Effects of macrophyte cutting on a whole lake ecosystem

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General Abstract

Macrophytes are of significant importance to aquatic ecosystems, generating primary production in nearshore environments and providing physical structure and habitat for organisms in the littoral zone of lakes. Macrophyte cutting is a common practice near human settlements, used to dampen the negative perceived effects they have on human activities. As such, understanding the impacts of vegetation cutting on both the lower and higher trophic levels can provide insight into impacts on the whole lake ecosystem. Impacts of macrophyte cutting on the whole-lake ecosystem were assessed at Lake 191 of the IISD-ELA, where 2 years of pre-experimental monitoring (1994 - 1995) were followed by 3 years of macrophyte cutting (1996-1998). After cutting occurred, macrophytes were allowed to re-establish and post-experimental monitoring occurred from 1999 until up to 2003. Results from this experiment showed decreased light penetration and decreased relative macrophyte biomass at 0.5m depth in 2000. Phytoplankton community composition became more variable, and biomass increased during macrophyte cutting. *Daphnia pulex*, *Daphnia catawba*, and *Daphnia schoedleri* collectively and *Diaptomus oregonensis* saw the greatest biomass changes within the zooplankton community. Growth rates of yellow perch declined following macrophyte cutting; by contrast, northern pike growth increased throughout macrophyte harvest, but slowed following macrophyte cutting. These changes in growth appeared to be density dependent for northern pike, but not for yellow perch. Stable isotope values of carbon and nitrogen (used to evaluate source energy in fish) were relatively stable for yellow perch throughout the experiment, however, carbon signatures for northern pike shifted towards more negative values suggesting changes in the source of carbon (towards pelagic resources) during manipulation, as well as a steady decline in trophic position (as indicated by nitrogen isotopic values). My results suggest that macrophyte cutting does impact the ecosystem as a whole, however, contrary to predictions, changes were most pronounced in fish than in lower trophic levels. Future studies should focus on what percentage of macrophyte cutting might facilitate positive reactions throughout the trophic levels, while still permitting anthropogenic activities.

Lay Summary

Aquatic plants are of great importance to aquatic ecosystems as they allow for increased energy production, habitat, and protection for organisms from predation. Cutting of aquatic plants is a common practice to allow for human activities, like swimming, boating and fishing. Given their importance to the ecosystem, understanding how aquatic plants affect phytoplankton, zooplankton, and fish communities is of great importance. In the 1990's, a whole-lake experiment took place where half of the aquatic plants from the shoreline of a lake were cut. Here, I assessed the impacts on both lower (e.g., algae and small animals) and higher (e.g., fish) trophic levels to determine the overall impacts on the whole-lake ecosystem. My results suggest that the lower trophic levels of Lake 191 were not impacted to the degree expected. Surprisingly, relative aquatic plant biomass increased during cutting and decreased only after cutting. Algae showed an increase during cutting, but zooplankton (small animals in the water column) were variable. Yellow perch, a prey fish, declined in growth rate, increased in biomass, but showed no changes to abundance during cutting or diet sources. On the other hand, northern pike, a top predator, showed a decline in abundance and biomass and increase in growth during macrophyte cutting. After cutting, northern pike appeared to rely on offshore resources to a greater extent than they had previously, and their relative position in the food chain declined. Together, these results suggest that aquatic plant cutting can have negative impacts on biomass and abundance of the fish communities.

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Chapter 1: General Introduction

Macrophytes are aquatic plants situated in the littoral zone of the lake. They require sunlight, nutrients, and suitable sediment to grow and thrive, making the littoral zone the only area macrophytes can successfully inhabit (Barko et al., 1991). Aquatic macrophytes are of great importance to aquatic ecosystems as they help with nutrient cycling and ecosystem metabolism (O'Brien et al., 2014; Tamire & Mengistou, 2014). Thus, macrophytes are a main contributor to the primary productivity in the littoral zone of aquatic ecosystems (Nõges et al., 2009; O'Brien et al., 2014; Tamire & Mengistou, 2014). Macrophytes are also important for the physical processes that occur in a lake, like water movements, currents, and sedimentation. Macrophytes are known to reduce flow velocities within the littoral zone, which causes sedimentation at the lake bottom and can result in up to 29-fold reduction in sediment resuspension, decreasing turbidity (Madsen et al., 2001; Zhu et al., 2015).

In aquatic ecosystems, macrophytes and phytoplankton compete for the same resources, which can lead to dominance of one over the other if the right conditions are present. Phytoplankton, which can also inhabit the littoral zone, also require sunlight and nutrients (Baker & Newman, 2014). While phytoplankton thrive with high nutrients in the water column, macrophytes tend to require low water column nutrients to remain rooted in the sediment (Baker & Newman, 2014). With a greater cover of phytoplankton, light cannot penetrate as deep into the water, leaving the macrophytes without sunlight and nutrients. On the other hand, phytoplankton struggle to survive when macrophytes become too dense as there are not enough nutrients in the water column due to sedimentation (Baker & Newman, 2014). Upon sudden increased nutrients in the water column from disturbances like macrophyte cutting, phytoplankton that utilize the surface of the water and grow quickly often dominate phytoplankton communities, like cyanophytes (Wojciechowski et al., 2018; Zhu et al., 2015). Macrophytes can also provide refuge for large zooplankton grazers, which has been shown to be a major determinant of phytoplankton densities in shallow lakes (Burks et al., 2006; Moss et al., 1994; Scheffer 1999). However, macrophytes and phytoplankton can inhabit the same area if both are in moderate levels (Baker & Newman, 2014).

Macrophytes can be important in structuring communities in aquatic environments by providing habitat and cover to various species, further increasing species diversity (Gasith & Hoyer, 1998; Sollberger & Paulson, 1991; Thomaz & Cunha, 2010). As mentioned previously, zooplankton use the littoral zone for refuge and grazing, despite the presence of zooplanktivorous fish (Lauridsen & Lodge, 1996; Scheffer, 1999). While some nearshore zooplankton taxa use macrophytes as refuge, studies show that specific species of *Daphnia* usually found in offshore areas behaviourally avoid macrophytes all together, and only in the presence of fish do they partially overcome this behavioural avoidance of macrophytes (Lauridsen & Lodge, 1996; Pennack 1973). The increased structural complexity of the macrophyte stands makes foraging more difficult for some large predators (Burks et al., 2006; Sass et al., 2006).

Another important group that relies on macrophytes for habitat, survival, and resources is macroinvertebrates (Cyr & Downing 1988a; Cyr & Downing 1988b). Macroinvertebrates can be found on both submergent and emergent macrophytes, with a greater abundance found on macrophytes with a large, colonizable surface area

(Schramm et al., 1987). Macroinvertebrates are commonly used as bio-indicators in aquatic ecosystems because they spend a significant time of their short lives in the water and are easy to sample (Uherek & Pinto 2014). As macroinvertebrates are lower in the trophic level, they can also serve as an important food source for fish in higher trophic levels. When fish are present in lakes, invertebrate abundance and density tends to increase with habitat complexity, but this pattern tends not to be present in fishless lakes (Rennie & Jackson 2005). As such, the structure of macrophytes provide a greater surface area for colonization of smaller organisms, like algae and invertebrates in lakes with fish. This, in turn, can attract species of higher trophic levels, including larval and juvenile fish, because of increased resource availability (Grenouillet et al. 2002; Vadeboncoeur et al., 2014).

Egg deposition in the littoral zone of the lake is common for a number of fish species including yellow perch (*Perca flavescens*) and northern pike (*Esox lucius*). Yellow perch deposit large masses of eggs on dead, submerged vegetation in a strand that can be up to 2 metres in length (Newsome & Tompkins, 1985). These egg strands are covered in a jelly-like substance, which is thought to repel predators and provide protection; suggesting protection in macrophyte stands from predation is not necessarily required for reproductive success (Čech et al., 2009; Newsome & Tompkins, 1985). After hatching, perch larvae move to the pelagic zone and remain there for 1-2 months before returning to the littoral zone (Wang & Eckmann, 1994). Adult perch select their habitat according to season. In spring and summer, they prefer coarse woody debris in the littoral zone. During autumn and winter, perch migrate to deeper zones in the lake (Westrelin et al., 2018). For northern pike, it is common to find eggs in shallow, vegetated habitats in the spring, which is thought to increase the survival of spawned eggs. Northern pike eggs are adhesive, allowing the eggs to attach to vegetation higher up; avoiding the lake bottom (Casselman & Lewis, 1996; Farrell et al., 1996; Dombeck et al., 1984). Once eggs hatch and young fish begin to get larger, northern pike can be found in moderately dense vegetation (Casselman & Lewis, 1996). As they grow larger, their habitat requirements and preferred depth range increases (Harvey, 2009; Kobler et al., 2008). In a shallow lake, it was seen that pike favour habitats that provide some degree of plant cover in both summer and winter (Kobler et al., 2008).

Aquatic macrophyte removal, which can be conducted by introduced invasive species (eg. *Ctenopharyngodon idella*), mechanical removal, or the use of herbicides, is a common management technique used to reduce the negative perceived effects they have on human activities and development. Whether the plant matter is left in the lake or removed completely, this practice is likely to have significant impacts on the habitat, diet, abundance and composition of fish and plankton populations (Espinosa-Rodriguez et al., 2020; Greer et al., 2012; Sass et al., 2006; Pothoven et al., 1999). Changes to the macrophyte community can alter habitat for both invertebrate and fish populations (Espinosa-Rodriguez et al., 2020; Smokorwski & Pratt, 2007). Removing macrophytes also reduces environmental heterogeneity, which can in turn reduce nearshore zooplankton biodiversity (Espinosa-Rodriguez et al., 2020). This decrease in nearshore zooplankton biodiversity can also impact higher trophic levels. Decreases in the abundance and growth rates of fish have been previously observed following removal of aquatic macrophytes from riverine environments (Garner et al., 1996; Greer et al. 2012). With less macrophyte biomass, available shelter for fish becomes limited. Species that depend on macrophytes for shelter from predators are then exposed, which may lead to an increase in predation and subsequent decrease in prey availability and survival of juvenile fish (Thomaz & Cunha, 2010). A decrease in prey density may further lead to decreased growth rates in consumer species. However, Trebitz and Nibbelink (1996) demonstrated using a simple simulation model that with plant removal in the 20 – 40% range, bluegill sunfish (*Lepomis macrochirus*) growth can actually increase due to edge effects, although these findings were not followed up with empirical observations.

The responses of some species to vegetation removal can be linked to their known life history requirements. For example, the preference for sparsely vegetated habitats by longear sunfish (*Lepomis megalotis*) accounted for an increase in species abundance following removal (Bettoli et al., 1993). Similarly, yellow perch prefer sparsely vegetated habitats (Westrelin et al., 2018), whereas northern pike prefer areas that are moderately vegetated (Kobler et al. 2008). One might then expect abundance of perch and northern pike to be related to their life history requirements in relation to the importance of macrophytes for feeding, cover and reproduction. If so, then based on these previous observations, macrophyte removal might be expected to cause a decline in northern pike abundance and perch abundance. Vegetation can lead to a clear-water state in shallow lakes by stabilizing lake sediments, which can further inhibit resuspension (Hamilton & Mitchell, 1996) and lead to a greater availability of smaller prey such as zooplankton (Barko et al., 1991; Burks et al., 2006; Scheffer et al., 1993). Phytoplankton-induced turbidity can cause the visual field in waters to decline, which in turn can cause slower growth rates in northern pike as pike larvae struggle to visualize and catch zooplankton (Salonen & Engström-Öst, 2013). When changes in spawning and nursery habitats of northern pike occur, they are forced to spawn in less desirable areas, which may affect recruitment (Massa & Farrell, 2019).

Based on the ecological importance of submergent macrophytes to habitat and species distribution (Espinosa-Rodriguez et al., 2020; Gasith & Hoyer, 1998; Smokorwski & Pratt, 2007; Sollberger & Paulson, 1991; Thomaz & Cunha, 2010), reproductive success of fishes (Casselman & Lewis, 1996; Dombeck et al., 1984; Farrell et al., 1996; Pothoven et al., 1999), and fish foraging abilities (Garner, 1996; Thomaz & Cunha, 2010), macrophyte cutting is likely to have major impacts at the whole ecosystem level. To better understand these impacts at the whole-ecosystem level, a whole-lake macrophyte cutting experiment was conducted in Lake 191 of the International Institute for Sustainable Development – Experimental Lakes Area (IISD – ELA) in Northwestern Ontario. Pre-experimental monitoring was conducted from 1994 – 1995. The littoral zone was divided into 80 sections that were 50m in width and half of the sections containing macrophytes were chosen at random for macrophyte cutting (Figure A1). Macrophytes were cut every 2-3 weeks from June – August during 1996 – 1998 using a commercial Hockney type weed cutter (Crary Company, West Fargo, N.D.) at the sediment interface, to a maximum depth of 1.5 m (where macrophytes stopped growing). All cut plant material was left in the lake. In 1999, cut areas were not manipulated and allowed to recover and post experimental monitoring of the lake occurred until 2003. Total relative biomass of macrophytes, or the relative amount of biomass expressed as the sum of the mean biomass of cut and uncut regions (each making up 50% of the total macrophyte cover of the lake) over all years was calculated using percent cover and biomass of cut and uncut areas (Figure A2; see Chapter 2 methods for further details on methods used to calculate this metric). Data collection on limnological and biotic parameters was also collected, however, these data have to this point only been summarized qualitatively in unpublished, largely descriptive reports (e.g., Jansen 2000, unpublished), and only report data and trends to 1999. As such, there is a need for the key components of the biological community in this experiment to be examined rigorously, provide a more complete description of the period post-manipulation, as well as make the findings of the study readily accessible to policy makers and the broader scientific community.

This thesis aims to evaluate the changes in the aquatic community of Lake 191 of the IISD – ELA before, during, and after macrophyte cutting, which has not been previously been examined across trophic levels in the detail described here. This was broken down into four objectives as follows:

1. To determine the changes in community composition and biomass of phytoplankton and zooplankton, relative to reference lakes in the region.

    H-1.1: The nearshore zooplankton community composition associated with macrophytes will shift to resemble a more pelagic assemblage following macrophyte cutting, whereas the offshore zooplankton community composition will remain stable or show only minor changes away from littoral-associated species.

    H-1.2: The phytoplankton community composition will shift to primarily phytoplankton groupings that will utilize the nutrients released from the decomposing plant material, such as cyanophytes.

H-1.3: Phytoplankton biomass will increase following macrophyte cutting as nutrients are released from the cut plant material and competition for sunlight and nutrients decreases.

H-1.4: The zooplankton biomass will decrease following macrophyte cutting as their refuge is removed and predation risk from fish increases.

2. To assess population abundance, biomass, and growth changes over time for *Esox lucius* and *Perca flavascens*; the dominant species in the experimental lake.

H-2.1: *Perca flavascens* and *Esox lucius* population abundance of fish greater than 100mm will decrease following macrophyte cutting as their primary habitat is disturbed.

H-2.2: Biomass for both *Perca flavascens* and *Esox lucius* for fish greater than 100mm will decrease when as their population abundance decreases. Once recovery begins, biomass will increase as habitat recovers.

H-2.3: Growth of *Perca flavascens* will decrease as their food source and foraging area decreases and competition for food increases.

H-2.4: As *Esox lucius* population abundance decreases, growth will increase as there becomes less competition for food and their primary food source, *Perca flavascens*, become easier to catch.

H-2.5: *Perca flavascens* maximum size will decrease as they are more vulnerable to predation from *Esox lucius,* a species that feeds based on gape size and prefers larger prey.

H-2.6: *Esox lucius* maximum size will not be affected as they mature later and grow at a slow rate.

3. To determine changes in resource use and trophic position for *Esox lucius* and *Perca flavascens* using stable isotope analysis, relative to Lake 239.

    H-3.1: Following the cutting of macrophytes, yellow perch $\delta^{13}C$ isotopic signatures will decrease to align more with offshore food sources (zooplankton and macroinvertebrates in the pelagic zone). Their $\delta^{15}N$ isotopic signatures will remain the same.

    H-3.2: Following the cutting of macrophytes, *Esox lucius* will rely more on offshore food sources as the nearshore food sources become sparse. Their $\delta^{13}C$ isotopic signatures will decrease to align more with offshore food sources. Their $\delta^{15}N$ isotopic signatures with remain unchanged as they will still feed on the same trophic level, but will switch to a diet of prey fish that are benthivorous instead of planktivorous.

4. To synthesize results from the first three objectives to determine the overall impacts of macrophyte cutting on a whole lake ecosystem.

Chapter 2: Impacts of macrophyte cutting on phytoplankton and zooplankton communities in Lake 191

2.1 Abstract

Aquatic macrophyte cutting can reduce environmental heterogeneity, causing changes in biodiversity and community composition of aquatic communities. However, the impacts of macrophyte cutting on lower trophic levels are less-well characterized. This study aimed to determine changes in water quality, as well as the community composition and biomass of phytoplankton and zooplankton from a whole-lake macrophyte cutting experiment conducted at Lake 191 of the IISD-ELA from 1994-2002. Approximately 50% of macrophyte cover was removed from the littoral zone of the lake from 1996-1998. Phytoplankton community composition became more variable during macrophyte cutting. Phytoplankton biomass increased in 1996 immediately following cutting, which was followed by a decrease to pre-experimental levels in subsequent years. Light penetration was relatively constant during the cutting period, but decreased sharply in 2000 when macrophyte biomass was at its lowest. Zooplankton community composition and biomass did not show dramatic changes during macrophyte cutting, though *Diaptomus oregonensis* increased in biomass during the recovery period. *Daphnia pulex, Daphnia catawba,* and *Daphnia schoedleri* collectively also appeared to increase during the experiment. These results suggest that lower trophic levels were not as impacted as predicted from smaller scale experiments, which in itself provides important insights into the impacts of macrophyte cutting on lower trophic levels.

2.2 Introduction

Macrophytes are crucial primary producers of aquatic ecosystems and contribute significantly to ecosystem function by providing both food and structural habitat for organisms (Nõges et al., 2009; O'Brien et al., 2014; Tamire & Mengistou, 2014). Located near the shoreline of waterbodies, macrophytes are often seen as a nuisance for human activities such as swimming, boating, and other water activities (Thiemer et al., 2021). Macrophyte cutting in the littoral zone is a common practice, often facilitated through mechanical means, species introductions, or herbicides (Hussner et al., 2017). Given the importance of aquatic macrophytes to the health and functioning of aquatic ecosystems, there are often impacts on the environment when this cutting in the littoral zone takes place.

Phytoplankton have the same requirements as macrophytes (sunlight and nutrients) to grow and thrive; suggesting phytoplankton abundance may trade off with macrophyte densities in the littoral zone (Baker & Newman, 2014). It is suggested that shallow lakes can have two alternate states of equilibria; one where macrophytes dominate in a clear-water state with moderate nutrient availability (eg. phosphorus), and another where phytoplankton dominate in a turbid state and high nutrient availability (Jackson 2003; Scheffer et al., 1993). Lakes are then able to switch between these states under certain conditions, such as a temporary reduction in turbidity of the lake facilitating a clear water state, or a sudden increase in turbidity causing a shift to a turbid state. Removing macrophytes from a shallow lake may cause changes towards increased turbidity and nutrients by allowing for sediment resuspension, making limited nutrients more available to phytoplankton. Phytoplankton abundance and biomass can be positively influenced by changes in nutrients like phosphorus (Elser et al., 2007; Schindler 1977), and phytoplankton community compositions can change to being dominated by groupings like cyanophytes post-disturbance (Wojciechowski et al., 2018; Zhu et al., 2015). Other studies have demonstrated an increase in chlorophyll *a* concentration, which is an indicator of an increase in primary production, and thus phytoplankton, after macrophyte removal and shredding (Bicudo et al., 2007; James et al., 2002). Measuring and analyzing changes in environmental parameters over time can aid in understanding what is happening in the ecosystem. Total phosphorus can aid in determining nutrient availability over time in aquatic ecosystems, chlorophyll *a* can help measure phytoplankton in the water column, and light penetration can aid in understanding clarity of water, which leads to an understanding of whether or not high phytoplankton biomass would be expected. Furthermore, phytoplankton and macrophytes play a major role in supporting primary consumers as zooplankton rely on phytoplankton as a food source (Paterson 1993) and abundance of invertebrate taxa are positively linked to macrophyte biomass (Cyr and Downing 1988b; Rabe and Gibson 1984; Rennie and Jackson 2005).

Macrophytes can also influence the physical environment in aquatic ecosystems. When macrophytes are present in river beds, streams, and littoral zones of lakes, they can reduce flow velocities within these areas, causing sedimentation, a reduction in turbidity, and an increase in light penetration, all which promote further macrophyte growth (Madsen et al., 2001). While macrophytes reduce sediment resuspension, wind on lakes with large bodies of open water can cause resuspension of sediments (Evans, 1994). Zhu et al. (2015) found that annual average of sediment resuspension was 29-fold lower in areas with macrophytes than areas without, which further solidifies the idea that macrophytes promote sedimentation. For sediment resuspension to occur, erosion, or disturbance to the sediment, needs to occur (Masden et al., 2001). An example of sediment disturbance could be macrophyte cutting, in which the macrophytes are mechanically cut. In the absence of macrophytes, nutrients that are resuspended in the water column, like phosphorus and nitrogen, can be utilized by phytoplankton as there are no competitors, allowing for an increase in phytoplankton growth (Zhu et al., 2015).

