6280	Wisconsin Codes Chapter NR 107	Not Regulated
CHEMICAL CONTROL	Provincial Pesticides Act and/or Canada Federal Fisheries Act Section 35(1) and 35(2) (HADD Provisions)	Manitoba Pesticide Regulation 94/88R of the Environment Act And/or Canada Federal Fisheries Act Section 35(1) and 35(2) (HADD Provisions)	Minnesota Rules – Chapter 6280, and The United States Federal Insecticide, Fungicide, and Rodenticide Act	Wisconsin Codes Chapter NR 107, and The United States Federal Insecticide, Fungicide, and Rodenticide Act	Michigan State Codes Chapter PA 004199, Sec. 12562, and The United States Federal Insecticide, Fungicide, and Rodenticide Act
BIOLOGICAL CONTROL	Indirectly addressed by Canada Federal Fisheries Act Section 35(1) and 35(2) (HADD Provisions)	Indirectly addressed by Canada Federal Fisheries Act Section 35(1) and 35(2) (HADD Provisions), and Manitoba Fishery Regulations Subsection 16(2) (prohibition of use of exotic species in Manitoba)	Indirectly addressed by Minnesota Rules – Chapter 6216 (prohibition of use of exotic species in Minnesota waters)	Indirectly addressed by Wisconsin codes Chapter NR 19.05 (prohibition of use of exotic species in Wisconsin waters)	Indirectly addressed by Michigan Compiled Laws, under PA 324.48735 and , R 299.1052 of the Michigan Administrative Rules

The states and provinces differ in how they govern the mechanical harvest of macrophytes. As summarised in Table 2, Ontario, Manitoba, and Michigan do not directly regulate the mechanical harvest of macrophytes, while Minnesota and Wisconsin have specific mechanical harvest regulations (DFO 1986, L. Esman, pers. comm., Department of Environmental Quality, Lansing, Michigan 1999, Minnesota Department of Natural Resources 2000, Wisconsin Department of Natural Resources 2000). Ontario and Manitoba indirectly regulate mechanical harvest of macrophytes through the use of Sections 35 (1) and (2) of the HADD provisions of the Federal Fisheries Act (DFO 1986). Michigan does not indirectly regulate mechanical harvest of macrophytes.

Ontario, Manitoba, and Wisconsin do not have operational guidelines for the administration of mechanical harvest regulations (DFO 1986, Wisconsin Department of Natural Resources 2000). Further, Ontario and Manitoba do not have operational guidelines for non-mechanical harvest of macrophytes (DFO 1986). Individual habitat managers interpret and apply these provisions on a case-by-case basis (K. Fisher, pers. comm., Freshwater Institute, Winnipeg, Mb. 1999).

The Minnesota Department of Natural Resources (MDNR) differs from the other agencies in that habitat managers are provided with operational guidelines that govern both mechanical and non-mechanical harvest of aquatic macrophytes (Minnesota Department of Natural Resources 2000). These guidelines are separated into three categories: activities requiring a permit, activities that do not require a permit, and activities prohibited by the MDNR. Activities that require a permit include: the removal of free-floating macrophytes and/or floating bogs, the destruction of aquatic macrophytes in public waters not associated with the riparian areas of a landowner, the installation and/or operation of an untended automated aquatic plant control device, and the creation of a channel that exceeds 4.3 metres in width (Minnesota Department of Natural Resources 2000).

Physical control of macrophytes without a permit is allowed by the MDNR under the following conditions: cutting or pulling aquatic macrophytes for the purpose of constructing shooting and/or observation blinds, and cutting or pulling submerged aquatic macrophytes to maintain a site for swimming or boat docking. Swimming and/or boat docking areas may not extend along more than one half the length of the landowners total shoreline to a maximum of 14 metres. Additionally, these areas may not exceed 210 square metres in area. Boat channels extending to open water may be maintained, but may not exceed 4.3 metres in width. The rules governing macrophyte removal specify that all cut macrophytes must be removed from the water body at the time of cutting.