Zooplankton can rely on macrophytes for refuge from predators and for grazing (Burks et al., 2006; Lauridsen & Lodge, 1996; Moss et al., 1994; Scheffer 1999). However, some species of zooplankton, like *Daphnia,* have been found to avoid the shoreline altogether because of the presence of zooplanktivorous fish (Gliwicz and Rykowska, 1992). Macroinvertebrates are commonly found to use both emergent and submergent vegetation for refuge, habitat, and survival (Cyr and Downing 1988a; Cyr and Downing 1988b; Schramm et al., 1987), especially in the presence of fish (Rennie and Jackson 2005). Other macrophyte removal studies have found that phytoplankton biomass increases following macrophyte removal, but few studies have addressed the effects of macrophyte removal on zooplankton, and those that have been conducted report conflicting results. Choi et al. (2014) found that the removal of free-floating macrophytes in a lake in South Korea resulted in larger, more pelagic zooplankton and an increase in overall zooplankton abundance, richness, and diversity, along with increased phytoplankton biomass. In agreement with these findings, Misteli et al. (2023) found that both zooplankton and phytoplankton abundance increased following macrophyte removal. Mangas-Ramírez and Elías Gutiérrez (2004) found that calanoids decreased following mechanical removal of water hyacinth, whereas cyclopoids and cladocerans remained relatively unchanged. One important factor to consider when looking at changes in zooplankton communities following manipulations are fish that prey on zooplankton. Prey fish, like yellow perch, use zooplankton as a primary food source (Thorpe 1977; Paszkowski & Tonn, 1994), which may impact zooplankton communities following macrophyte cutting.

No current literature looking at macrophyte removal from the littoral zone of the lake assesses the impacts on a whole-lake ecosystem, and most studies only focus on a single type of plant removed (submerged and emergent), removal of a single plant species, or responses by a single organism group (Thiemer et al., 2021). The goal of this study was to analyze the impacts of macrophyte cutting on water quality, biomass and community composition of phytoplankton and zooplankton of a whole lake undergoing macrophyte cutting. Lake 191 is a small, shallow lake at the IISD – ELA in northwestern Ontario, which had 50% of macrophyte cover removed from the littoral zone of the lake. Following the cutting of macrophyte cover in Lake 191, I predict that the lake will shift to having high phytoplankton biomass and higher nutrients (e.g. phosphorus) immediately following macrophyte cutting, and with this, an increase in cyanophytes will occur. Given that phytoplankton biomass increases with higher turbidity, I predict that water clarity will decrease following macrophyte cutting. Conversely, as macrophytes are allowed to recover and plant biomass increases, because macrophytes were not entirely removed from the lake, the lake will be able to make the shift back to macrophyte-dominance. In terms of zooplankton, I predict that community composition after macrophyte cutting will shift to a make-up of larger, more pelagic taxa as there becomes more open water present in the lake, as observed elsewhere (e.g. Choi et al. 2014). Further, I predict zooplankton biomass will decrease following macrophyte cutting as their refuge is removed, they become more vulnerable, and predation risk from prey fish, like yellow perch, increases.

2.3 Methods

2.3.1 Study Site

The International Institute for Sustainable Development – Experimental Lakes Area (IISD-ELA) is located 52 km southeast of Kenora in Northwestern Ontario at 93°30'- 94°00'W, 49°30'-49°45'N (Brunskill & Schindler 1971). The IISD-ELA is comprised of 58 lakes set aside for whole-lake experimentation. A whole-lake macrophyte cutting experiment was conducted in Lake 191 from 1994 – 2003, with the primary purpose of understanding the impacts of littoral zone alteration on lake biota. Lake 191 is a shallow, brown water lake that contains an extensive macrophyte community (Table 2.1). Background monitoring occurred from 1994 – 1995. The entire shoreline was divided into 80 sections that were 50m in width. Of these 80 sections, 38 were determined to have macrophytes (Figure A1). Half of these 38 sections were randomly chosen for macrophyte cutting from 1996 – 1998 using a commercial Hockney type weed cutter (Crary Company, West Fargo, N.D.). Macrophytes were cut at the sediment interface, to a maximum depth of 1.5 m (where macrophytes stopped growing) and was repeated on a bi- or tri-weekly basis each year between June (1997, 1998) or July (1996) until the end of August. This effectively supressed macrophyte growth in the cut regions of the littoral zone, as macrophyte growth occurs from June – August in boreal lakes and plants die off in early fall (remaining dormant until water temperature increases in May). The cut plant material was left in the lake. This was followed by up to 4 years of post-experimental monitoring (1999-2003), depending on the parameter being measured.

Percent cover and biomass (g/m^2) of macrophytes were measured from 1994 – 2001 and 1996 – 2001, respectively, in both cut and uncut areas at 0.5 m depth (Table 2.2; Table 2.3). From this, total relative macrophyte biomass at 0.5m (i.e., biomass in the region of macrophyte cover prior to cutting, as the sum of cut and un-cut regions) was calculated using the estimated average percent cover and biomass estimates for each region (g/m^2; Figure A2). For 1994 and 1995, no biomass data were present. To estimate biomass of macrophytes for these years, a relationship between biomass (y) and percent cover (x) was determined using linear regression (Figure A3). From this, the percent cover for these years was inserted into the equation from the line of best fit that was generated ($y = -3.8 + x$), and macrophyte biomass estimates were produced ($F_{1,10} = 50$, $p < 0.05$). To facilitate comparisons across years, relative biomass was the sum of cut and uncut areas in the lake for all years (assuming cut regions in 1994 and 1995 was the same). While macrophyte biomass in previous reports (Huebert unpublished 1995, 1996, 1997) was measured from 0 – 1m, for the purpose of this study 0.5 m was chosen as the measurement point as this is the area most likely inhabited by phytoplankton, zooplankton, and fish.

Results from the Lake 191 experiment were compared with data collected from three unmanipulated reference lakes in the IISD-ELA: Lakes 239, 373, and 442. While these three lakes differ in size, depth, and species make-up from Lake 191, the goal of their inclusion for comparison was to rule out changes due to regional temporal variability during the time period of the experiment, which I assumed would manifest in all lakes under investigation (Table 2.4).

2.3.2 Chemical and physical parameters

Chemical, physical, and biotic parameters were collected in Lake 191 over the duration of the experiment (Table 2.5). Water samples for total phosphorus ($\mu g \cdot L^{-1}$, estimated as the sum of total dissolved phosphorus and suspended phosphorus) dissolved organic carbon (DOC; µg L-1), and chlorophyll *a* ($\mu g \cdot L^{-1}$, as an indicator of primary production), and algal identification were collected biweekly to monthly, along with temperature and light profiles during the ice-off season.

Light profiles (PAR profiles) were collected using an LI-192 Underwater Quantum Sensor, starting at just above the lake surface (0 m) and lowered in 0.5 m increments until the light measured was 1% or less of the surface light measurement. Light ratios (LR) at each depth on a given sampling date were calculated using the following equation:

$$LR = \frac{I_z}{I_0} \text{ (eq. 2.1)}$$

Where I_z is the light value ($\mu E \bullet m^{-2} \bullet s^{-1}$) at depth z and I_0 is the light value at the surface. Using light ratios, light extinction coefficients (k) were calculated for all summer dates by linear regression using R version 4.2.0 (R Core Team, 2022), using the following equation (Wetzel, 2001):

$$\ln(LR) = k * \ln(z) \text{ (eq. 2.2)}$$

Since k estimates are a measure of the slope describing the logarithmic decline of light ratios with depth (where the negative value of the term is ignored); because there is no intercept in the equation, steeper slopes represent a more rapid elimination of light with depth (Wetzel 2001). Each sampling event for which light data existed for Lake 191 were examined individually to ensure light ratios were calculated correctly and there were no outliers. The corresponding *p*-values for each *k* estimate were examined and dates with *p*-values > 0.05 were eliminated from the data (7.9% of all dates). In Lake 191, no PAR profiles were recorded for the year 1999.

As a secondary measurement of light penetration in Lake 191, secchi disk depth (m) was taken at the deep-water station in the centre of the lake biweekly from 1994 – 2002. This was done by lowering the secchi disk into the water on the shaded side of the boat until the observer could no longer see the quadrats shown on the disk. The disk was brought back up slowly in the water column until the quadrats could just be seen, and this depth was recorded to the nearest shallowest 0.25m increment.

To estimate thermocline depths for delimiting depth boundaries for water sampling, temperature was determined using a Flett Research Mark II digital telethermometer at 1m intervals until temperature changed >1°C/m, at which the bottom of the epilimnion was defined. Water samples were collected using an integrated water sampler over the deep station in each lake (Shearer 1978). Integrated epilimnion samples were collected from the lake surface to 0.5 m above the bottom of the thermal epilimnion or to 1% of the surface PAR (whichever was shallowest on the day of sampling). Depths of the strata were predetermined using the temperature and light profiles (Findlay et al., 2009). Since Lake 191 is shallow (Table 2.4), only epilimnion samples were collected, and only epilimnetic water chemistry parameters were examined for the three reference lakes for comparison.

Chemical parameters were analyzed by the Analytical Chemistry Laboratories at the IISD-ELA using the collected water samples. For chlorophyll *a*, high pressure liquid chromatography (HPLC) with a methanol, acetone, and water mixture was used. Suspended phosphorus and total dissolved phosphorus were analyzed using automated colourimetry and the manual technique of photo-oxidation of acidified samples and colourimetry, respectively (for more information, refer to Prokopowich 1979). For dissolved organic carbon, the dissolved inorganic carbon was removed from the sample by acidification. From here, the dissolved organic carbon samples were analyzed by gas stripping and conductimetric analysis for carbon dioxide (for more information, refer to Prokopowich 1979; Stainton et al., 1977).

2.3.3 Phytoplankton and zooplankton

A 125 mL aliquot of the water samples described above was taken and fixed in Lugol's solution for phytoplankton identification. Phytoplankton from epilimnetic water samples were identified and enumerated using the Utermöhl technique as modified by Nauwerck (1963). These cell counts were converted to wet-weight biomass (mg/m^3) by estimating cell volumes, which was done by measuring 30-50 cells of an individual species and applying the geometric formula of best fit for each cell shape (Vollenweider 1968; Rott 1981). A specific gravity of 1 is assumed for these biomass estimates.

Zooplankton samples were collected during the open water season from 1994 – 2001. For Lake 191 and reference Lakes 373 and 442, a flexible vinyl tube (7.6 cm diameter at the mouth) was used at 5-7 open-water stations in each lake (Salki 1993). The volume of the tube was then poured through a net (of 72 μm from 1994 – 1998, after 1998 53 μm net) and the collected contents were transferred into 45ml glass vials and preserved using a 5% formalin solution (Salki 1993, 1995). Similar methods were applied to 6-10 nearshore stations at each sampling event in Lake 191. Common species were identified to stage and species from subsamples using a compound microscope. Larger, less abundant species were enumerated using a dissecting scope. For Lake 239, a two-barreled closing sampler with a 53 μm mesh net was used and two hauls were collected from 1m above the lake bottom to the surface at the deepest part of the lake. Biomass estimates were determined by multiplying density estimates (numbers/L) by an estimate of the average mass (μg dry weight per individual) based on Malley et al. 1989 and Paterson (unpublished data). Zooplankton were then grouped into common taxa to harmonize the datasets across lakes and over time periods for analysis (Table 2.6).

2.3.4 *Statistical Analysis*

Environmental variables – namely, total phosphorus ($\mu g \cdot L^{-1}$), chlorophyll *a* ($\mu g \cdot L^{-1}$), DOC ($\mu g \cdot L^{-1}$), secchi depth (m), and calculated k estimates were plotted to determine changes over the duration of the experiment. Associations between these variables were then evaluated using a correlation matrix to determine the collinearity between the three variables in Lake 191. To check the normality of each variable, histograms were evaluated prior to running the correlation matrix. Total phosphorus displayed a right-skewed distribution, so this variable was log-transformed. After running the correlation matrix, a multiple linear regression model was run using the row scores from the first axis (axis explaining the most variance) against each environmental variable to see the relationship between the independent variables (total phosphorus, chlorophyll a, k estimates, DOC, and secchi depth) and the dependent variable (phytoplankton and zooplankton row scores). A linear model was then run, and variance inflation factors (VIF) were calculated to measure the degree to which the independent variables were influenced by correlation with one another. To check for normality and homogeneity, diagnostic plots were run. Since chemistry and light profiles are sampled at centre buoy in the middle of the lake, the nearshore zooplankton from Lake 191 were not included in this analysis. All sampling dates were crosschecked with each other to ensure a consistent timeframe. Any dates that were more than 7 days apart, or dates that were missing from the corresponding dataset, were removed from the analysis all together (for dates that were not identical and were kept in the analysis, see Table A1.; Table A2.).

Correspondence analysis (CA) is a type of multivariate analysis commonly used in ecology to analyze count and biomass data (ter Braak and Verdonschot 1995). A CA using the FactoMineR package in R version 4.2.0 (R Core Team, 2022) was used to assess the impacts of macrophyte cutting on community changes for phytoplankton and zooplankton over three time periods: pre-experimental monitoring (1994–95), cutting period (1996–98), and post-experimental monitoring (1999–2003). For both phytoplankton and zooplankton in Lake 191, initial correspondence analyses were run using all sampling dates. On this initial CA, data were examined to evaluate seasonal effects on communities, comparing periods across the 4 seasons, where dates corresponding to each season were chosen based on the spring and autumn equinox and the summer and winter solstice (Table 2.7). Seasonal differences were clearly apparent from this initial analysis, and the decision was made to retain only summer sampling dates to ensure among-year comparisons were not influenced by potential differences in the representation of samples within seasons among years. Phytoplankton biomass (mg/m^3) in all lakes were grouped as follows: Cyanophyte, chlorophyte, euglenophyte, chrysophyte, diatom, cryptophyte, and dinophyte. Groups that represented less than 1% of total phytoplankton biomass in a given lake were removed from the matrix for the CA. Rare taxa for zooplankton were dealt with in the same fashion as outlined above for phytoplankton. Row scores from both phytoplankton and zooplankton CA's were extracted into a comma separated values (csv) file for use in the multiple regression described above.

From both the nearshore and offshore CA's for Lake 191, zooplankton taxa of interest were identified from the biplots by determining which taxa appeared to have the strongest associations with the first two dimensional axes. The annual biomass of these identified taxa were then plotted to evaluate changes over time. For phytoplankton in Lake 191, all 7 groups were plotted in similar fashion.

Biomass over time for littoral and pelagic groupings of zooplankton taxa was assessed for Lake 191 and compared to the three reference lakes. For the groupings, littoral Cladocera and littoral Cyclopoids (See Table 2.6 for full list of species in these two groups) represented all littoral taxa in Lake 191, while all other taxa were classified as pelagic. For the purpose of this study, "littoral" taxa were defined as zooplankton that live on macrophytes or are benthic, and "pelagic" taxa were defined as zooplankton that inhabit the water column. To standardize values across lakes, zooplankton data was standardized using z-scores (Z) from the following equation:

$$Z = \frac{x - \mu}{\sigma} \quad \text{(eq. 2.3)}$$

Where x is the raw score (e.g., biomass), μ is the lake-specific population mean over all years of observation included in the study, and σ is the lake-specific population standard deviation (estimated over the same set of observations as the mean). A 95% confidence interval range was produced using the reference lakes z-scores for both zooplankton and phytoplankton using the following equation:

$$\mu \pm t\ \frac{\sigma}{\sqrt{n}} \text{ (eq. 2.4)}$$

Where μ is the population mean, σ is the population standard deviation, t is the value from the t-distribution table (1.96), and n is the sample size. The calculated upper and lower confidence intervals were then plotted on the annual plots. Total annual biomass plots were made in the same way for both zooplankton and phytoplankton summer sampling dates in Lake 191 to see trends over the years of the experiment. For zooplankton, Lake 442 was missing data for 1997, therefore, only Lakes 239 and 373 were considered for the confidence interval range for this year. Similarly, for phytoplankton, Lake 442 was missing data for 1996 and 1997. The situation was the same in that only the other two lakes were considered in the confidence interval range.

2.4 Results

2.4.1. Water chemistry, light

Mean annual plots for environmental variables for Lake 191 showed general stability in total phosphorus and chlorophyll *a*, but large changes in *k* estimates, secchi depth, and dissolved organic carbon (Figure 2.1). Variability in total phosphorus increased once manipulation started, and while an increase after cutting followed by a gradual decrease over the years may be apparent, high interannual variability makes it difficult to definitively say this is a trend (Figure 2.1a). Light extinction coefficient estimates for Lake 191 increased in 2000 (the first year after manipulation), indicating lower light penetration (since light extinction coefficients are a measure of the absorption relationship, a higher k-value means light cannot penetrate as deep in the water). This was followed by a gradual increase back to normal ranges in subsequent years (Figure 2.1c). Similarly, secchi depth decreased over time following macrophyte cutting and was lowest in 2000 (Figure 2.1D). Dissolved organic carbon spiked in 2000 and dropped back down to normal range the following year (Figure 2.1E). Relative biomass of macrophytes was lowest in 2000 (Figure A2).

2.4.2 Phytoplankton community

Phytoplankton total annual biomass in Lake 191 increased the first year of manipulation (1996), exceeding the range of variation expected based on reference lakes and gradually decreased until 1999 (Figure 2.2). In 2000, it increased again and remained slightly higher than pre-manipulation levels for the following 2 years, but remained within the range of annual variation expected based on reference lakes. The years of 1994 (pre-manipulation) and 1999 (post-manipulation) were below the range of interannual variation expected based on reference lakes, whereas 1996 and 1997 (during manipulation) were above of the 95% confidence interval bounds produced by reference lakes (Figure 2.2).

The first and second axes of the phytoplankton CA explained a total variance of 63.68%, with the first axis explaining almost double that of the second axis (axis 1 = 40.21%, axis 2 = 23.27%; Figure 2.3). Increased variability can be seen for the manipulation period, followed by a narrowing of the community diversity in the post-manipulation period suggesting a reduction in taxonomic diversity compared with the pre-manipulation time period. Chrysophytes and Cyanophytes were both present in the pre-manipulation and manipulation ellipses, but not in the post. All other phytoplankton groups were present in all three time periods. Reference Lakes 239, 373, and 442 did not show similar results (Figure 2.3). A multiple regression of the environmental variables*,* *k* estimates, total phosphorus, and chlorophyll *a*, dissolved organic carbon, and secchi depth, with the first axis row scores of the Lake 191 phytoplankton community was not significant ($F_{5,16} = 1.307$, p-value = 0.3101).

Some groups of phytoplankton in Lake 191 accounted for more biomass than others. Based on Figure 2.4, the y-axes show that Cyanophyte, Chrysophyte, and Cryptophyte (panels A, D, and F) had the most biomass in comparison to the other 4 groups. Chlorophytes and Dinophytes appeared to show changes most associated with the manipulation period (Figure 2.4 B and G). Chlorophyte biomass increased immediately following macrophyte cutting and did not decrease until the last year of monitoring. Dinophyte biomass increased in gradually until 1997 and dropped below pre-manipulation levels in 1999. Cryptophyte biomass (Figure 2.4 F) increased to above pre-manipulation levels in 1997, which was followed by a drop in 1999 before increasing again. However, variability in 1994 was high for this group, so it is harder to say if these changes are different in comparison to pre-manipulation period. Several taxa (Cryptophytes, Chrysophytes and Dinophytes) all seemed to show consistent increases in biomass during the post-manipulation period (Fig 2.4 D,F,G) whereas Cyanophytes and Chlorophytes declined during this period (Fig 2.4 A,B).

2.4.1 Zooplankton community

Annual biomass of total zooplankton dropped in 1997, the second year of macrophyte cutting. This was followed by an increase back to pre-experimental levels the following year (Figure 2.5). Among year variability was encompassed by variability observed in our reference lakes for 1996, 1999, and 2000, but was lower than expected based on interannual variation among reference lakes in 1995 and 1997. Annual biomass for pelagic zooplankton closely mirrored annual biomass for total zooplankton (Figure 2.6), indicating that most zooplankton in the total biomass dataset were pelagic. Littoral zooplankton annual biomass was highly variable, encompassed by the reference lake intervals for 1997, 1998, and 2001, and was highest in 1994 and 1999, but below the envelope of reference lake variability for these taxa in 1995, 1996, and 2000 (Figure 2.7).

The first and second axes of the CA on the offshore zooplankton community cumulatively explained 58.9% of the total variance (Figure 2.8). The CA on the offshore zooplankton community in Lake 191 indicated that the zooplankton community is represented primarily by the first dimensional axis. During macrophyte cutting, offshore zooplankton community diversity increased. While the community again narrowed during the post-cutting period, it did not return to the region of pre-cutting diversity. Reference lakes 239, 373, and 442 did not show similar trends (Figure 2.8). From the CA's done on both the offshore and nearshore zooplankton communities, taxa of interest were identified (e.g., those that appeared to have large influence on the first two axes). For the CA on the offshore zooplankton community in Lake 191, *Holopedium glacialis* appeared to be representative of axis 1 and was present in all time period ellipses, while *Daphnia* group 1 was strongly representative of the y-axis and was not present in any of the time period ellipses (Figure 2.8). *Diaphanosoma birgei* and *Bosmina longirostris* were only represented in the ellipse that represents the macrophyte cutting period. *Diaptomus oregonensis* adults appeared to influence the post-experimental monitoring community in both axes directions and was not present in the pre-experimental monitoring ellipse.