There are six macrophyte control methods prohibited by the MDNR. First, the placement of plastic mats, plastic sheets, filter fabric, or similar materials (collectively known as bottom weed barriers, or BWB's) on the macrophyte beds of public waters to destroy or prevent their growth is prohibited. Second, the removal of macrophytes to improve the appearance of undeveloped shoreline only for aesthetic purposes is forbidden. Third, the control of aquatic macrophytes in areas posted or designated by the commissioner as scientific and/or natural areas is unlawful. Fourth, pesticide control of aquatic macrophytes in natural environment lakes (established pursuant to chapter 6120.3000 of the Minnesota Rules) and pesticide control of aquatic macrophytes in watercourses or portions of watercourses classified as wild (as defined under either the Minnesota or federal Wild and Scenic Rivers Acts, section 103F.325 and sections 1271 to

1287 respectively) is prohibited. Fifth, it is unlawful to remove or destroy aquatic macrophytes within a posted fish spawning area. Sixth, organised lakewide cutting and removal programs are restricted to a maximum area not to exceed 50% of the total littoral area as determined by the commissioner (Minnesota Department of Natural Resources 2000).

6.3.2 Chemical Control Regulations

The regulations used by all five jurisdictions to regulate the chemical control of macrophytes are similar (Tables 2 and 3). First, the jurisdictions rely on a system that implies a high level of agreement between local (i.e. provincial and state) and federal government. Chemical application is regulated through both local and federal regulations (Table 3, from DFO 1986, Manitoba Department of Conservation 2000, Michigan Department of Natural Resources 2000, Wisconsin Department of Natural Resources 2000). Second, the regulations employ a formal permitting process (Table 3) (DFO 1986, Manitoba Department of Conservation 2000, Michigan Department of Natural Resources 2000, Wisconsin Department of Natural Resources 2000). However, there are differences in the permit requirements of each jurisdiction (Table 3).

Table 3: Administrative Agencies in the United States and Canada responsible for the Chemical Control of Aquatic Macrophytes.

CHEMICAL CONTROL COMPONENTS	ONTARIO	MANITOBA	MINNESOTA	WISCONSIN	MICHIGAN
IDENTITY OF APPROVAL AGENCY	Federal: DFO [Fisheries Act (HADD Provisions)], and Provincial: PMRA (Pesticides Act)	Federal: DFO [Fisheries Act (HADD Provisions)]	Federal: EPA (FIFRA), and State: MDA (Minnesota Rules – Chapter 6280)	Federal: EPA (FIFRA), and State: WDNR, WDATCP (Wisconsin Codes Chapter NR 107)	Federal: EPA (FIFRA), and State: MDA, MDEQ (Michigan State Codes Chapter PA 004199, Sec. 12562)
PERMIT REQUIREMENTS	Training Program	Method of application; Map of application area	Map of application area; Amount of chemical and rate of application	Application area map; plant community summary; Chemical amounts; alternative feasibility report	Map of application area; Amount of chemical and rate of application

6.3.3 Biological Control Regulations

All of the jurisdictions rely on indirect means to regulate the biological control of macrophytes (Table 2) (DFO 1986, Manitoba Department of Conservation 2000, Michigan Department of Natural Resources 2000, Wisconsin Department of Natural Resources 2000). Further, there are differences between the methods that Ontario and the remaining jurisdictions use to regulate biological control agents. Manitoba, Michigan, Minnesota, and Wisconsin can partially prevent the use of biological agents to control macrophytes based on state regulations that prohibit the possession and/or transportation of exotic species (i.e. *Ctenopharyngodon idella*) (Manitoba Department of Conservation 2000, Michigan Department of Natural Resources 2000, Wisconsin Department of

Natural Resources 2000). Ontario is the only jurisdiction that does not outlaw the possession, transportation, or translocation of non-native species into local waterbodies (Ontario Ministry of Natural Resources 2000). Instead, habitat managers in Ontario determine on a case-by-case basis whether or not the use of biological control agents leads to a compromise of the HADD provisions of the Federal Fisheries Act (DFO 1986).

6.4 Critique of Aquatic Macrophyte Regulations

This critique is organised according to the method of macrophyte control (i.e. physical, chemical, biological). Within each method the regulations will be critiqued according to jurisdiction. The regulations are critiqued in relation to the results of both the Lake 191 experiment and studies reviewed in chapter two.