A correlation matrix revealed some evidence of covariation among predictor variables, however, all VIF's were <2 (Zuur et al. 2010). A multiple regression of total phosphorus, chlorophyll *a*, and *k* estimates dissolved organic carbon, and secchi depth for the offshore zooplankton community axis 1 row scores was not significant ($F_{3,24} = 1.191$, p-value = 0.3458). Diagnostic plots revealed normality and no evidence of homogeneity or outliers.

Mean annual biomass plots for specific taxa identified as important in the offshore zooplankton community from CA's revealed that in 1997, zooplankton mean annual biomass was at or near 0 for all taxa of interest (Figure 2.9). For *H. glacialis* (Figure 2.9 D), the lack of overlap in standard error bars suggests that zooplankton biomass in 1997 was different from the pre-experimental monitoring period and the post-experimental monitoring period up until 2001. *D. birgei* increased in 1996 and 1998, which was followed by a decrease to pre-manipulation levels in post-manipulation years. *D. oregonensis* increased in 1998, continuing to increase until the end of post-experimental monitoring. The first two axes of the CA on the nearshore community explained 67.85% of the total variance, and, while lacking the pre-experimental ellipse due to a low number of row (site) scores in that period, little to no shifts in the community were seen (Figure 2.10). For the nearshore zooplankton community in Lake 191, *Leptodora kindtii* and *D. oregonensis* adults were represented by both the first and second axes, however, were not present in either macrophyte cutting or post-experimental monitoring ellipses (Figure 2.10). *D. birgei* was represented by only the manipulation period, which was also seen in the offshore zooplankton CA. For the nearshore zooplankton taxa of interest, *D. birgei, D. oregonensis* and Cyclopoida nauplii mean annual biomass dropped in 1997, followed by an increase in 1998 (Figure 2.11).

2.5 Discussion

The results of this study showed impacts of macrophyte cutting on light penetration and the phytoplankton community. For zooplankton, however, impacts were difficult to discern. In terms of environmental parameters like total phosphorus, chlorophyll *a*, DOC, secchi depth, and light extinction coefficients, this experiment showed little to no effect on the first two, but dramatic (though delayed) decrease in light penetration, secchi depth, and an increase in DOC. While total phosphorus appeared to increase at the start of manipulation and gradually decrease over the years, there was a large amount of variation over all years. James et al. (2002) found an increase in total phosphorus from a range of 0.03-0.08mg/L to a high of 1.81mg/L 7 days after mechanical shredding of macrophytes, and total phosphorus in their study was found to decrease about a week after the highest recorded amount. While the results in Lake 191 were variable, the initial increase observed follows that of James et al. (2002) and makes sense given that plant material in both cases was left to decompose in the water, releasing nutrients into the water column (Marinho et al., 2010). However, one important difference between my study and the one by James et al. (2002) is that in their study, macrophyte shredding only occurred once, whereas it occurred over years in Lake 191. The steady decrease in total phosphorus in Lake 191 in the years following (1997 – 2002) does not entirely match up with the findings of James et al. (2002), as they found a decrease in total phosphorus 15 days after shredding ceased, in which case we might expect the total phosphorus in Lake 191 would decrease only after the cutting ended in 1999. The decrease in total phosphorus in 1997 and 1998 in the present study could be explained by the increase in relative macrophyte biomass at 0.5m, which increased by 2-3 times what it was prior to macrophyte cutting (mainly due to an increase in percent cover and biomass in uncut regions). It is possible that the new plants in the lake were using the nutrients released by the dead plant material, which is why I didn't observe a consistent increase in total phosphorus over the cutting years.

The decrease in light penetration and secchi disk depth observed in Lake 191 occurred only after macrophyte cutting stopped and when relative macrophyte biomass was at its lowest. This is supported by current literature, where Harpenslager et al (2022) found an increase in light attenuation (decrease in light penetration) following macrophyte removal due to an explosion in growth of phytoplankton, however unlike our study, cut plant material was removed and the bottom 50 cm of the lake was not mowed. In support of our observations, James et al. (2002) also found that turbidity, which is tightly related to light penetration and secchi depth, increased dramatically over the 14-day period after mechanical shredding. Dissolved organic carbon in Lake 191 spiked in 2000, where it increased by up to 300 µg/L in comparison to all other years. This is important as DOC absorbs ultraviolet light and leads to rapid attenuation, or lower light penetration, in higher concentrations (Dodds & Whiles, 2010), further supporting the results that in 2000, light penetration in Lake 191 was at its lowest. However, it is unclear if these changes in dissolved organic carbon are from a delay in impacts from macrophyte cutting or environmental factors, such as increased precipitation in that year causing increased fluxing of DOC from adjacent wetlands. Further analysis of regional precipitation patterns and DOC concentrations in reference lakes would be required to definitively evaluate this as a possible effect. In Lake 191, the changes observed in environmental parameters appear to be delayed and do not occur directly after cutting begins, but instead in the post-manipulation period. This could be due to the length of the experiment in Lake 191, as no other experiment in the current literature was run for the same length of time, which as a result has a higher chance for extenuating environmental effects to potentially impact results.

An increase in chlorophyll *a,* which is a measurement of primary productivity, was commonly found as a result of the increase in total phosphorus and nutrients in previous studies where macrophytes were fully removed (Bicudo et al., 2007; Choi et al., 2014; Espinosa-Rodríguez et al., 2020; Harpenslager et al., 2022) and a study where macrophytes were shredded and left (James et al., 2002), but not observed in the current study. Although I did not see an increase in chlorophyll *a*, there was a marked increase in the phytoplankton biomass immediately following cutting. James et al. (2002) suggested that the high chlorophyll *a* concentration at the experimental site meant there was high algal productivity, which would coincide with our increase in phytoplankton biomass found in Lake 191 following cutting. This initial increase in phytoplankton biomass observed is supported by the increase in total phosphorus as phosphorus is one of the nutrients phytoplankton use to grow. Similarly, the increase in relative biomass of macrophytes at 0.5m in 1997 could explain the decrease in phytoplankton biomass around the same time period as an increase in macrophyte cover and biomass would not be expected to accompany increases in phytoplankton biomass. As chlorophyll *a* is an indirect measure of the amount of phytoplankton in the water, the increase in phytoplankton biomass but no change in chlorophyll *a* suggests that chloroplast densities post-cutting may be lower in phytoplankton than prior to manipulation. From lab experiments in current literature, it was determined that algae increase their chlorophyll *a* content when light is low to maximize light absorption (Beardall & Morris, 1976). The increase in phytoplankton biomass following macrophyte cutting is further supported by other studies where complete macrophyte removal occurred (Choi et al., 2014; Misteli et al., 2023).

Based on the results of this study, *Daphnia* appeared to be the most affected zooplankton taxa in response to macrophyte cutting. *Daphnia* are a group of zooplankton commonly found in the centre of the lake, far from the littoral zone. Gliwicz and Rykowska (1992) suggest that high predation risk in the littoral zone from littoral fish, like juvenile perch, may be a factor in the evolution of shore-avoidance in some zooplankton species. Further, they saw smaller body sizes and clutches (number of eggs in a brood) in the nearshore populations of two *Daphnia* species, suggesting nearshore-oriented *Daphnia* populations may be more susceptible to predation due to lower reproductive rates. Similarly, if small zooplanktivorous fish increased in abundance during macrophyte cutting, predation from these small zooplanktivorous fish could be a potential cause of declines observed here in 1997. In the results of the study in Lake 191, while total zooplankton biomass crashed in 1997, the biomass of *Daphnia* group 1 (*D. pulex, D. catawba, D. schoedleri*) in the offshore zooplankton community was largely negligible during the duration of the experiment apart from 1998, when biomass spiked. While Rabe and Gibson (1984) saw an increase in *Daphnia* in shallow sites following macrophyte removal, it is hard to say the results in Lake 191 are due to macrophyte cutting as the increase in *Daphnia* group 1 was only in 1998 and not observed in any other year. Further, while Gliwicz and Rykowska's (1992) suggest that *Daphnia* commonly avoid macrophyte covered areas, and while this might explain the increased abundance of *Daphnia* during an active cutting year, it was not observed in the other two cutting years.

Total biomass of zooplankton in Lake 191 for pelagic and offshore sites saw a large decrease in zooplankton in 1997, followed by an increase in 1998. Total biomass for littoral taxa, however, saw no real changes over time. While these changes were observed, the pre-manipulation years were very different from each other, making it hard to tell if changes observed during manipulation are truly due to macrophyte cutting. One possible suggestion for the one-year crash in zooplankton biomass in Lake 191 is increased predation. It is possible that zooplankton were being fed on to a greater degree in this year by fish before a different food source was found. However, if this is the case, it is unclear why this effect would only be seen for one year during the experiment. While few studies have assessed changes in zooplankton communities and biomass following macrophyte cutting, Bickel and Closs (2009) found that total invertebrate biomass and abundance significantly increased following macrophyte removal. Other studies have found conflicting results regarding zooplankton abundance, with Choi et al. (2014) finding an increase in abundance of zooplankton in intermediate levels of macrophyte removal, and Garner et al (2006) finding a decrease in zooplankton abundance and a shift in community composition towards smaller zooplankton species following weed cutting. Mitseli et al (2023) found no change in the abundance of zooplankton following removal.

These differing results in literature may be due to different methods of cutting and removal (i.e. applied over different time periods, different percentage of cutting).

Unfortunately, no data during the current study were collected to characterize macroinvertebrates. Despite the importance of macroinvertebrates in aquatic ecosystems and their prevalence in macrophyte-covered waters (Cyr & Downing 1988a; Cyr & Downing 1988b; Jeppesen et al. 1997; Schramm et al., 1987), few studies have looked at the impacts of macrophyte removal on this group of invertebrates; including the current study. Studies that have evaluated impacts of macrophyte removal on this taxa are mixed; Misteli et al. (2023) found that macroinvertebrates associated with macrophytes decreased in abundance directly following macrophyte removal, which could be due to a high by-catch along with removed plant matter. On the contrary, Aasland (2021) found that while macroinvertebrate community composition shifted, density, diversity, and taxa richness of macroinvertebrates did not change following macrophyte removal in an oligotrophic river. Rennie and Jackson (2005) found that macroinvertebrate density in lakes with fish were positively correlated with plant biomass. This suggests that macroinvertebrate density may have scaled with total relative macrophyte biomass at 0.5m (Figure A2), in that it increased during cutting when total relative macrophyte biomass is at a high, and decreased during post-manipulation when total relative macrophyte biomass was at its lowest.

In Lake 191, macrophyte cutting had some impacts on environmental parameters and lower trophic levels. Total relative macrophyte biomass at 0.5m increased during macrophyte cutting and declined during recovery. This increase in total relative macrophyte biomass at 0.5m during macrophyte removal was supported by current literature (Thiemer et al., 2021). The decline in total relative macrophyte biomass following cutting is not supported by patterns in light penetration, as when macrophyte biomass declines, we can expect an increase in turbidity and a decrease in water clarity (Madsen et al., 2001). In terms of phytoplankton and chlorophyll *a,* there was no increase observed during the period of low total relative macrophyte biomass, which is unexpected given that when macrophyte biomass is low, typically phytoplankton biomass increases (Zhu et al., 2015). There was an increase in 2000 in DOC, which absorbs UV light and causes a decrease in light attenuation (Dodds & Whiles, 2010), which could be the cause of increased turbidity. While a decrease in zooplankton biomass was observed, variation among the pre-experimental monitoring years was high, making it difficult to discern if this was due to macrophyte cutting. A change in community composition to larger, more pelagic zooplankton was not observed during macrophyte cutting, which was expected given the increase in open water.

This study aimed to determine the changes in zooplankton and phytoplankton biomass and community composition following macrophyte cutting. The results saw some changes in environmental parameters and phytoplankton biomass, but little to no changes in zooplankton community or biomass. One limitation in terms of the analysis on the zooplankton community is the lack of macroinvertebrate data for Lake 191. Given the importance of macroinvertebrates on aquatic ecosystems, perhaps more concrete observations on the lower trophic levels would be seen following macrophyte cutting if such data had been collected. It is also possible that had there been enough data to view the time periods in a different way (eg. yearly instead of by the three periods), the results may have shown greater impacts for environmental variables and zooplankton.

Nevertheless, it was determined that the lower trophic levels in Lake 191 were not impacted dramatically, which was unexpected given past studies on phytoplankton and zooplankton and the overall importance of macrophytes on aquatic environments in general.

Tables

Table 2.1. List of macrophyte species present in Lake 191 from 1994 – 1997 (Huebert 1997, unpublished).

Species
Utricularia vulgaris
Carex spp.
Sparganium fluctuans
Isoetes echinospora
Nuphar lutea spp. variegatum
Eleocharis palustris
Utricularia intermedia
Equisetum fluviatile
Eriocaulon septangulare
Scirpus subterminalis
Dulichium arundinaceum
Nitella sp.
Callitriche palustris
Nymphaea odorata
Iris versicolor
Moss
Sagittaria latifolia
Eleocharis acicularis
Potamogeton epihydrus
Myriophyllum sp.

Table 2.2. Percent cover of macrophytes for Lake 191 from 1994 – 2001 in the 0.5 m contour. From 1996 – 2001, cut and uncut sections of the lake were separated into two separate categories. No data was available on macrophyte cover for 2002 or 2003 (Huebert report; Mills pers. comm).

Year	*% Cover*	
1994	27	
1995	26	
1996	Uncut – 53	Cut – 11
1997	Uncut – 63	Cut – 2
1998	Uncut – 43	Cut – 3
1999	Uncut – 48	Cut – 3
2000	Uncut – 27	Cut – 3
2001	Uncut – 19	Cut – 18

Table 2.3. Biomass (g/m^2) of macrophytes for Lake 191 from 1996 – 2001 in cut and uncut sections from the 0.5m contour of the lake. No data was available on macrophyte cover for 2002 or 2003 (Huebert report; Mills pers. comm).

Year	*Biomass (g/m^2)*	
1996	Uncut – 55	Cut – 7.9
1997	Uncut – 68	Cut – 0.1
1998	Uncut – 57	Cut – 0.2
1999	Uncut – 22	Cut – 1.1
2000	Uncut – 14	Cut – 1.1
2001	Uncut – 28	Cut – 1.1

Table 2.4. Comparison of physical parameters for Lake 191, Lake 239, Lake 373, and Lake 442.

	Lake 191	**Lake 239**	**Lake 373**	**Lake 442**
Surface area (ha)	16.3	54.3	27.3	16.0
Maximum depth (m)	4.1	30.4	20.8	17.8
Mean depth (m)	2.09	10.5	10.7	9
Trophic status	Oligo/Mesotrophic	Oligotrophic	Oligotrophic	Oligotrophic

Table 2.5. Parameters collected and used for analysis for Lake 191 and reference lakes.

Chemical	*Physical*	*Biotic*
Chlorophyll a (μg·L^{-1})	Temperature	Macrophyte cover and biomass
Total dissolved phosphorus (μg·L^{-1})	Light (PAR) profiles	Phytoplankton populations
Suspended phosphorus (μg·L^{-1})	Secchi disk depth (m)	Zooplankton populations
Dissolved organic carbon (μg·L$^{-1)}$		Fish populations

Table 2.6. Taxa groupings used for zooplankton biomass in all lakes.

Group	Species included
***Eubosmina* group**	*Eubosmina sp., Eubosmina longispina*
***Daphnia* group 1**	*Daphnia pulex, Daphnia catawba, Daphnia schoedleri*
***Daphnia* group 2**	*Daphnia galeatamendotae, Daphnia dubia, Daphnia laevis, Daphnia longiremis, Daphnia dentifera*
Littoral Cladocera group	*Acantholeberis curvirostris, Acroperus harpae, Alona affinis, Alona sp., Camptocercus sp.,* unidentified chydorids, *Ilyocryptus sp., Macrothrix laticornis, Latona setifera, Ophryoxus gracilis, Eurycercus lamellatus, Pleuroxus denticulus, Scapholeberis kingii, Simocephalus exspinosus, Simocephalus sp.*
Littoral Cyclopoid group	*Eucyclops agilis, Eucyclops speratus, Macrocyclops albidus* adults (c6), *Macrocyclops albidus* copepidids (c4-5), *Paracyclops poppei* adults (c6), *Paracyclops poppei* copepodids (c4-5)
Calanoid 4-5 group	Calanoid copepedids C4-5, *Diaptomus ashlandi* copepedids C4-5, *Diaptomus leptopus* copepedids C4-5, *Diaptomus minutus* copepedids C4-5, *Diaptomus oregonensis* copepedids C4-5, *Diaptomus sicilis* copepedids C4-5, *Epischura lacustris* copepedids C4-5
Cyclopoid 4-5 group	Cyclopoid copepodids C4-5, *Cyclops vernalis* copepedids C4-5, *Cyclops bicuspidatus tomasi* copepedids C4-5, *Mesocyclops edax* copepedids C4-5, *Orthocyclops modestus* copepedids C4-5, *Tropocyclops extensus* copepedids C4-5

Table 2.7. Season breakdown with dates used for zooplankton and phytoplankton correspondence analyses.

Season	**Dates**
Winter	December 21st – March 19th
Spring	March 20th – June 20th
Summer	June 21st – September 21st
Fall	September 22nd – December 20th

Figures

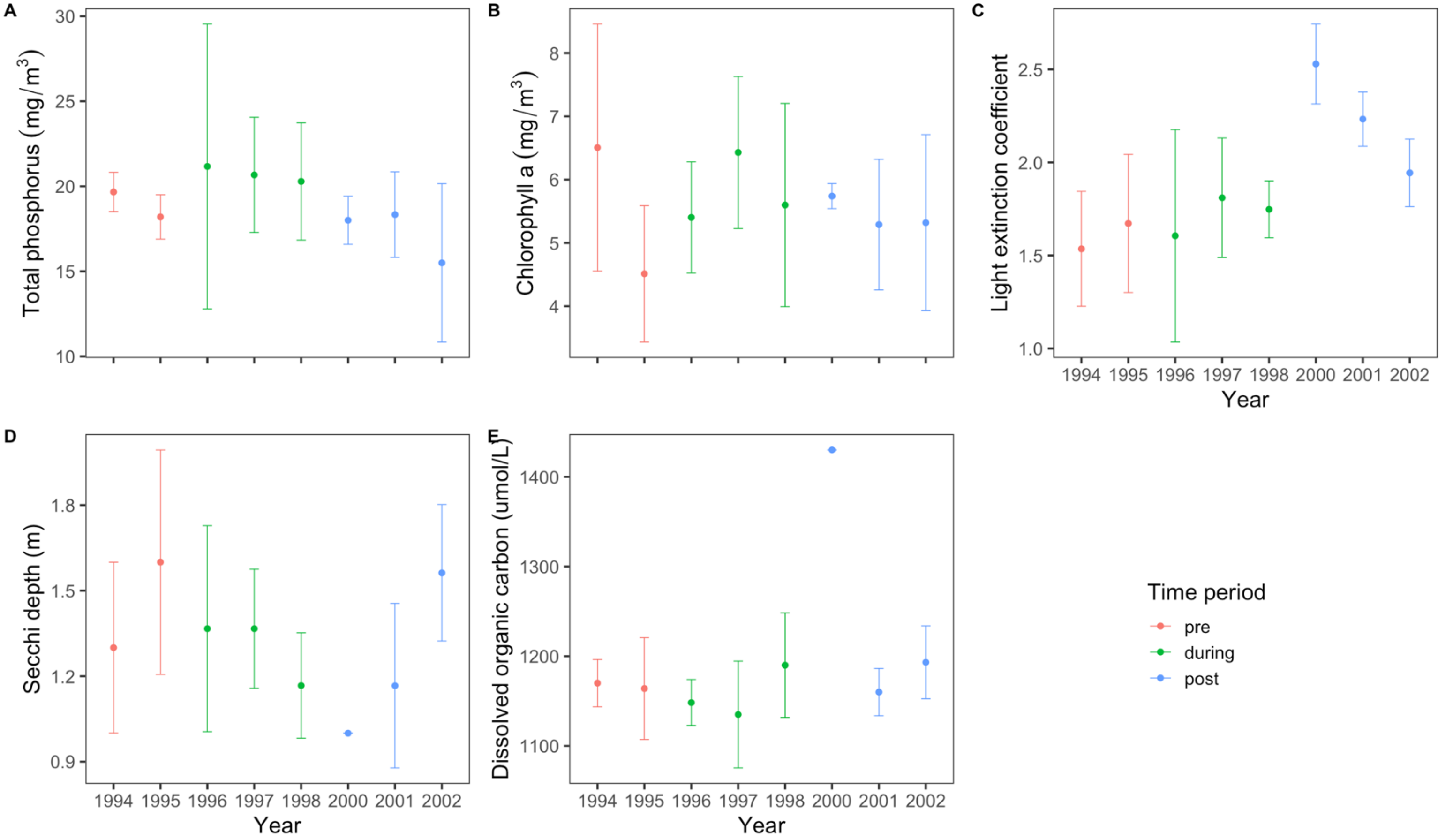

Figure 2.1. Mean annual plots for environmental variables in Lake 191 as follows: A) Total phosphorus (mg/m^3); B) Chlorophyll a (mg/m^3); C) light extinction coefficients; D) Secchi depth (m); and E) Dissolved organic carbon (umol/L). Standard deviation error bars and time periods are plotted on each graph where pink represents pre-experimental monitoring, green represents during macrophyte cutting, and blue represents post-experimental monitoring. Note scale differences on the y-axes.

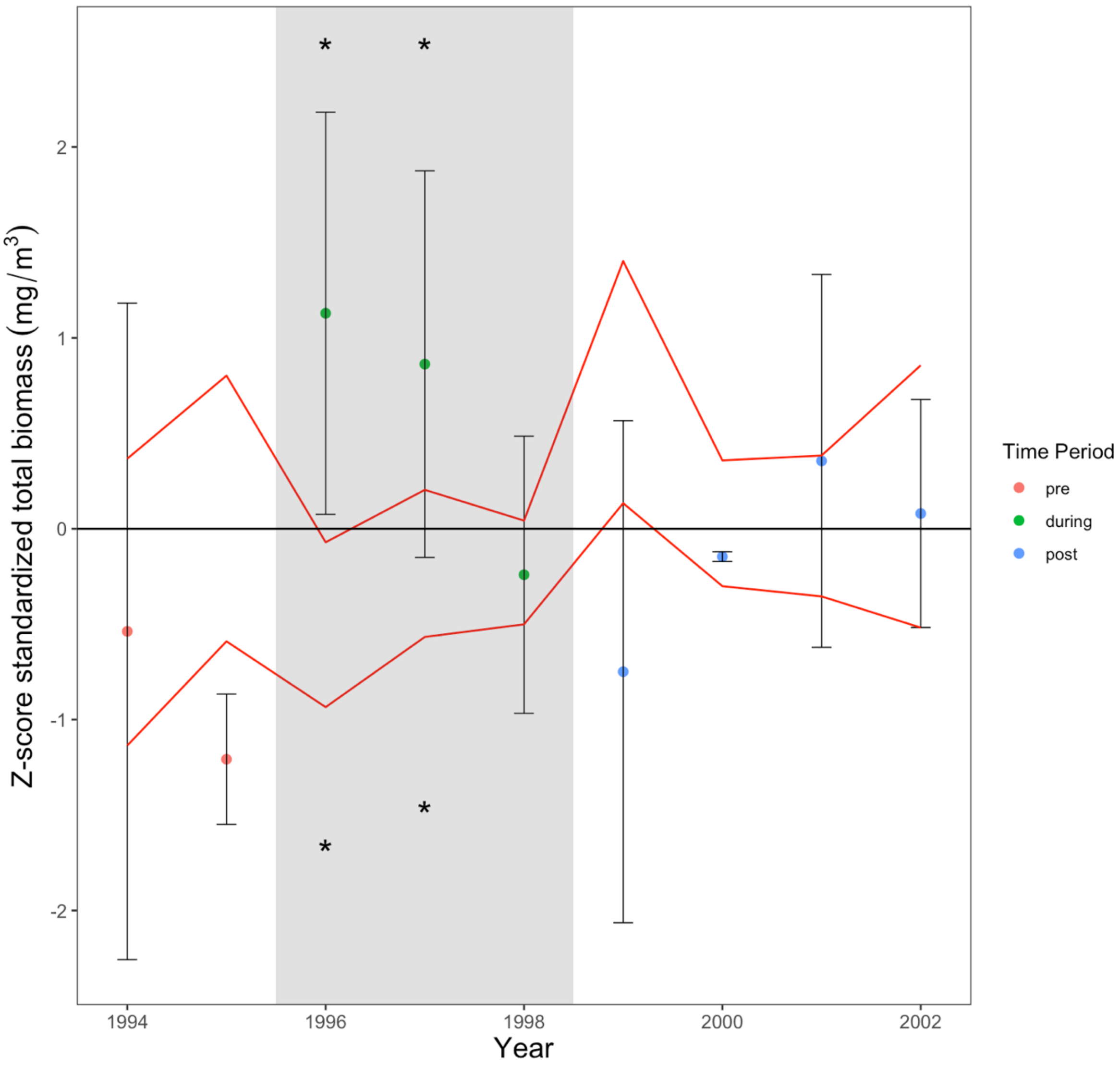

Figure 2.2. Phytoplankton annual biomass standardized by z-scores. Time periods are plotted on each graph where pink represents pre-experimental monitoring, green represents during macrophyte cutting, and blue represents post-experimental monitoring. Macrophyte cutting years are highlighted in grey. Red lines represent 95% confidence intervals calculated from the z-scores of three reference lakes: Lake 239, Lake 373, and Lake 442. For 1996 and 1997, only Lakes 239 and 373 were included in the CI range as 442 was missing data for these years (denoted by asterisks).

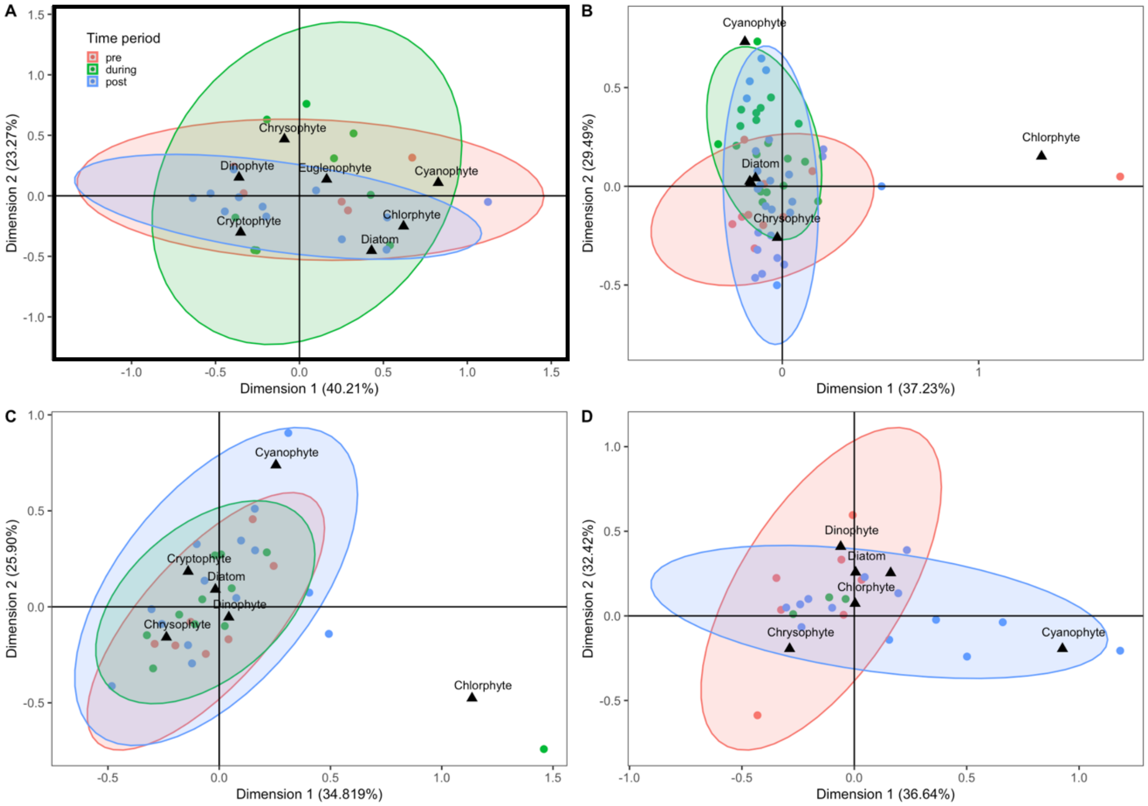

Figure 2.3. CA's of the phytoplankton communities from A) Lake 191, B) Lake 239, C) Lake 373, and D) Lake 442 for all summer dates. Time periods are shown using points and ellipses where pink represents pre-experimental monitoring, green represents during macrophyte cutting, and blue represents post-experimental monitoring. Note that in D), too few points are present to show a "during" ellipse.

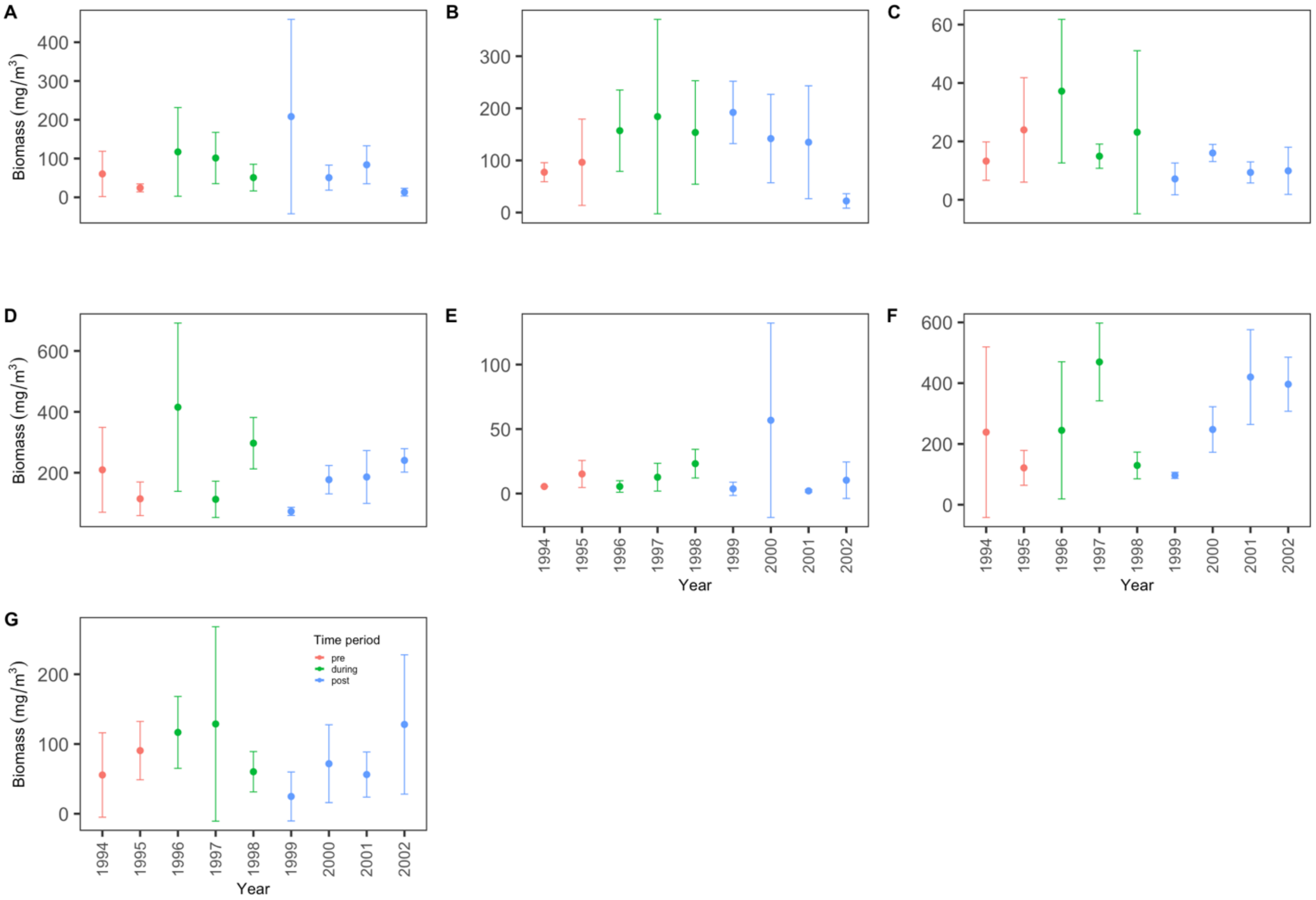

Figure 2.4. Lake 191 phytoplankton mean annual biomass mg/m^3 for all phytoplankton groups: A) Cyanophyte; B) Chlorophyte; C) Euglenophyte; and D) Chrysophyte; E) Diatom; F) Cryptophyte; and G) Dinophyte, with standard deviation error bars. Time periods are plotted on each graph where pink represents pre-experimental monitoring, green represents during macrophyte cutting, and blue represents post-experimental monitoring. Macrophyte cutting years are highlighted in grey. Note scale differences on the y-axes.

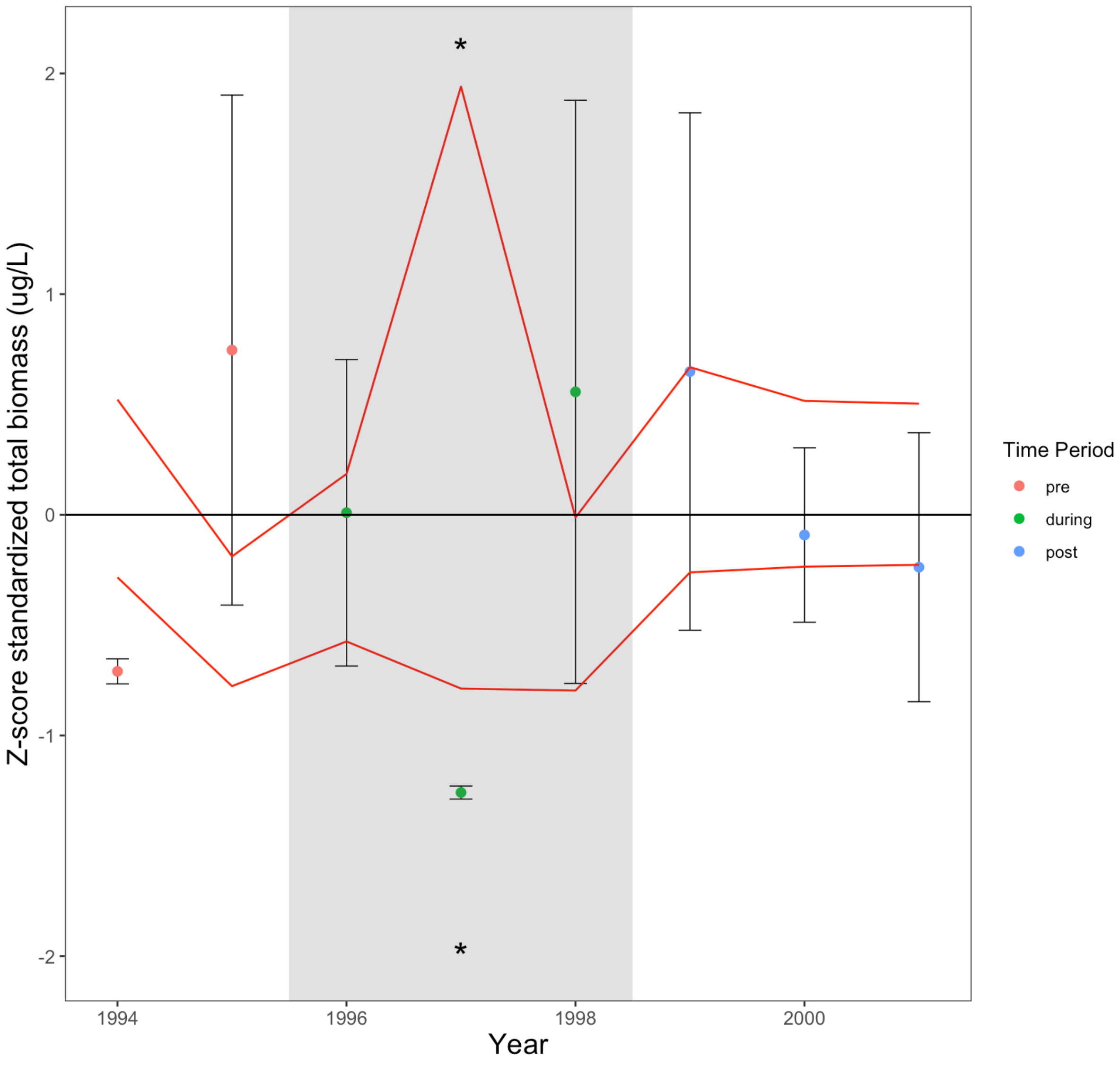

Figure 2.5. Zooplankton total annual biomass standardized by z-scores. Time periods are plotted on each graph where pink represents pre-experimental monitoring, green represents during macrophyte cutting, and blue represents post-experimental monitoring. Macrophyte cutting years are highlighted in grey. Red lines represent 95% confidence intervals calculated from the z-scores of three reference lakes: Lake 239, Lake 373, and Lake 442. For 1997, only Lakes 239 and 373 were included in the CI range as 442 was missing data for this year (denoted by asterisks).

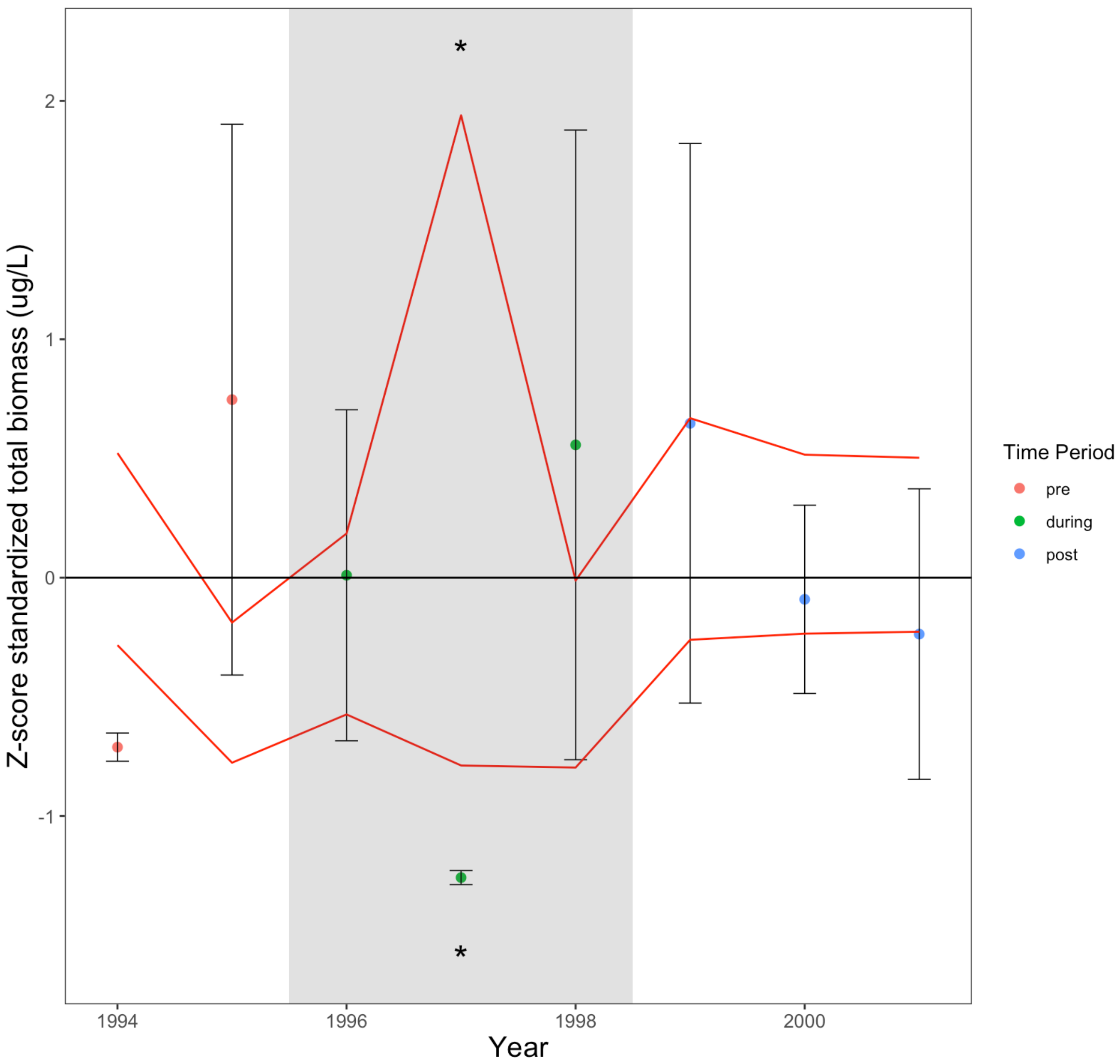

Figure 2.6. Z-score standardized total biomass for pelagic zooplankton taxa only. Time periods are plotted on each graph where pink represents pre-experimental monitoring, green represents during macrophyte cutting, and blue represents post-experimental monitoring. Macrophyte cutting years are highlighted in grey. Red lines represent 95% confidence intervals calculated from the z-scores of three reference lakes: Lake 239, Lake 373, and Lake 442. For 1997, only Lakes 239 and 373 were included in the CI range as 442 was missing data for this year (denoted by asterisks).