6.4.1 Physical Control of Regulations

The physical control regulations reviewed in section 6.3.1 may not be comprehensive enough to protect fish habitat. There are no guidelines associated with the physical control regulations in Ontario, Manitoba, and Wisconsin. Additionally, there are no regulations in Michigan that address the physical control of macrophytes. The manner in which the regulations are applied is not explicitly outlined (DFO 1986, Wisconsin Department of Natural Resources 2000, L. Esman, pers. comm., Michigan Department of Environmental Quality, Lansing, Michigan 1999). The application of such generalized regulations may not take into account the differences between lakes that have macrophyte exotics and lakes that have a natural species community. Macrophyte communities in the lakes in these jurisdictions vary (Minnesota Department of Natural Resources 2000, Wisconsin Department of Natural Resources 2000, Michigan Department of Natural Resources 2000). Some of these lakes have eutrophication and exotic macrophyte species problems while other lakes do not. Having to apply the same general regulations for all bodies of water, whether they have macrophyte nuisance issues or not, may prove to be deleterious to fish populations.

Guidelines for the physical removal of macrophytes should be based on the make-up of individual macrophyte communities in each lake. Different guidelines are necessary for lakes where the community is dominated by exotic macrophytes or influenced heavily by eutrophication than for pristine lakes with natural macrophyte communities. Clearly, applying harvesting as advocated by Olsen et al. (1998) to pristine, nutrient poor lakes, like ELA lake 191, would have consequences habitat managers want to avoid: fewer large predators and many forage fishes. Alternatively, not harvesting in lakes dominated by exotic macrophytes, like *Myriophyllum spicatum*, perpetuates fish communities with few large fishes that sport-fisherman prefer. It is essential that habitat managers recognise the differences in macrophyte policy that are necessary for each community.

6.4.2 Chemical Control Regulations

There are two main problems with the chemical control regulations in all jurisdictions reviewed in this paper. First, the operational guidelines that resource agencies use to apply the chemical regulations do not take into consideration the differences between lakes based on macrophyte communities. Lakes that do not have macrophyte nuisance problems are regulated in the same manner as lakes that have problems (DFO 1986, Manitoba Department of Conservation, Michigan Department of Natural resources 2000, Minnesota Department of Natural Resources 2000, Ontario Ministry of Natural Resources 2000, Wisconsin Department of Natural Resources 2000).

Second, these jurisdictions do not have comprehensive permitting processes for the application of aquatic herbicides (Table 3) (DFO 1986, Manitoba Department of Conservation 2000, Michigan Department of Natural Resources 2000, Minnesota Department of Natural Resources 2000, Ontario Ministry of Natural Resources 2000, Wisconsin Department of Natural Resources 2000). Four of the five jurisdictions do not require landowners that are applying for chemical use permits to attend training programs (Table 3). This may allow some landowners to receive permits to apply herbicides without a complete understanding of how to avoid negative impacts on fish populations and avoid hazards to their own health. Not all of the jurisdictions require applicants to submit detailed information about both the area intended for treatment and their intended methods of treatment. This may lead resource agencies to issue application permits with incomplete information on the areas that are going to be treated and the amounts of herbicide used in each treatment (Table 3).

6.4.3 Biological Control Regulations

The selected jurisdictions do not directly regulate the biological control of macrophytes (Table 2). Methods that are used to biologically control macrophytes are relatively new, and their effects on native ecosystems are poorly understood (Newman 1996). Thus, the possibility that these control methods could adversely effect native fish populations has not been adequately examined. One method currently being researched involves stocking native weevils (*Euhrychiopsis lecontei*) that consume and destroy Eurasian watermilfoil (Newman 1996). Because *E. lecontei* is not an exotic species, state regulations do not prohibit the use of this organism to control macrophytes. Additionally, this control method is not directly addressed in the HADD provisions of the Federal Fisheries of Canada (Table 2).

7. SUMMARY, CONCLUSIONS, AND RECOMMENDATIONS

7.1 Summary

In this study I examined the effects of macrophyte harvesting on the feeding relationships of northern pike, yellow perch, and pumpkinseed in a boreal lake in the ELA, summarised regulations that relate to habitat modification, and recommended management measures based on the findings of the investigation. This project was undertaken to assist habitat managers and research scientists in understanding the effects of habitat loss on native fish populations in Canada, and to examine the current regulations that relate to habitat modification and management.