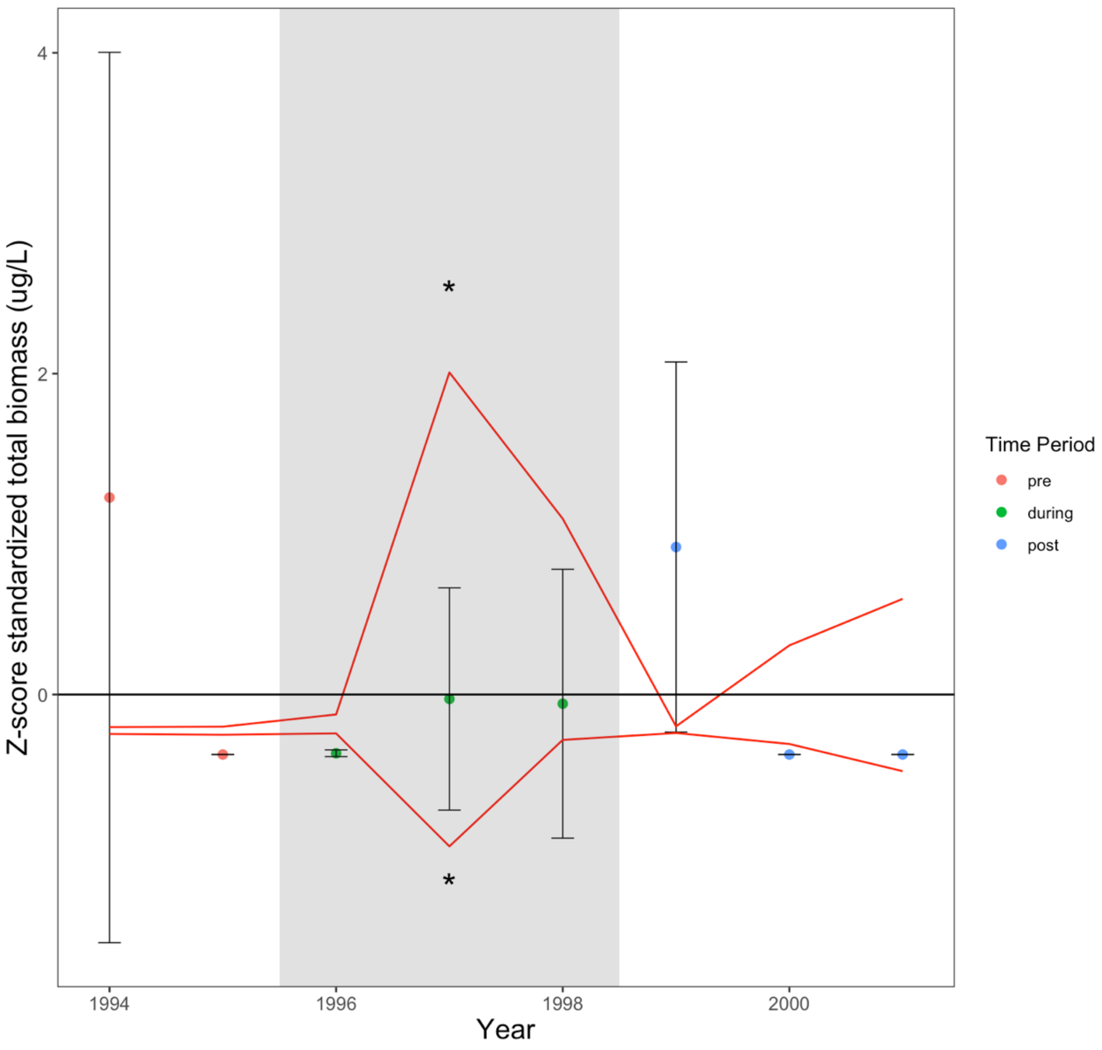

Figure 2.7. Z-score standardized total biomass for littoral zooplankton taxa (littoral Cladocera and littoral Cyclopoid, outlined in Table 2.5). Time periods are plotted on each graph where pink represents pre-experimental monitoring, green represents during macrophyte cutting, and blue represents post-experimental monitoring. Macrophyte cutting years are highlighted in grey. Red lines represent 95% confidence intervals calculated from the z-scores of three reference lakes: Lake 239, Lake 373, and Lake 442. For 1997, only Lakes 239 and 373 were included in the CI range as 442 was missing data for this year (denoted by asterisks).

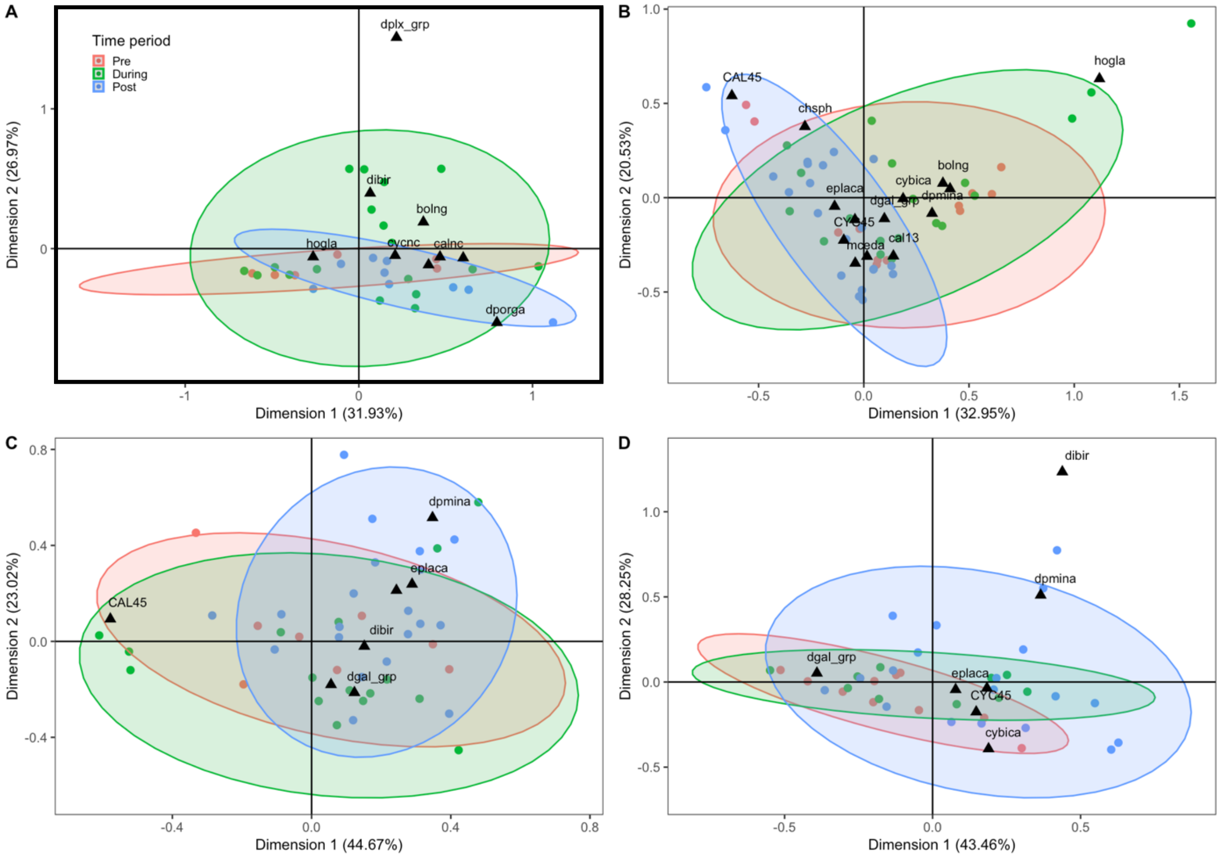

Figure 2.8. CA's of the offshore zooplankton communities from A) Lake 191, B) Lake 239, C) Lake 373, and D) Lake 442 for all summer dates. Time periods are shown using points and ellipses where pink represents pre-experimental monitoring, green represents during macrophyte cutting, and blue represents post-experimental monitoring. The plotted taxa abbreviations are as follows: bolng = *Bosmina longirostris*; calnc = Calanoida nauplii; cal13 = cyclopoida copepedids 1-3; CAL45 = calanoid 4-5 group; chsph = *Chydorus sphaericus*; cybica = *Cyclops bicuspidatus thomasi* adults; cycnc = Cyclopoida nauplii; CYC45 = cyclopoid 4-5 group; dibir = *Diaphanosoma birgei*; dplx_grp = *Daphnia* group 1; dgal_grp = *Daphnia* group 2; dpmina = *Diaptomus minutus* adults; dporga = *Diaptomus oregonensis* adults; eplaca = *Epischura* adults; and hogla = *Holopedium glacialis*.

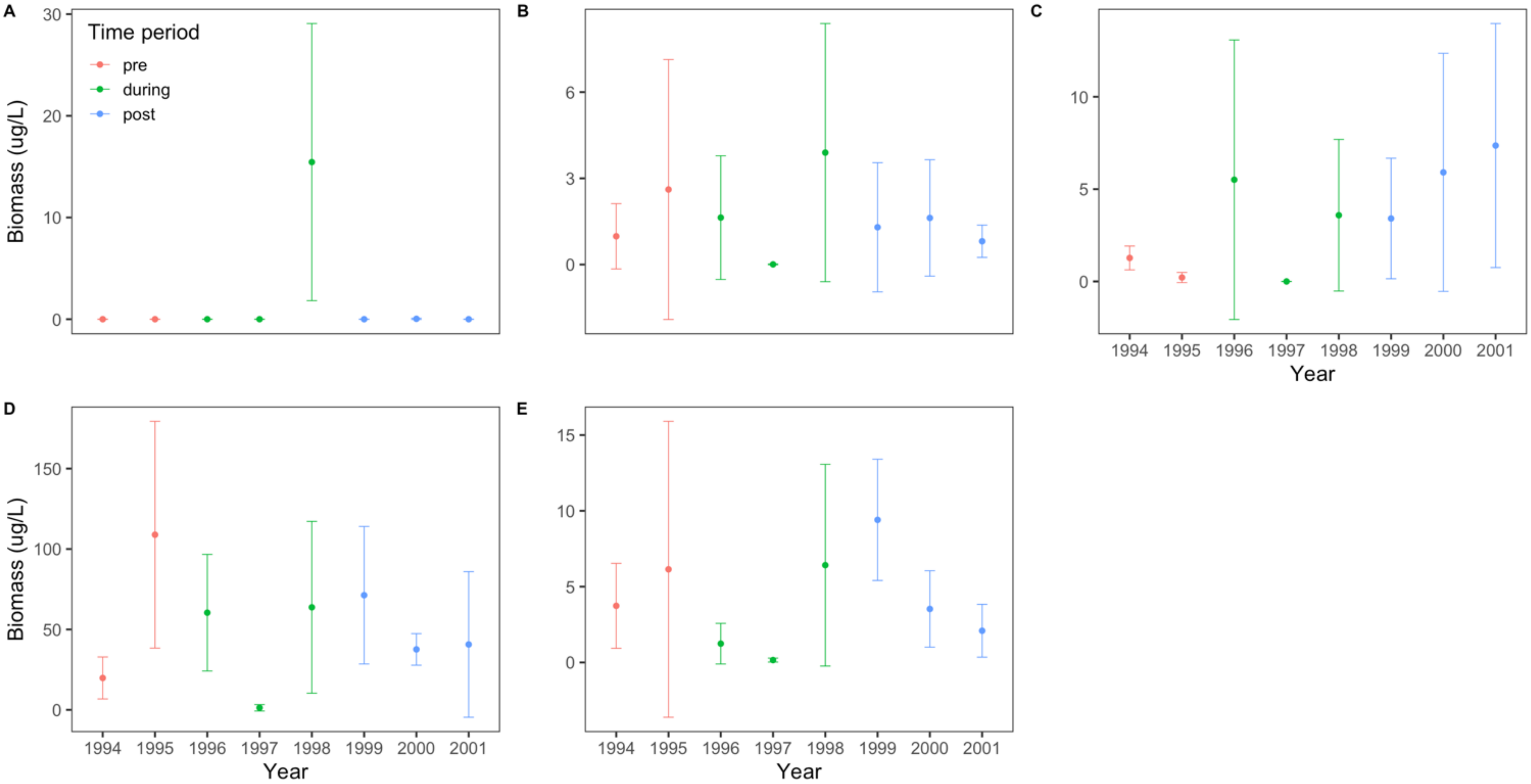

Figure 2.9. Lake 191 offshore mean annual biomass (µg/L) for taxa of interest identified from the CA as follows: A) *Daphnia* group 1; B) *Diaphanosoma birgei*, C) *Diaptomus oregonensis* adults; D) *Holopedium glacialis*; and E) *Bosmina longirostris*. Standard deviation error bars and time periods are plotted on each graph where pink represents pre-experimental monitoring, green represents during macrophyte cutting, and blue represents post-experimental monitoring. Note scale differences on the y-axes.

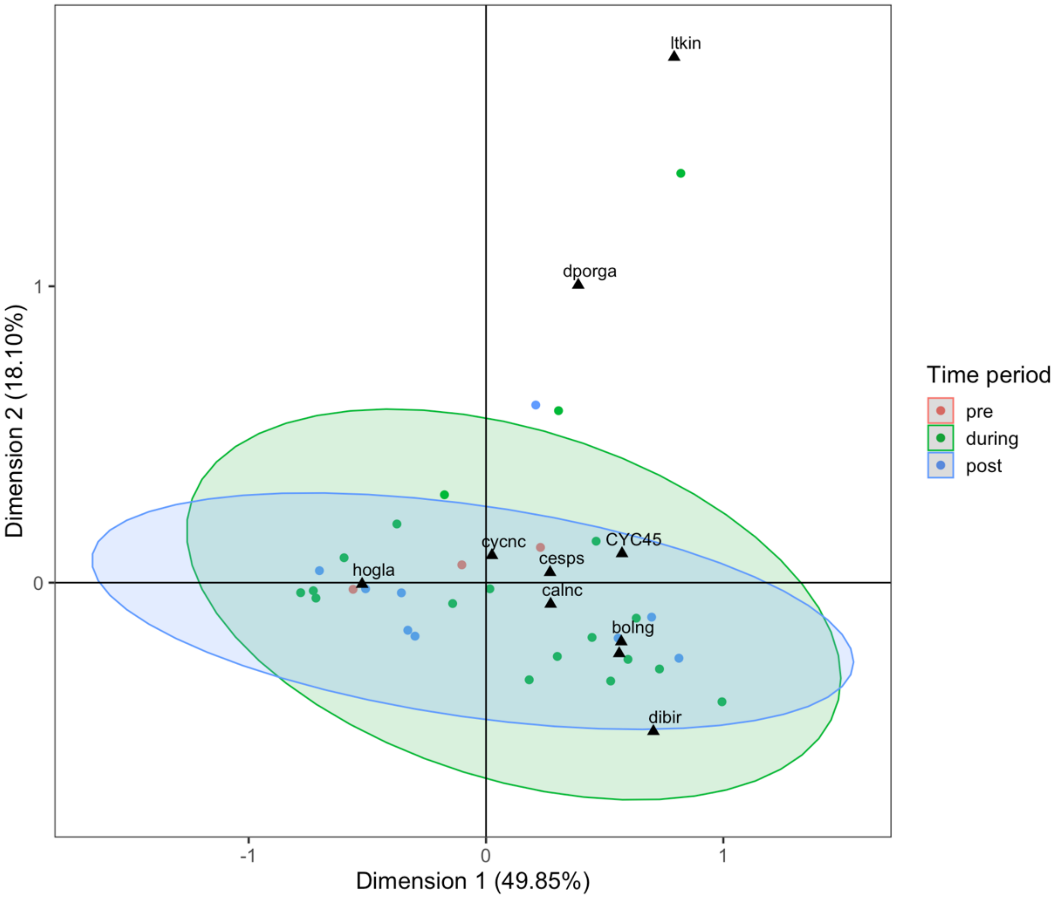

Figure 2.10. CA of the nearshore zooplankton community in Lake 191 for all summer dates. Time periods are shown using points and ellipses where pink represents pre-experimental monitoring, green represents during macrophyte cutting, and blue represents post-experimental monitoring. Note that there is no ellipse for the pre-experimental monitoring period due to too few points. The plotted taxa abbreviations are as follows: bolng = *Bosmina longirostris*; calnc = Calanoida nauplii; cesps = *Ceriodaphnia* sp.; cycnc = Cyclopoida nauplii; CYC45 = cyclopoid 4-5 group; dibir = *Diaphanosoma birgei*; dporga = *Diaptomus oregonensis* adults; hogla = *Holopedium glacialis*; and ltkin = *Leptodora kindtii.*

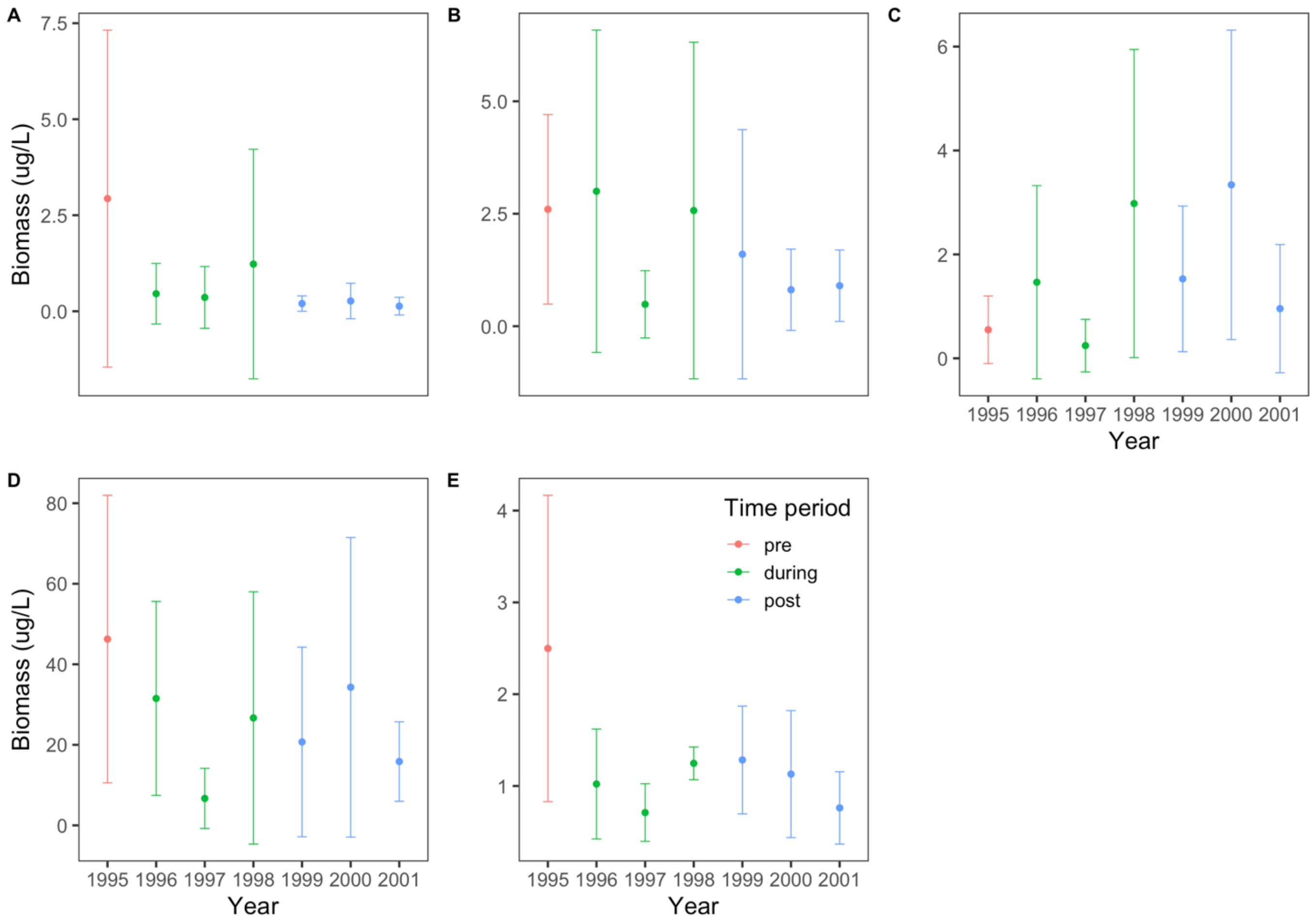

Figure 2.11. Lake 191 nearshore mean annual biomass (µg/L) for taxa of interest identified from the CA as follows: A) *Leptodora kindtii*; B) *Diaphanosoma birgei*; C) *Holopedium glacialis*; D) *Diaptomus oregonensis* adults; and E) Cyclopoida nauplii. Standard deviation error bars and time periods are plotted on each graph where pink represents pre-experimental monitoring, green represents during macrophyte cutting, and blue represents post-experimental monitoring. Note scale differences on the y-axes.

Chapter 3: Macrophyte cutting impacts on fish populations

3.1 Abstract

Macrophytes structure aquatic communities, and their removal can impact community structure and function in lakes. As part of a whole lake ecosystem study, changes in ecosystem function and structure as it relates to fish population dynamics, growth, and energy acquisition were investigated at Lake 191 of the IISD-Experimental Lakes Area. Macrophytes were cut from 50% of the area they occupied initially from the littoral zone of the lake and regrowth in harvested regions was suppressed for 3 years. Perch were the dominant prey fish species in the lake, approximately 3 times more abundant than the only other prey species present, pumpkinseed. Abundance both yellow perch and northern pike and biomass of northern pike were lowest during macrophyte cutting, followed by an increase 2 years after cutting. Growth rates of yellow perch declined following macrophyte cutting; by contrast, northern pike growth increased throughout macrophyte harvest, but slowed following macrophyte cutting. These changes in growth appeared to be density dependent for northern pike, but not for yellow perch. Stable isotope values of carbon and nitrogen (used to evaluate source energy in fish) were relatively stable for yellow perch throughout the experiment, with a decline in carbon isotopic values for perch in 1997. Signatures for northern pike towards more negative values suggest changes in the source of carbon (towards pelagic resources) during manipulation as well as a steady decline in trophic position. These results suggest cutting of macrophytes disturbed essential habitat, which in turn altered the demographics and growth of both a dominant prey fish species and a top predator as open water increased, increasing exposure of prey fish (and possibly also pike) to pike predation.