There were three methods used to determine the implications of feeding relationships on the effects of macrophyte removal on trophic levels in Lake 191. Fish diets were analysed using the percent composition by number method, the Relative Importance Index established by George and Hadley (1979), and a comparison of the relationship between predator size class and prey type. The most common food of northern pike was YOY northern pike. Northern pike did not consume preyfish at levels that have been reported in similar studies of diet composition (Frost 1954, Lawler 1965). The results of diet analysis for yellow perch indicated seasonal variation in the occurrence of prey items. Yellow perch consumed benthic invertebrates and zooplankton according to their seasonal availability. Pumpkinseed consumed high percentages of benthic invertebrates throughout the season. Both yellow perch and pumpkinseed consumed conspecifics and YOY northern pike.

The regulations of two provinces (Ontario and Manitoba) and three states (Michigan, Minnesota, and Wisconsin) that relate to the control of aquatic macrophytes were examined. This information is summarised in Tables 2 and 3. The similarities and differences between regulatory systems in these states and provinces were also reviewed in this study. Finally, the regulations that relate to the control and/or removal of macrophytes were critiqued in reference to both the results of the Lake 191 experiment, and similar studies on fish habitat modification.

7.2 Conclusions

The feeding relationships between northern pike, yellow perch, and pumpkinseed provide information to interpret population changes of these species and lower trophic levels in Lake 191. Stomach content analysis of northern pike in Lake 191 indicated that northern pike were not utilising alternative prey species that had increased in abundance after macrophyte harvesting. Instead, northern pike preferentially consumed juvenile northern pike. Differences between YOY northern pike, yellow perch, and pumpkinseed habitat selection, predator avoidance behaviours, and fin morphology have led to northern pike preference for cannibalism. The differences in vulnerability to predation by northern pike between YOY northern pike and preyfish may have been due in part to loss of refuge via macrophyte removal.

Different size classes of northern pike selected different prey items. Small size classes, and thus young age classes, of northern pike preferred cannibalism to consumption of preyfish. Large size classes of northern pike did not consume a high percentage of northern pike. The small size classes of northern pike may have been conditioned to select conspecifics based on their ease of capture relative to preyfish.

Seasonal variation in the diets of yellow perch and pumpkinseed indicated that these fish were neither obligate planktivores nor obligate benthivores. They likely switched prey depending on availability. Previous studies have shown that flexibility in prey selection leads to a competitive advantage in terms of nutrient procurement (Mills et al. 1987). The differences in diet breadth between preyfish and northern pike may help to explain both yellow perch abundance increases, and decreases in northern pike abundance.

When yellow perch and pumpkinseed consumed zooplankton they selected mostly large species. The increase in preyfish abundance, coupled with their preference for large zooplankton, may be responsible for the shift in the zooplankton community observed by Salki (in prep. 2000). Large numbers of small planktivorous fish may have consumed enough large zooplankton to shift the community composition from larger bodied to smaller bodied zooplankton. This may explain how zooplankton abundance increased at the same time that biomass decreased. Because macrophyte harvesting is responsible for the changes in yellow perch abundance, it is indirectly responsible for the changes in the zooplankton community.

Benthic invertebrates were a more important component of preyfish diet than zooplankton. The difference between the importance of these two food types may have implications on the effects of macrophyte removal on preyfish abundance. Monohan and Caffrey (1996) found that removing littoral zone macrophytes allowed planktivorous fish access to benthic invertebrates that would otherwise be inaccessible. Benthic invertebrates are larger and more calorically dense than zooplankton (Driver 1981, Karamushko 1996). Macrophyte removal may have allowed preyfish access to a high quality food source that was previously less available. Abundance of yellow perch and pumpkinseed increased by low levels of predation by northern pike and increased access to benthic invertebrates.

Evidence of northern pike consumption of northern pike was found in smaller than expected sizes of both yellow perch and pumpkinseed. This provides further evidence for increased predation of YOY northern pike. Yellow perch and pumpkinseed consumption of northern pike, high levels of northern pike cannibalism during a period when preyfish abundance were increasing, and the removal of littoral zone vegetation combine to emphasise the role of cover for juvenile northern pike survival.

The regulations that govern macrophyte control in the selected jurisdictions seemed insufficient to protect fish habitat. Outside of Minnesota, the states and provinces reviewed in this study have not adopted specific guidelines for the administration of their macrophyte control regulations. Additionally, the regulations used by the selected jurisdictions do not adequately cover the differences between aquatic plant communities and other factors, such as eutrophication. The permitting processes utilised by the jurisdictions to regulate chemical control of macrophytes may not be comprehensive enough to ensure the protection of fish habitat.