3.2 Introduction

The importance of macrophytes to primary productivity and community structuring is well represented in literature (Gasith & Hoyer 1998; Tamire & Mengistou, 2014; Thomaz & Cunha, 2010). Macrophytes provide habitat complexity, offering protection and substrate to many organisms (Burks et al., 2006; Thomaz & Cunha, 2010). Many species of fish rely directly on macrophytes in the littoral zone for habitat and foraging (Christie et al., 2002). Thus, understanding the impacts of macrophyte habitat disturbance on fish communities is important to ensure healthy fish populations and aquatic ecosystems. While macrophyte removal is a common management technique used across North America to dampen the effects they have on human activities (cottages, recreational fishing, swimming, etc), this removal can impact the habitat, diet, abundance, and composition of fish and other organisms in a lake (Pothoven et al., 1999). The responses of some species to vegetation removal can be linked to their known life history requirements (Bettoli et al., 1993); in the absence of macrophytes, we may see a decrease in abundance for fish species that heavily rely on aquatic vegetation for survival, feeding and reproduction, like northern pike (*Esox lucius*; Casselman & Lewis, 1996; Kobler et al., 2008).

Macrophytes can be used by fish as cover, either to avoid or facilitate predation. Yellow perch (*Perca flavascens*) and pumpkinseed (*Lepomis gibbosus*), two species of prey fish, often use macrophytes for habitat and to avoid predation (Jacobsen & Perrow, 1998). Macrophyte habitats are typically occupied by fish during the day when visibility is better and oxygen is high from photosynthesizing plants, and horizontal migrations commonly occur at dusk when visibility and chance of predation are lower to facilitate foraging in open waters (Jacobsen and Perrow 1998; Shoup et al., 2003). Northern pike, a sit-and-wait predator species, extensively use macrophytes as cover to forage for food, for habitat partitioning, and for reproduction throughout the year (Casselman and Lewis 1995; Cook and Bergersen 1988; Farrell et al., 1996; Kobler et al., 2008). They commonly associate with areas where vegetative density is high and the water is relatively shallow, suggesting that the littoral zone and higher macrophyte densities are key to the growth and survival of northern pike (Cook and Bergersen 1988; Diana et al., 1977; Kobler et al., 2008).

The littoral zone is commonly used for reproduction by many fish species. Egg deposition on macrophytes is done by both yellow perch and northern pike. While yellow perch deposit large masses of eggs on dead vegetation, a coating of jelly-substance provides protection and deters predators, suggesting macrophytes are not required for protection from predation for eggs (Čech et al., 2009; Newsome & Tompkins, 1985). Northern pike deposit their eggs high up on macrophyte strands to avoid the lake bottom (Casselman & Lewis, 1996; Farrell et al., 1996; Dombeck et al., 1984). These eggs are adhesive, but do not have the same protection yellow perch eggs have, suggesting macrophytes are the main source of protection from predators for northern pike eggs. Pumpkinseed do not use macrophytes as a means for egg deposition, and instead are nest breeders that seek out sand and gravel for reproduction (Moyle & Cech, 1996).

Fish often rely on more than one source of food throughout life. Fishes' dietary requirements often change depending on life stages, and appropriate access to food allows for proper growth of fish; for many species, macrophyte stands can play an important role in facilitating feeding at critical life stages. Generally, all early larval fish utilize zooplankton as a food source (Garner, 1996). Once they develop into juveniles, specialized diets can form depending on the species of fish. Yellow perch in particular are known for their horizontal migration into the pelagic zone and back into the littoral zone for food the first several months of life (Wang & Eckmann, 1994). Yellow perch diet consists mainly of zooplankton in early years of their lives, later incorporating macroinvertebrates in their diet. Once they become larger (usually at older ages), they tend to incorporate some fish (through cannibalism and smaller prey fish) into their diet (Thorpe 1977; Paszkowski & Tonn, 1994). Pumpkinseed also feed on zooplankton, but benthic macroinvertebrates, like snails, are also important in their diet (Coleman & Wilson, 2010; Collingsworth & Kohler, 2010; Keast 1978). They exhibit morphological changes as they age, such as specialized jaws for crushing gastropod shells (Keast 1978), which often differs between habitat types, like littoral and limnetic habits (McCairns & Fox, 2004). Pumpkinseed also exhibit horizontal migrations similar to perch and are more active at night (Klinard et al., 2018). Based on this, it can be assumed that both perch and pumpkinseed rely on a mix of resources from both littoral and pelagic areas. Eurasian perch (*Perca fluviatilis)* in particular have been found to display resource polymorphism, where individuals in littoral areas feed more on invertebrates and fish, and individuals in pelagic areas feed more on zooplankton (Quevedo et al., 2009: Svanbäck & Eklöv, 2002; Svanbäck et al., 2008).

While environmental factors like temperature, pH, oxygen, and photoperiod influence growth rate of fishes, nutrition quality and quantity of prey are also important factors to consider (Dutta 1994), which are likely to vary under a scenario of macrophyte habitat disturbance. A study done by Schindler et al. (2000) demonstrated that growth rates of bluegill sunfish (*Lepomis macrochirus)* were negatively impacted by residential development along the shoreline, which could be due to loss of critical nearshore habitat. It has also been suggested that interspecific competition can cause declines in the density of macroinvertebrates, which in turn can cause declines in growth of both bluegill and pumpkinseed fish when competing for the same resources and refuge from predation (Mittelbach 1988). While yellow perch and pumpkinseed do not eat exactly the same diet, their resource overlap is sufficient such that yellow perch can compete with sunfish, which can influence growth of both species (Schindler et al., 2000). Maximum length in fishes is linked to most basic parameters of fish population dynamics, including mortality, length at maturity, and growth rates (Froese & Binohlan, 2000; Pauly 1980; Welcomme, 1999). All of these traits are important in understanding the overall health of fish populations.

To assess the impacts of changes in food webs of the direction and flow of energy in aquatic ecosystems, stable isotope analysis is commonly used. Stable isotope ratios of carbon and nitrogen allow for characterization of energy sources and trophic positions, respectively (Hecky & Hesslein, 1995). While analyzing stomach contents of fish can provide important information regarding what an individual consumed that day, and aid in knowing taxonomic resolution, stable isotopes provide a more information regarding which trophic levels and carbon sources are integrated into the tissues of an organism (Hecky & Hesslein, 1995). Additionally, since tissue turnover rates in fish range from days to years, depending on the tissue under consideration, stable isotope analysis of fish tissues can allow for an understanding of diet and trophic position over longer time periods compared to analyzing stomach contents (Hesslein et al., 1993). Nitrogen isotope ratios become higher as trophic levels increase, allowing for estimation of consumer trophic levels, whereas carbon is comparatively more stable across trophic levels (Vander Zanden & Rasmussen, 1999; Vander Zanden & Rasmussen, 2001). Because carbon is relatively stable and shows minor fractionation between consumers and sources, consumer organisms typically assume the carbon signatures of their diet (Hecky & Hesslein, 1995). This, combined with the observation that different energy sources can have distinct carbon isotope ratios, make them useful for differentiating between energy obtained between distinct sources, such as from littoral areas and pelagic areas (Post, 2002). In lakes, littoral $\delta^{13}C$ baselines tend to be more enriched, and therefore, less negative in values than pelagic sources (France 1995). While carbon and nitrogen in an organism can inform both source of energy and trophic position, differentiating changes in $\delta^{13}C$ and $\delta^{15}N$ and whether or not they are due to food web structure and carbon flow, or just changes in the baseline can be challenging without baseline values (Post, 2002).

The purpose of this study was to evaluate changes in the dominant prey and predator fish species in a small, shallow lake during a macrophyte cutting experiment. As macrophyte cover is reduced, I predict a decrease in northern pike biomass because of their preference for vegetated areas for foraging and protection for young of year (Casselman & Lewis, 1996; Kobler et al., 2008). Cannibalism is known to be common among pike, and as such, with the removal of vegetation used for refuge I expect an increase in cannibalistic behaviour (Craig, 2008). I predict that this cannibalism, in turn, will decrease abundance of northern pike. Although yellow perch can move between vegetation and open water, Jacobsen & Perrow (1998) saw most 0+ perch still inhabited macrophytes regardless of whether or not predators were present. Based on this, I suspect yellow perch biomass and abundance will decrease as macrophytes are cut and predation upon them increases. I expect growth of prey fish species to decrease as key refuge is removed and foraging for food becomes more difficult. A decrease in northern pike abundance is expected to result in increased growth as a consequence of density dependence, and increased access to prey fish resources as a result of macrophyte cutting. Northern pike prefer larger prey items, as such, I expect maximum size of yellow perch will decrease as larger individuals are preyed upon preferentially as they become easier for pike to access. I expect both yellow perch and northern pike carbon isotopes to become more negative to represent an increase in reliance on open water resources, due to the large reduction in littoral habitat area. I predict that yellow perch will be forced to feed on zooplankton and macroinvertebrates outside of the littoral zone, representing more pelagic carbon signatures (lower $\delta^{13}C$) and no change in trophic position. For northern pike, as their preferred littoral habitat and foraging area is reduced by half, their $\delta^{13}C$ isotopic signatures are also predicted to decrease to reflect an increased reliance on offshore food sources. I further predict their $\delta^{15}N$ isotopic signatures to display no change as they will still be feeding on the same species of prey fish, but in open-waters.

3.2 Methods

3.2.1 Study site

A whole-lake macrophyte cutting experiment was conducted in Lake 191 at the IISD-ELA, a freshwater research facility which is located southeast of Kenora in Northwestern Ontario at 93°30’- 94°00’W, 49°30’-49°45’N (Brunskill & Schindler 1971). Lake 191 is a shallow, brown water lake in the southern part of this region that contains an extensive macrophyte community and a simple fish community composed of primarily northern pike (*Esox lucius)*, yellow perch (*Perca flavascens*), pumpkinseed (*Lepomis gibbosus*), and few white sucker (*Catotomus commersonii*). From 1994 – 1995, 2 years of background monitoring occurred before 50% of the macrophytes were mechanically cut at the sediment interface from the littoral zone (max depth of 1.5 m) for each of three years on a bi- or tri-weekly basis from June – August (1996-1998) (Figure A1). This was followed by up to 4 years of post-experimental monitoring (1999-2003). Results from the Lake 191 experiment were compared with data collected from two unmanipulated, reference lakes in the region, Lake 239 and Lake 468 (Table 3.1). While both of these lakes are much larger than Lake 191 and harbour a different fish community, neither have undergone manipulations, and no other lakes with perch in the region that were sampled at the same time that could provide information on perch over a similar time period.

3.2.2 Fish

In Lake 191, fish were sampled in the spring and fall for each of 1994 – 2003 using seine nets, trap nets, and angling (northern pike) over a period of 3-4 weeks for each season. Trap nets were deployed in the spring and fall in reference Lake 239 for yellow perch and northern pike capture, whereas fish capture in Lake 468 was primarily facilitated by gillnetting in the fall (3-4 overnight sets per year; Mills et al 2002). In Lakes 191 and 239, all captured fish were first anaesthetized, then were marked by either fin scarring (for fish > 100 mm; Welch & Mills, 1980) or by tagging with modified carlin tags (White & Beamish 1972) for fish >375mm. For small fish (< 100 mm), typically only fork length and species were noted. For all fish > 100 mm, total length (mm), fork length (mm), weight (g), sex, and capture status (e.g., newly captured or recaptured fish based on fin scars or tagging information) were recorded. Sampling in Lake 468 was destructive and fish that were not already dead upon pulling gillnets were euthanized by blunt force trauma to the cranial region followed by cervical dislocation. Fin rays were also sampled from a subsample of fish from all lakes for age determination. For northern pike, the first 1-3 leading pectoral fin rays on one side of the fish were clipped as close to the attachment point on the body as possible. For yellow perch, the same technique was used to obtain the first 1-3 leading rays of the pelvic fin. Collected fin ray samples were placed in fin envelopes and set aside to dry.

Ages were assigned to fish using cross sections of fin-rays (Mills & Beamish 1980). Dry fins were mounted and cured with a clear epoxy. After curing, these fin ray sections were cut into cross-sections approx. 0.5mm thick using an Isomet low-speed jewellery saw. Cross sections were mounted on slides and ages were determined using a compound microscope (Mills & Beamish 1980). Age classes were assigned to each fish by a single interpreter at Fisheries and Oceans Canada, which were used in later analysis of fork length and weight at specific age classes. Changes in maximum size over time was assessed by calculating the 95% quantile of fish captured annually based on fork lengths for yellow perch, pumpkinseed, and northern pike in Lake 191 and were compared to those from fish in Lake 239. Pumpkinseed were not present in either Lake 239 or 468 (or any other ELA lakes with regular monitoring), so trends for this species could not be compared to a reference system.

While pumpkinseed were not sampled as extensively as northern pike and yellow perch and Lake 191, they were still present in the lake, and as such, it was important to evaluate their relative importance to the fish community. Using beach seine data from

Lake 191 for the years of 1997 – 2003, the total catch in each region was summed, and divided by the number of seines performed to estimate a mean catch per unit effort (CPUE) for each region (cut, uncut) in each year. This was then used to analyze the relative abundance of perch and pumpkinseed to determine the more dominant prey fish species. Total CPUE and CPUE in both cut and uncut areas (for 1996 – 2003 only) for young of year (YOY) northern pike was also calculated based on seine data (Figure A7; for 1994 – 1999, values were estimated from Jansen, 2000 unpublished. 2000 – 2003 were calculated using YOY seine data).

To estimate population abundance for yellow perch and northern pike, mark-recapture methods were used for fish >100mm. Seasonal- and year-specific fin nicks were given to all captured fish >100 mm in length to identify when they were caught (Table A3; Table A4). After receiving their nicks and having measurements taken, these fish were placed in a bin to recover from anesthesia and returned to the lake alive. At every sampling occasion, fish were checked for previous fin nicks to determine if the fish had been previously handled. If a fish had nicks on their fins, they were recorded at the time of capture to determine when they were previously handled. These fin nicks were used to build capture-recapture histories for the population for analysis in Program Mark (see below). For Lake 239, yellow perch were not used in population abundance and biomass estimates as mark-recapture methods were not applied to this species during this time period. While fin nicks were the primary source of information for capture-recapture histories in yellow perch, individual tagging was the primary information source for northern pike, and fin nicks were used to augment these histories for untagged fish (i.e., northern pike with only fin nicks to determine capture histories made up a relatively small proportion of the data compared to individually tagged fish). To estimate the size distribution of yellow perch, pumpkinseed and northern pike <100mm, length-frequency distributions were produced using the collected fish data from Lake 191 and reference Lake 239 (for perch only). This was done by plotting histograms of all fork lengths of the collected fish on a log-transformed y-axis. From here, I was able to visualize changes in the size-distribution of the population over the years of the experiment and compare this to the reference lake.

To provide insights into how changes in size of fishes were impacted in Lake 191, annual changes in growth (fork length- and weight-at-ages) for yellow perch and northern pike were estimated. Because fish that that have not yet reached sexual maturity invest energy only into somatic growth, the most pronounced changes in growth were expected in younger age classes. For perch, age of maturity is thought to range from 2-4 years, and for northern pike, age of maturity is said to be 1-4 years (Malette & Morgan, 2005; Scott & Crossman 1973). For this experiment, ages of 2-6 for yellow perch and 1-4 for northern pike were chosen based on data availability. I applied a minimum sample of 2 individuals to characterize each age class.

3.2.3 Population estimation

Capture histories were created using mark-recapture data collected for northern pike (Lakes 191 and 239) and yellow perch (Lake 191) as described above. The open-population POPAN method in Program MARK was used for both northern pike and yellow perch (Program MARK version 9.0; Arnason et al. 1998). As the POPAN model is a modified version of the Cormack-Jolly-Seber (CJS) model, the following assumptions were made with respect to our data (Amstrup et al., 2010):

1. Every marked animal present in the population at a sampling period has the same probability of being recaptured or resighted.
2. Every marked animal present in the population immediately following a sampling period has the same probability of survival until the next sampling period.
3. Marks are not lost/overlooked.
4. Sampling periods are very short.
5. All emigration from a sampled area is permanent.
6. The fate of each animal with respect to capture and survival is independent of the fate of others.

Fully time-dependent models where survival (ϕ), capture probability (p), and probability of entrance into the population (*pent*) were attempted first for northern pike in Lakes 191 and 239 and for yellow perch in Lake 191. For yellow perch, a fully time-dependent model would not converge. Every combination of time-dependent and constant survival, capture probability, and entrance probability was then evaluated for each lake/species combination. Models were also formulated with parameter estimates specific to the experimental time-period (pre, during, post) and evaluated against my full suite of models. Akaike's Information Criterion (AIC_c) and ΔAIC_c values were used to select the model of best fit, where a ΔAIC_c of <10 indicated the models to be evaluated based on the ΔAIC_c weights. If the weight of the top model is close to 1, the top model was the model of best fit. The further the ΔAIC_c of a model is from 1, the more likely it is that the next closest model is the top model (To see full table of models for Lake 191 and Lake 239, see Tables 3.2, 3.3, and 3.4).

Goodness of fit testing was done for all POPAN models where a fully time-dependent model was able to be fit (Lake 191 and Lake 239 northern pike) using the Program RELEASE test, which test for the first two assumptions outlined above, respectively. The outcome of this test was used to calculate a ĉ value, which was calculated using the Chi-squared and degrees of freedom given from Program RELEASE for the sum of test 2 and test 3 (Lake 191 pike: $X^2 = 163.194$, df = 67, p = 0.000; 239 pike: $X^2 = 128.569$, df = 111, p = 0.1217). A ĉ value of 1 represents a well fit model. If $\hat{c} > 1$, then the adjustment was applied. The ĉ values were calculated by dividing the Chi-squared value by the degrees of freedom. This gave us the following ĉ values: 2.436 for Lake 191 pike and 1.158 for Lake 239 pike. These were then applied to the models to determine adjusted ΔAIC_c values.

3.2.4 Fish biomass

Biomass (kg/ha) of northern pike populations for Lakes 191 and 239 and yellow perch for Lake 191 were estimated as the product of mean weights of fish >100mm and abundance estimates, scaled to lake surface area. While many yellow perch were measured, few individuals were weighed, therefore, mean weights were calculated using length-weight regressions for fish greater than 100mm. For northern pike, nearly all fish that were measured were also weighed at sampling, and mean weights were calculated using the measured weights. In Lake 239, there were too few northern pike captured in 1995 to calculate mean weights. As such, the mean weights for 1994 and 1996 were averaged to produce an estimate.

3.2.5 Stable isotope analysis

Using collected fin ray sections, stable isotope samples were prepared for yellow perch and northern pike in both Lake 191 and Lake 239 by weighing 0.20 – 0.50mg of tissue in a small, tin cup (Elemental Analysis, 5 x 3.5mm) on a Sartorius microbalance (when possible, higher weights in that range were always used). If a weight within this range could not be achieved for a given sample, samples from multiple fish were combined into a composite sample (Lake 239: 2 samples in 1983; 3 samples in 2000; 1 sample in 2003). The years of 1994 – 2003 were used for northern pike in both lakes. For yellow perch, there were no samples for the pre-manipulation years (1994 – 1995) for Lake 191 and no samples from 1994 – 1998 for Lake 239. As such, the years 1973 and 1983 were used to represent the pre-manipulation period in each lake, though 1983 samples were available for Lake 239 only. Six individual fish were selected from each year for each fish species in both lakes, with an emphasis on fish collected in the fall; with the exception of the year 2000 for Lake 239 northern pike (5 samples used), and the years 1973, 1983, and 1999 for Lake 239 yellow perch (3, 2, and 2 samples used, respectively). For these years and species, additional fin samples to facilitate stable isotope analyses were unavailable, so all available samples were used. In the case where fall samples were not available, spring or summer samples were used (See Table A5. for breakdown of fall data for each year). To standardize for body size, northern pike samples were kept within 200mm of each other for each year. As yellow perch samples were scarce, body size standardization was not possible (See Table A6. for mean size of fishes for each year).

For northern pike and yellow perch samples in both lakes, it was rare to find fin ray samples that were not at least partially covered in epoxy from the ageing process. For most northern pike samples, the distal tips of the fin samples were exposed, and a sample was able to be retrieved for stable isotope analysis (100% of northern pike samples in Lake 191 and 86.79% of northern pike samples in Lake 239 were not fully covered in epoxy). However, since perch are smaller fish, all fin ray samples from Lake 239 and few from Lake 191 were completely coated in epoxy. To remove the fish fin rays from the epoxy, an Isomet low-speed jewellery saw was used to cut cross sections from the sample. Fine point tools (eg. sewing needles) were used to push the fin ray out of the epoxy layer. The fin ray was then dissected using the tools to ensure no epoxy was left on the fin samples and placed in a tray to be weighed. About 20 samples out of 46 that were cut out of epoxy were viewed under a dissecting scope to ensure this technique of removal from the epoxy was sufficient and no epoxy was left on the fin rays.

Duplicate samples were produced every 10 samples to ensure sample results were consistent and the results from these duplicate samples were averaged in final analyses. Paired *t*-tests showed no significant differences among paired $\delta^{13}C$ duplicate samples ($t_{19} = 0.471$, $p = 0.643$) or $\delta^{13}N$ duplicate samples ($t_{19} = 0.939$, $p = 0.360$). All stable isotope samples were analyzed at Isotope Tracer Technologies Inc. in Waterloo, Ontario using Delta^{plus} Isotope Ration Mass Spectrometry (IRMS) coupled with an Elemental Analyzer EA 1110 CHN. The typical standard deviation for the instrument was ±0.3% and ±0.15% for nitrogen and carbon, respectively. For the purpose of this study, isotopic $\delta^{15}N$ and $\delta^{13}C$ signatures were used for all analyses, which were calculated using the following equation:

$$\delta = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] * 1000 \text{ (eq. 3.1)}$$

Where R_{sample} is the measured isotopic ratio of the sample and $R_{standard}$ is the measured isotopic ratio of the standard material.

While our preference was to examine isotopic changes over time with a two-factor Analysis of Variance (ANOVA), Comparing differences in trends between lakes among years, data exploration demonstrated that the variance in stale isotopic values for Lake 239 was much greater than that of Lake 191. This would violate the assumptions of homogeneity of variance using a 2-factored approach, and as such, the decision was made to run single-factor ANOVA's for the northern pike for each $\delta^{15}N$ and $\delta^{13}C$ signature in Lake 191 and Lake 239 with year as the independent variable, as variance was more equal within lakes than between lakes. In cases where ANOVAs were significant, a post-hoc Tukey's test of unplanned comparisons was conducted.

3.3 Results

Yellow perch appeared to be the dominant prey fish species in Lake 191 in comparison to pumpkinseed, as yellow perch abundance surpassed pumpkinseed in all years in cut areas of the littoral zone and nearly all years in the uncut zones (all except 1998 and 2001; Figure 3.1). In uncut areas across all years, yellow perch made up 66.3% of CPUE on average, while pumpkinseed only made up 33.69%. In cut areas across all years, yellow perch made up 80.3% of CPUE on average, and pumpkinseed made up 19.7%. Length-frequency distribution plots for pumpkinseed (Figure 3.2) and yellow perch (Figure 3.3) displayed a shift from an even distribution across all size classes in pre-manipulation years to an explosion of population for fish <100mm from 1996 onwards. For northern pike, in 1999 there appeared to be fewer fish caught based on the length-frequency distribution as there were fewer bars on the histogram. After this year, an increase in smaller size classes can be seen from 2000 – 2002 (Figure 3.4). In comparison, reference Lake 239 did not show similar results and stayed relatively consistent with the length-frequency distributions over all years for both yellow perch and northern pike (Figure 3.5; Figure 3.6).

The abundance of yellow perch > 100 mm significantly increased in 2000, one year after macrophyte cutting was ceased (Figure 3.7 A). Once macrophyte cutting began, population abundance estimates for northern pike in Lake 191 demonstrated a significant decline (from a mean of 628 for the pre-manipulation period to a low of 408 in 1997; Figure 3.7 B). This decline continued through to 1999, after which an increase in population to at or slightly above pre-manipulation was seen from 2000 – 2002. Northern pike in reference Lake 239 showed no similar trends, with the population remaining stable throughout the sample time period, indicating the changes seen in Lake 191 northern pike were not likely due to regional variation (Figure 3.7 C).

Mean weight of yellow perch in Lake 191 increased in in 1996 and 1997, followed by a decrease in mean weights in 1998 to pre-manipulation levels (Figure 3.8 A). Yellow perch in Lake 239 did not show any similar trends. Northern pike mean weight remained relatively stable, with a peak in 1999 followed by an immediate decrease in the subsequent year (Figure 3.8 B). Mean weights in Lake 239 northern pike did not show similar trends and peaked in 2000 before declining again (Figure 3.8 D).

Combining mean size and abundance results to estimate biomass, yellow perch biomass of fish > 100 mm in length increased throughout manipulation, dropping to pre-manipulation levels in 1999 (Figure 3.9 A). In 2000, biomass of yellow perch drastically increased by 2 times pre-manipulation levels to 15 kg/ha, remaining high for the following two years. Northern pike biomass was low during macrophyte cutting (Figure 3.9 B), but observed values were similar to those seen in 1995, one year prior to manipulation, which were much lower than those observed in 1994. Biomass of northern pike subsequently increased during the recovery period in comparison to the macrophyte cutting period; biomass of northern pike was highest in 2000, which was followed by a decline in 2002. Biomass of northern pike in reference lake 239 remained stable throughout the years of the experiment, indicating changes seen were not due to regional variation (Figure 3.9 C).

While no yellow perch growth data from Lake 191 were available prior to macrophyte cutting, their growth rates were stable during macrophyte cutting but declined after macrophyte cutting ceased for ages 2-5 (Figure 3.10 A and C). In reference Lake 468, no similar changes over time as were observed in Lake 191 were apparent (Figure 3.10 B and D).

Northern pike growth showed different trends in comparison to yellow perch, with growth dramatically increasing during macrophyte cutting, followed by declines that appear to be similar to growth declines in perch after cutting was ceased (Figure 3.11 A and C). For age classes 1-3, an increase in fork length by about 100mm occurred from 1996 – 1999. In age class 4, the increase in average annual fork length was seen from 1996 – 2002. Average annual weight for northern pike in Lake 191 showed similar trends to average annual fork length, with an increase in weight from the 1996 – 1999 for all age classes. These increases were more prevalent in the older two age classes (ages 3-4), with age class 3 increasing by ~300g from 1996-1999 and age class 4 increasing by ~400g from 1996 – 2002. Reference Lake 239 did not have data present for every average weight and fork length for every age class in every year, however, from the data present, no similar trends as those observed in Lake 191 were observed (Figure 3.11 B and D).

Maximum size declined for both pumpkinseed and yellow perch, the two prey fish species present in Lake 191 (Figure 3.12 A) by about 140mm and 180mm, respectively. By contrast, northern pike maximum size were not impacted. Yellow perch and northern pike maximum size remained stable from 1994 – 2003 in Lake 239 along with yellow perch in Lake 468 (Figure 3.12 B).

Based on stable isotopes of carbon, yellow perch showed a dip in carbon isotopic values in 1997 and no changes in other years (Figure 3.13). However, values across all years were variable in all years. No trends in nitrogen isotopic values were observed. There were no apparent patterns in Lake 239 yellow perch. A single-factor ANOVA was done on yellow perch $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures, which revealed that there were no differences in means over the duration of the experiment (Lake 191 $\delta^{13}C$: $F_{8,46} = 0.957$, $p > 0.05$; Lake 191 $\delta^{15}N$: $F_{8,46} = 1.839$, $p > 0.05$). In contrast, $\delta^{13}C$ isotopic signatures of northern pike declined steadily from 1997 to 2000 relative to prior years in the dataset, suggestive of a period of increasing pelagic carbon resource use, before returning to steadily from pre-manipulations from 2001-2003. A single-factor ANOVA on northern pike $\delta^{13}C$ isotopic signatures over time revealed a significant difference in means over the duration of the experiment ($F_{9,50} = 2.435$, $p < 0.05$); A post-hoc tukey's test indicated $\delta^{13}C$ for northern pike in 2000 was significantly lower than those observed in 1997 and 2002 (Figure A2). A change in trophic position for northern pike in 2002 was visible from the $\delta^{15}N$ isotopic signatures for Lake 191. A single-factor ANOVA on northern pike $\delta^{15}N$ isotopic signatures also revealed a significant difference in means over time ($F_{9,50} = 7.457$, $p < 0.05$). Generally, $\delta^{15}N$ signatures appeared to decline over the duration of the study, appearing to be lowest 4 and 5 years after manipulation (Figure 3.14B). A post-hoc Tukey's test indicated the pre-experimental monitoring year 1994 was significantly greater than all years except 1996, 1998, 2000. A significant decrease in $\delta^{15}N$ values during the recovery period was observed in 2002, where this year was significantly lower than 2000. The years of 2002 and 2003 were also significantly lower than 1996, which indicates there are significant differences between these two recovery period years and the first year of manipulation (Figure A3). Reference lake 239 did not show these trends and had relatively higher variance for both $\delta^{15}C$ and $\delta^{15}N$ over time. Single-factor ANOVA's for both isotopic signatures for both fish species in Lake 239 showed no significant differences among years ($\delta^{13}C$: $F_{6,423} = 0.646$, $p > 0.05$ and $\delta^{15}N$: $F_{6,23} = 0.575$, $p > 0.05$ for yellow perch; $\delta^{13}C$: $F_{7,40} = 1.632$, $p > 0.05$ and $\delta^{15}N$: $F_{7,40} = 2.189$, $p > 0.05$ for northern pike).

3.4 Discussion

The fish community in lake 191 underwent many changes with the cutting of 50% of macrophytes present for a 3-year period. The abundance of yellow perch >100 mm in length appeared largely unaffected over the duration of cutting, instead increasing in 2000 during the post-manipulation period. In contrast, biomass estimates of large yellow perch (> 100 mm) showed an increase from 1996 – 1998, a single decrease in 1999, and a drastic increase from 2000 – 2003. Further, length-frequency distributions of both yellow perch and pumpkinseed showed a dramatic increase in the amount of smaller prey fish (< 100mm) from 1996 which was sustained until the end of monitoring in 2003. While the result of biomass of larger yellow perch goes against my original hypothesis that biomass would decrease as macrophytes are cut due to increased predation, the increase in larger perch density after cutting appear to have had denser refuge available to them, as relative macrophyte biomass at 0.5m in Lake 191 was highest from 1996 – 1998 (Figure A2). Since yellow perch rely on macrophytes for protection from predation when in the presence of predators (Jacobsen & Perrow, 1998), it is plausible that both smaller yellow perch (<100mm) congregated in the uncut areas when relative macrophyte biomass increased during the cutting period, allowing for an increase in smaller fish. Large yellow perch abundance remained unchanged as northern pike abundance declined, which indicates lower per capita predation on perch.

Shifts in size distributions for prey fish clearly indicate that reductions in maximum size of prey fish are not just due to an increased proportion of smaller prey fish, but also a reduction in larger-bodied prey fish over the course of the experiment. Together, this suggests that predation by northern pike on larger prey fish may also play a role in these patterns, as pike feed based on gape size. In a complete vegetation removal experiment where grass carp were introduced in Lake Conroe, Texas biomass and mean size of sunfish declined (Bettoli et al., 1993). Similar to yellow perch in our experiment, bluegill in Lake Conroe remained abundant. It is possible that large perch in Lake 191 were able to maintain their abundance because of their ability to graze on various prey, like zooplankton, macroinvertebrates, and small fish (Thorpe 1977; Paszkowski & Tonn, 1994; Persson et al., 1991). I speculate that the increase of biomass for yellow perch greater than 100mm could be due to the pulse of small fish from earlier years growing to a size larger than 100 mm, and as such, they were able to be nicked and enter the marked population. It is surprising that small prey fish became more frequent in the population with the removal of their spawning habitat, however, this is likely due to the increase in relative macrophyte biomass at 0.5 m, suggesting that cutting of macrophytes in Lake 191 may not have had the intended impacts on plant cover.

As predicted, northern pike abundance and biomass decreased following macrophyte cutting. This was followed by an increase in 2000 as the abundance and biomass of large perch increased. By comparison, abundance in unmanipulated Lake 239 was relatively stable. Declines in abundance for species that rely on macrophytes was observed in other ecosystems where macrophyte areas were cut and/or underwent removal; giant kokopu (*Galaxias argenteus)* and common bully (*Gobiomorphus cotidianus*) abundance declined after 60% of macrophytes were mechanically removed in streams in New Zealand (Greer et al. 2012). Another study examining large sized species (dace, chub, roach, perch, pike; small sized species were juveniles, gudgeon, minnow, and stone-loach) also found a decrease in abundance of fish populations following macrophyte removal, but struggled to discern these results from natural variation in the river (Swales, 1982). In their study, population abundance and density of large-sized species (dace, chub, roach, perch, pike) increased back to pre-removal levels the year following cutting, which was not observed in Lake 191. One possibility for the lag effect in population abundance and biomass returning to normal for northern pike could be the increase in large perch abundance as the increase in abundance and biomass for northern pike is observed when large yellow perch abundance increases. The decrease in abundance of northern pike during cutting may be due to increased cannibalism, as suggested by Robasco (2000). He came to this conclusion based on stomach content analysis on northern pike in Lake 191 in 1999. Craig (2008) suggests cannibalism among northern pike is a common occurrence, further providing support for this idea.

Growth of fish following cutting of aquatic vegetation is variable, and both an increase and decrease in growth following cutting is observed throughout the literature (Bettoli et al., 1992; Garner et al., 1996; Herwig & Wilson, 1997; Olson et al., 1998; Trebitz & Nibbelink, 1996; Unmuth et al., 1998; Unmuth et al., 1999). In Lake 191, both fork length and weight of yellow perch for all age classes demonstrated a lagged response, in that they declined after the cutting period in 2000 when abundance increased, suggesting this may be a result of density dependence. It is, however, important to note that in this study, there was no data for growth rates of yellow perch prior to macrophyte cutting, making assessments of pre-manipulation difficult. Trebitz and Nibbelink (1996) saw that in a modelling study with less than half the vegetation removed, bluegill feeding and growth rate increased in simulations, and only after more vegetation was removed was decreased fish growth observed. From this, it is possible that response of fish growth rates in Lake 191 were impacted by macrophyte cutting in a similar way, in that 50% of macrophytes resulted in too large of a clear-cut area in this system to benefit yellow perch growth and too little edge habitat was available. The decline in yellow perch growth in Lake 191 was further supported by the results of maximum size, where we saw a decline in the maximum size of prey fish in Lake 191 over the years, meaning there were not as many large fish as previously found in Lake 191. Based on the literature, it seems that with a greater percentage of macrophytes cut, prey fish growth will likely decrease. This is supported by Garner et al. (1996), in which they saw a decline in growth rates of roach after weed cutting where only a 2m marginal strip of macrophytes remained, which represented 40% removal of macrophytes. Another possible explanation for this result is density dependence in the perch population. The abundance of yellow perch increased when the recovery period began, and with an increase in fish abundance, growth would slow due to increased pressure on food sources.

In a study where removal of all macrophytes through introduction of grass carp occurred, largemouth bass, a piscivorous fish, displayed an increase in first-year growth rates as piscivory was initiated at smaller sizes (Bettoli et al., 1992). In Lake 191, we saw an increase in northern pike growth rates in 1996 when macrophyte cutting began for all age classes. The increase in growth rates for northern pike could be due to an increase in readily available food sources from increased exposure to prey (due to reduced prey refuge). Because growth for northern pike increased over a period of time with relatively stable abundance and biomass, this suggests that the increase in growth was not due to density dependence, indicating changes in food availability is a more likely explanation. Another example of increased growth rates following macrophyte cutting can be found in Olson et al. (1998). In this study, macrophytes were removed from 20% of the littoral zone of the lake and both bluegill and largemouth bass growth rates increased. This was attributed to the increase in edge habitat, allowing for greater access to food. Northern pike growth declined from 2000 to the end of the experiment. During this time, the abundance of northern pike increased, which suggests that there was an increase in northern pike young of year during recovery, which we can see in the size-frequency distributions for northern pike. Looking at the trends of young of year CPUE for northern pike from 1994 -2003, we can see a decrease in total CPUE starting immediately when cutting begins. Catch per unit effort in uncut areas for YOY pike increases following recovery in 1999 – 2002, suggesting there was an increase in YOY northern pike. This supports the increase in abundance of northern pike >100 mm in 2000 as when the YOY from the previous year grow, they would be included in this larger size class.

In 1997, yellow perch $\delta^{13}C$ stable isotopic values dropped, showing that there was a shift in diet for yellow perch to offshore resources. This corresponds with the crash of zooplankton biomass in 1997 observed in this study (Chapter 2). This provides additional evidence that the increase in smaller perch and pumpkinseed in 1996 caused the zooplankton biomass to dramatically decline in 1997. This is further supported by the fact that early larval fish utilize zooplankton as a food source when they are of small sizes (Garner, 1996). However, despite a sustained high abundance of small prey fish following 1997, both zooplankton densities and yellow perch $\delta^{13}C$ returned to values seen before this year. If high prey fish densities were responsible for reduced zooplankton densities, I would expect zooplankton densities to remain depressed in the years following 1997 when small fish densities remained high, and for yellow perch $\delta^{13}C$ to reflect primarily pelagic resource use.

As predicted, northern pike stable isotopic signatures represented a sustained shift in diet to pelagic sources and a shift to lower trophic levels indicating a greater reliance on more offshore resources, but only after the active cutting of macrophytes was ceased. The decrease in $\delta^{13}C$ found for northern pike in 2000, which indicates a shift to more pelagic sources, is supported by a number of other results. Relative macrophyte biomass at 0.5m in Lake 191 was lowest during the post-cutting period. This suggests that macrophytes were less dense during this time, making it possible that zooplanktivorous prey fish became more susceptible to predation. Supporting this finding, size-frequency distributions indicate that number of small prey fish remained high in the later years of the experiment. Yellow perch feed on zooplankton until they reach larger sizes (> 75 mm; Thorpe 1977; Paszkowski & Tonn, 1994), and are often found migrating between the littoral zone and the pelagic zone to feed (Wang & Eckmann, 1994). This may have caused the decrease in carbon isotopic values in northern pike, as northern pike would be feeding on smaller, zooplanktivorous yellow perch due to the decrease in maximum sizes of prey fish. This would further explain the decrease in trophic levels for northern pike as younger, smaller perch occupy lower trophic levels than their larger, older counterparts. While the years in which carbon and nitrogen isotopic appear lowest do not line up exactly (carbon was lowest in 2000, nitrogen was lowest in 2002), stable isotope analysis was done using fish fin tissues, which experience turnover on a rate of 2-4 months (Busst and Britton 2017). Given this longer tissue turnover rate, isotopic signatures derived from these tissues provide an understanding of diet and trophic positions over a longer period of time in comparison to stomach content analysis, which looks at diet only on a particular sampling occasion representing a few hours of feeding (Hesslein et al., 1993). Foraging lower in the food web can also lead to slower growth rates (Pazzia et al. 2002), which could explain why we see growth rates slow down around the same time trophic level drops in Lake 191. One can also speculate that the increase in both northern pike and yellow perch abundance around the same years led to lower preferred food availability in both species, where low mean and maximum size of yellow perch forced northern pike to make a switch to lower trophic levels, as larger yellow perch were not of sufficient density, forcing a switch to small prey fish and large macroinvertebrate prey (e.g. leeches and anisopterans; Venturelli & Tonn, 2006).

From this study, it is apparent fish communities in Lake 191 were greatly impacted by the cutting of 50% of macrophytes. While there was a delay in the response in yellow perch that was not expected, northern pike growth responded in a density dependent fashion as predicted only during the recovery period. Growth during the manipulation period increased over a period of stable abundance, suggesting this was due to food availability rather than density dependence. At the same time northern pike experienced a peak in abundance and biomass, they also exhibited a switch to pelagic diet and lower trophic position. This could be explained by northern pike running out of larger prey items in the years prior to 2000, causing them to switch to smaller yellow perch, thus lower trophic levels and offshore sources. At the same time, yellow perch abundance increased. This increase in yellow perch abundance signals that large yellow perch may be subjected to less predation around 2000, which would further explain the switch of northern pike diets. Though Robasco (2000) showed zooplankton composing a high percentage of northern pike diets, it is unclear why they make this switch when there is competition for zooplankton from prey fish. It has been suggested in former studies that partial removal of macrophytes will allow for open water, while still providing enough macrophyte biomass and edges to not greatly harm the fish communities (Bickel & Closs, 2009; Trebitz & Nibbelink, 1996). Given the decrease of northern pike abundance and overall shift in trophic position and diet, it is apparent that cutting of 50% of macrophytes was enough to cause a negative shift in predator fish populations in a small, shallow lake. Had there been consistent pre-experimental monitoring data for prey fish species, perhaps we would have been able to come to more concrete conclusions regarding why yellow perch did not display impacts to the magnitude expected.

Tables

Table 3.1. Comparison of physical parameters and exhaustive list of fish species present in Lake 191, Lake 239, and Lake 468.

	Lake 191	**Lake 239**	**Lake 468**
Surface area (ha)	16.3	54.3	301
Maximum depth (m)	4.1	30.4	25
Fish species present	Northern Pike (*Esox lucius)*, Yellow Perch (*Perca flavascens)*, Pumpkinseed (*Lepomis gibbosus),* White Sucker (*Catostomus commersonii)*	Northern Pike *(Esox lucius)*, Yellow Perch *(Perca flavescens)*, Iowa Darter *(Etheostoma exile)*, Cisco (*Coregonus artedi)*, Lake Trout *(Salvelinus namaycush)*, Slimy Sculpin *(Cottus cognatus)*, White Sucker *(Catostomus commersonii)*, Finescale Dace *(Chrosomus neogaeus)*	Lake Whitefish (*Coregonus clupeaformis)*, Lake Trout (*Salvelinus namaycush)*, Finescale Dace (*Chrosomus neogaeus)*, Blacknose Shiner (*Notropis heterolepis),* Bluntnose Minnow (*Plimephales notatus),* Longnose Dace (*Rhinichthys cataractae)*, Pearl Dace (*Margariscus nachtriebi)*, White Sucker (*Catostomus commersonii),* Yellow Perch (*Perca flavascens),* Northern Pike (*Esox lucius)*, Slimy Sculpin (*Cottus cognatus)*

Table 3.2. POPAN model output for 191 perch.