7.3 Recommendations

Suggestions for macrophyte control regulations and related future research include:

- More research needs to be done on the fish populations of Lake 191. Specifically, the feeding relationships between trophic levels, and the abundances of fish and zooplankton should continue to be monitored;
- The regulations that relate to the physical control of aquatic macrophytes should be revised to reflect a more adaptive management approach, in order to facilitate this;
    - Multiple experiments, similar to the Lake 191 removal experiment, should be conducted on different types of waterbodies, using different methods of macrophyte removal (i.e. hand cutting, and mechanical harvesting machinery), and with different percentages of littoral zone macrophyte removal;
    - Government agencies should publicize the potential impacts of macrophyte removal to relevant stakeholders (i.e. riparian landowners);
    - The results from the adaptive management experiments, and the input of relevant stakeholders should be utilised to draft a set of regulatory guidelines that address the control of macrophytes and can be applied to lakes with different macrophyte communities and trophic levels.

- The government agencies listed above should augment their current chemical control regulations in the following manner:
    - A provision that makes chemical application training compulsory should be added to all chemical control regulations. This will ensure that landowners are aware of the safest and least biologically dangerous methods of chemical application;
    - Application guidelines should be designed and implemented by all relevant government agencies. There is an abundance of literature on the effects of chemical herbicides on trophic levels of aquatic systems. Application guidelines should be based on the most conservative (in terms of habitat protection) control regimes, as indicated by the literature;
    - Landowners applying for chemical use permits should be required to include the following information: a map of the area to be treated, both the rates and total amounts of chemicals intended for use, a summary of the plant community, and a list of alternative control methods;

- At the current time none of the government agencies listed above has a regulation concerning biological control of aquatic macrophytes. The agencies should employ the set of steps suggested above for physical control regulations, but modify them such that they examine the effects of biological control of aquatic macrophytes.

GLOSSARY

- **Biomass**: the combined (total) weight of a given group of organisms (Murphy and Willis 1996).
- **Ecosystem**: the basic unit in ecology, including both the organisms and the non-living environment (Standard College Dictionary 1963).
- **Euryphagous:** eating various kinds of food (Standard College Dictionary 1963).
- **Eutrophication**: trophic state of a water body characterised by high inputs of nutrients and high biological production (Murphy and Willis 1996).
- **EPA**: the United States Environmental Protection Agency.
- **FIFRA**: the United States Federal Insecticide, Fungicide, and Rodenticide Act.
- **Frequency distributions**: an arrangement of statistical data that exhibits the frequency of the occurrence of the values of a variable (Murphy and Willis 1996).
- **Littoral zone**: the aquatic zone extending from the shoreline of lakes and oceans to depths where light is insufficient for growth of rooted macrophytes (Murphy and Willis 1996).
- **Macrophytes**: vascular plants and macroscopic algae that are rooted in the sediments below open water, and may be completely submerged, partly floating, or emergent (Murphy and Willis 1996).
- **Mesotrophic**: trophic state of a water body characterised by intermediate nutrients and intermediate biological production (Murphy and Willis 1996).
- **MDEQ**: the Michigan Department of Environmental Quality.
- **MDA**: the Minnesota Department of Agriculture.
- **NNLP**: the No Net Loss Policy of DFO Canada.
- **Oligotrophic**: trophic state of a water body characterised by low nutrients and low biological production (Murphy and Willis 1996).
- **OMNR**: the Ontario Ministry of Natural Resources.

- **Phytoplankton**: photosynthetic organisms in the plankton (Murphy and Willis 1996).

- **Population stunting**: low average growth in a population of organisms (Carlander 1969).

- **Recruits**: the number of fish surviving from the egg stage to a certain age or size when they are fully vulnerable to catch gear (Murphy and Willis 1996).

- **Size selection hypothesis**: relative over- or under-representations of specific sizes of forage fish in a population that is taken by a top-level predator (Murphy and Willis 1996).

- **Trophic status**: a relative descriptor of nutrient and organic content of a water body (Murphy and Willis 1996).

- **Zmax**: the metric that is used to express the maximum measured depth of a water body (Carlander 1969).

- **Zooplankton**: animals in the plankton, usually dominated by rotifers, copepods, and cladocerans (Murphy and Willis 1996).

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