Model	**AICc**	**ΔAICc**	**AICc Weights**	**Model Likelihood**	**Num. Parameters**
{Phi(exp)p(t)pent(t)}	1593.811	0	0.99926	1	26
{phi(*)p(t)pent(t)}	1609.221	15.4099	0.00045	0.0005	23
{Phi(exp)p(t)pent(exp)}	1610.21	16.3993	0.00027	0.0003	22
{Phi(t)p(exp)pent(t)}	1615.514	21.7028	0.00002	0	27
{Phi(*)p(t)pent(*)}	1681.819	88.0074	0	0	18
{Phi(exp)p(exp)pent(t)}	1692.751	98.9395	0	0	20
{Phi(t)p(exp)pent(exp)}	1742.261	148.4501	0	0	21
{Phi(*)p(*)pent(t)}	1790.834	197.0229	0	0	11
{Phi(exp)p(exp) pent(exp)}	1932.51	338.6992	0	0	10
{Phi(*)p(*)pent(*)}	3355.328	1761.5173	0	0	3
{Phi(t)p(*)pent(*)}	3381.635	1787.8237	0	0	16

Table 3.3. POPAN model output for Lake 191 pike.

Model	$\hat{C}$ adj.	QAICc	ΔQAICc	AICc Weights	Model Likelihood	Num. Parameters
{Phi(t)p(exp)pent(t)}	2.436	1522.4015	0	0.64798	1	31
{Phi(t)p(*)pent(t)}		1523.6352	1.2337	0.34968	0.5396	30
{Phi(exp)p(exp)pent(t)}		1534.5728	12.1713	0.00147	0.0023	21
{Phi(*)p(*)pent(t)}		1536.6541	14.2526	0.00052	0.0008	17
{Phi(t)p(exp)pent(exp)}		1537.4568	15.0553	0.00035	0.0005	22
{Phi(exp)p(exp)pent(exp)}		1570.3802	47.9787	0	0	10
{phi(t)p(t)pent(t)}		3612.064	2089.6625	0	0	47
{Phi(t)p(t)pent(exp)}		3620.3095	2097.908	0	0	35
{Phi(exp)p(t)pent(t)}		3633.4256	2111.0241	0	0	31
{Phi(*)p(t)pent(t)}		3636.2069	2113.8054	0	0	29
{Phi(exp)p(t)pent(exp)}		3653.8565	2131.455	0	0	23
{Phi(t)p(*)pent (*)}		43766.195	42243.794	0	0	16
{Phi(*)p(t)pent (*)}		181621.24	180098.84	0	0	17

Table 3.4. POPAN model output for Lake 239 pike.

Model	$\hat{C}$ adj.	QAICc	ΔQAICc	AICc Weights	Model Likelihood	Num. Parameters
{phi(*)p(t)pent(t)}	1.158	2382.84	0	0.98406	1	98
{p(t)phi(t)pent(t)}		2391.086	8.2458	0.01594	0.0162	123
{phi(t)p(*)pent(t)}		2650.106	267.2664	0	0	73
{phi(*)p(*)pent(t)}		2687.059	304.2194	0	0	25
{phi(t)p(*)pent(*)}		2761.278	378.4381	0	0	51
{phi(t)p(t)pent(*)}		37746.67	35363.8312	0	0	97
{phi(*)p(t)pent(*)}		40477.52	38094.6766	0	0	50
{phi(*)p(*)pent(*)}		41067.36	38684.517	0	0	2

Figures

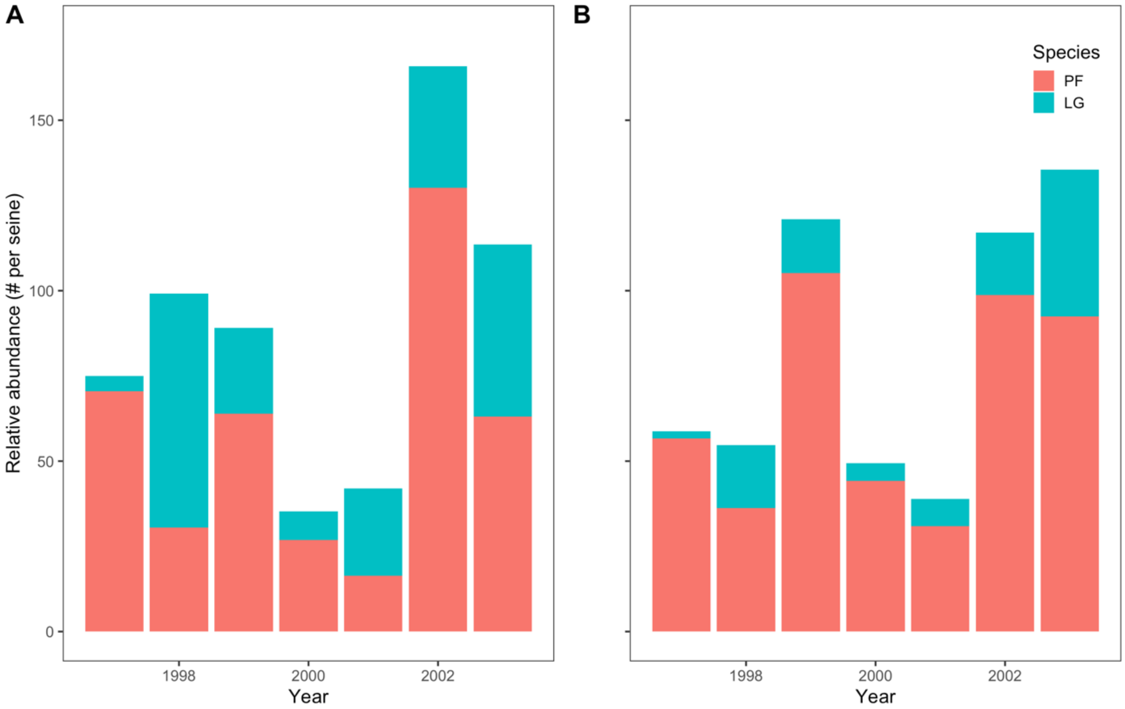

Figure 3.1. Average annual seine haul catch (total catch/total # of seines) for Lake 191 perch (PF, pink) and pumpkinseed (LG, blue) in A) uncut zones, and B) cut zones from 1997 - 2003. Y-axes for both A and B have been made to have the same scale.

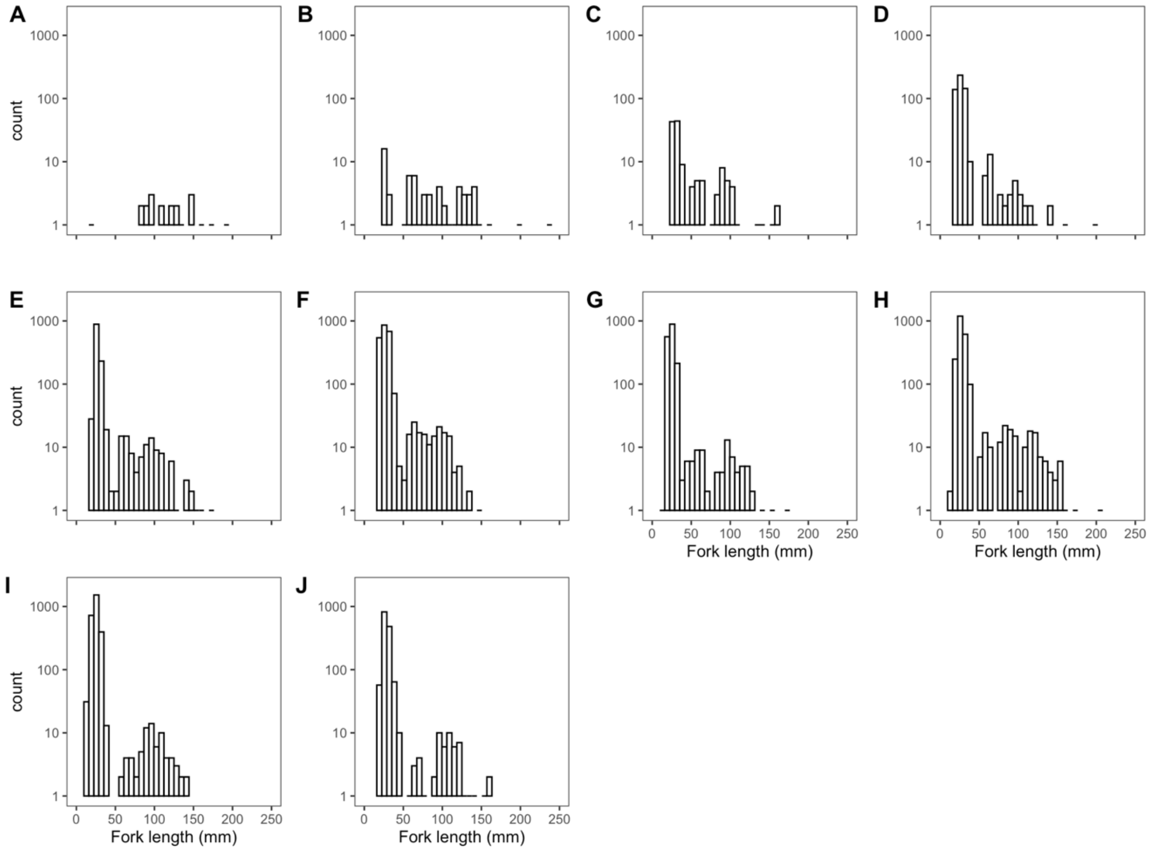

Figure 3.2. Length-frequency distribution of pumpkinseed in Lake 191 for the years of 1994 – 2003, A-J, respectively, where the y-axis has been log-transformed to better visualize changes in frequencies for in each year. Years of cutting (1996-1998) are panels C-E.

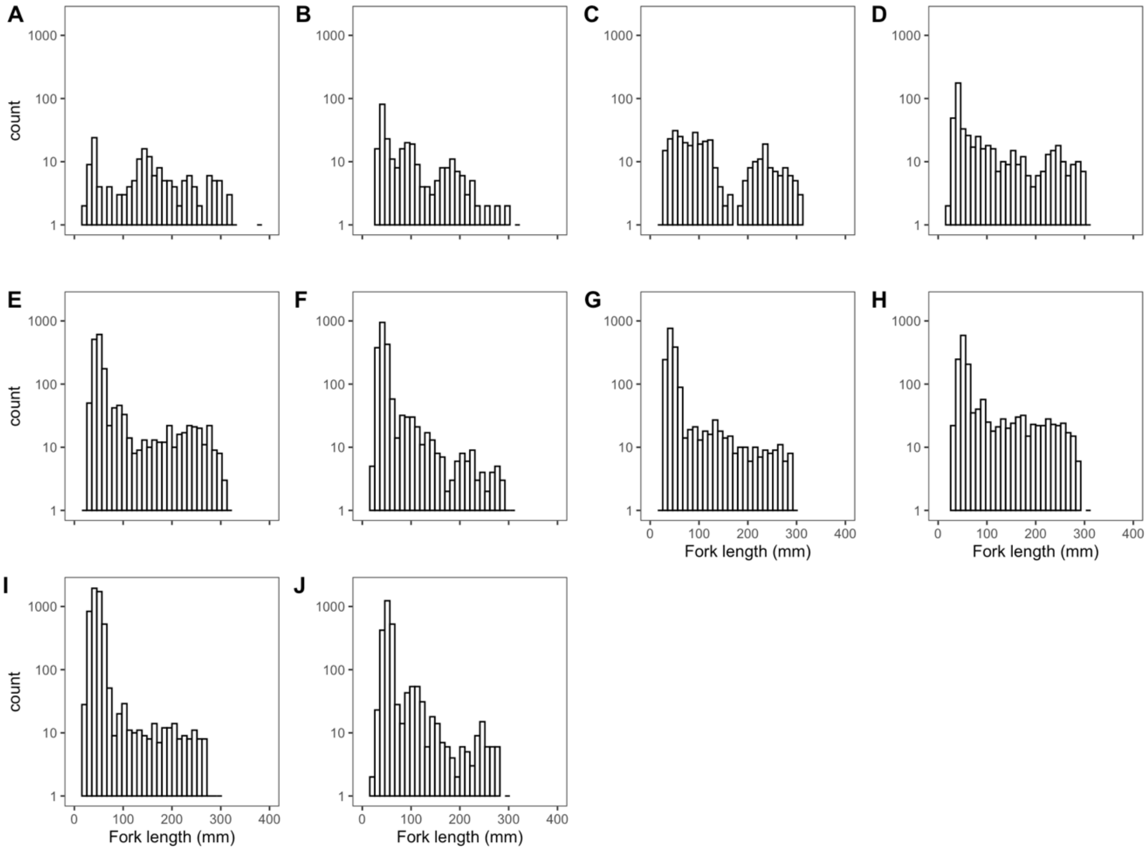

Figure 3.3. Length-frequency distribution of yellow perch in Lake 191 for the years of 1994 – 2003, A-J, respectively, where the y-axis has been log-transformed to better visualize changes in frequencies for in each year. Years of cutting (1996-1998) are panels C-E.

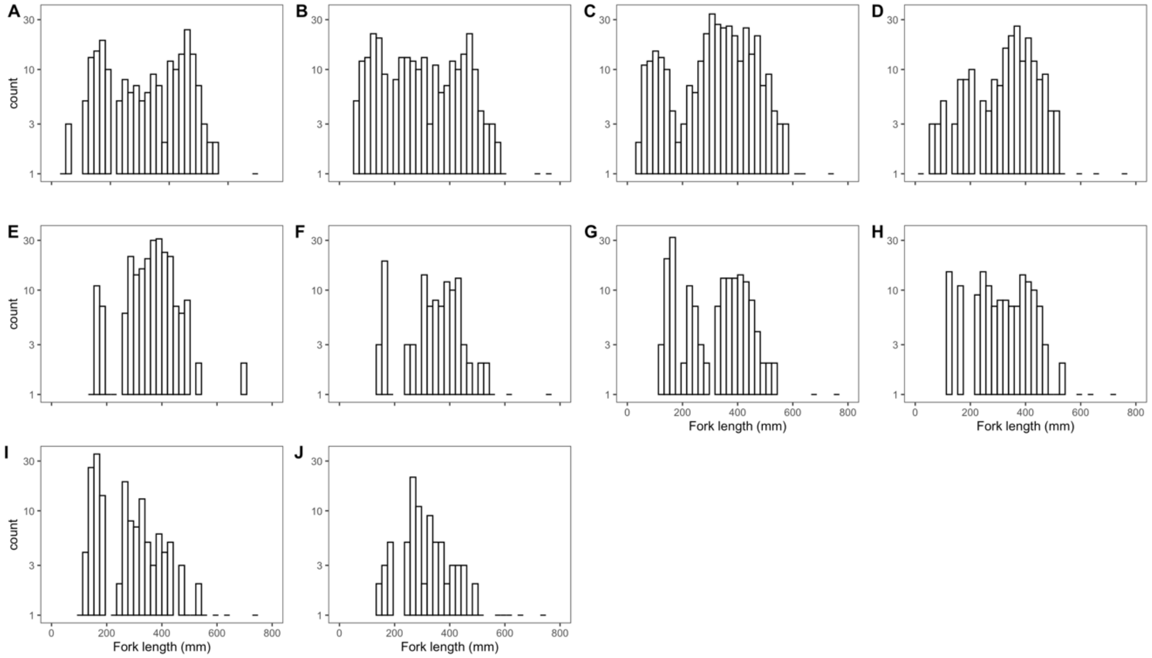

Figure 3.4. Length-frequency distribution of northern pike in Lake 191 for the years of 1994 – 2003, A-J, respectively, where the y-axis has been log-transformed to better visualize changes in frequencies for in each year. Years of cutting (1996-1998) are panels C-E.

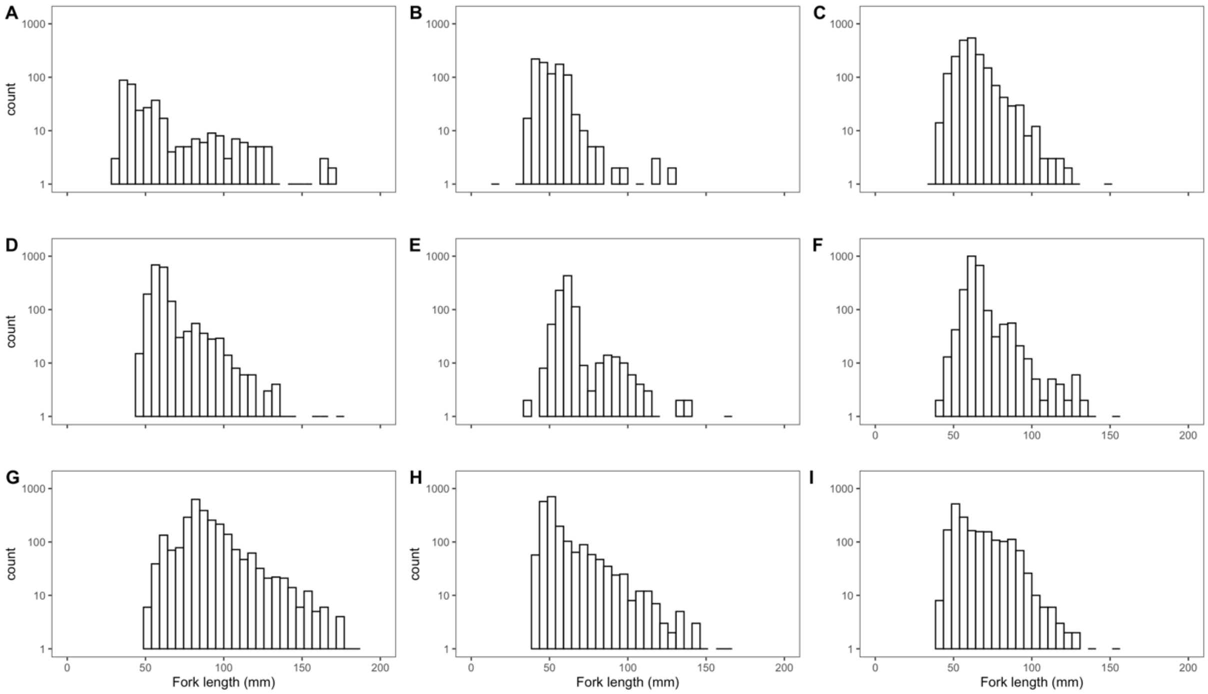

Figure 3.5. Length-frequency distribution of yellow perch in Lake 239 for the years of A) 1994; B) 1995; C) 1996; D) 1998; E) 1999; F) 2000; G) 2001; H) 2002; I) 2003. The y-axis has been log-transformed to better visualize changes in frequencies for in each year.

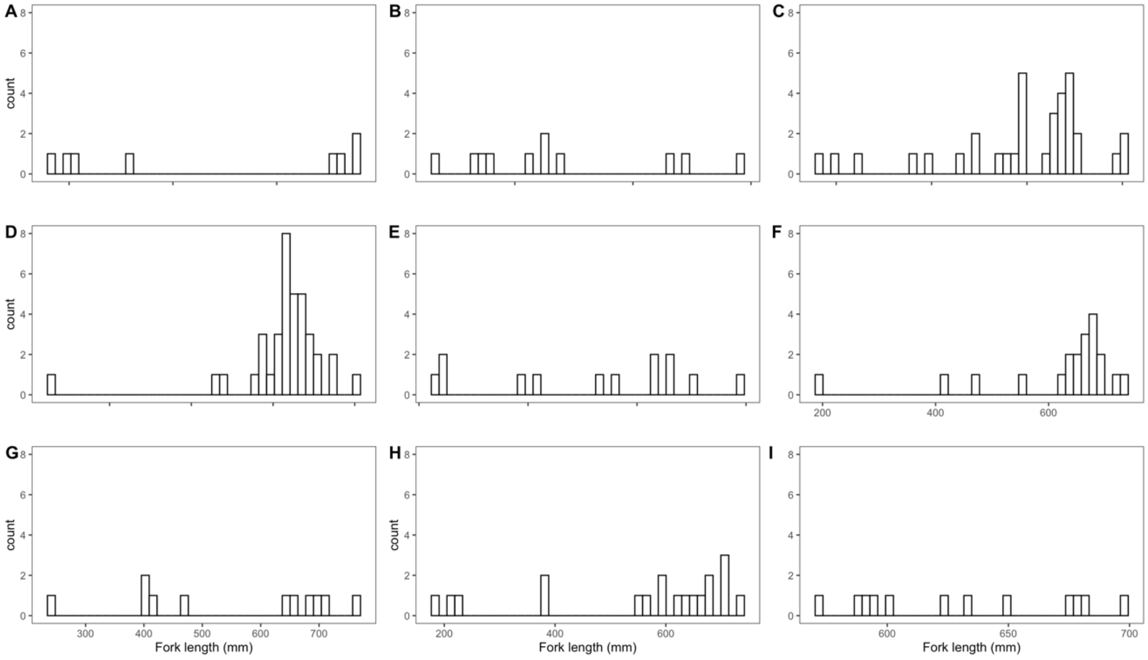

Figure 3.6. Length-frequency distribution of northern pike in Lake 239 for the years of A) 1994; B) 1995; C) 1996; D) 1998; E) 1999; F) 2000; G) 2001; H) 2002; I) 2003.

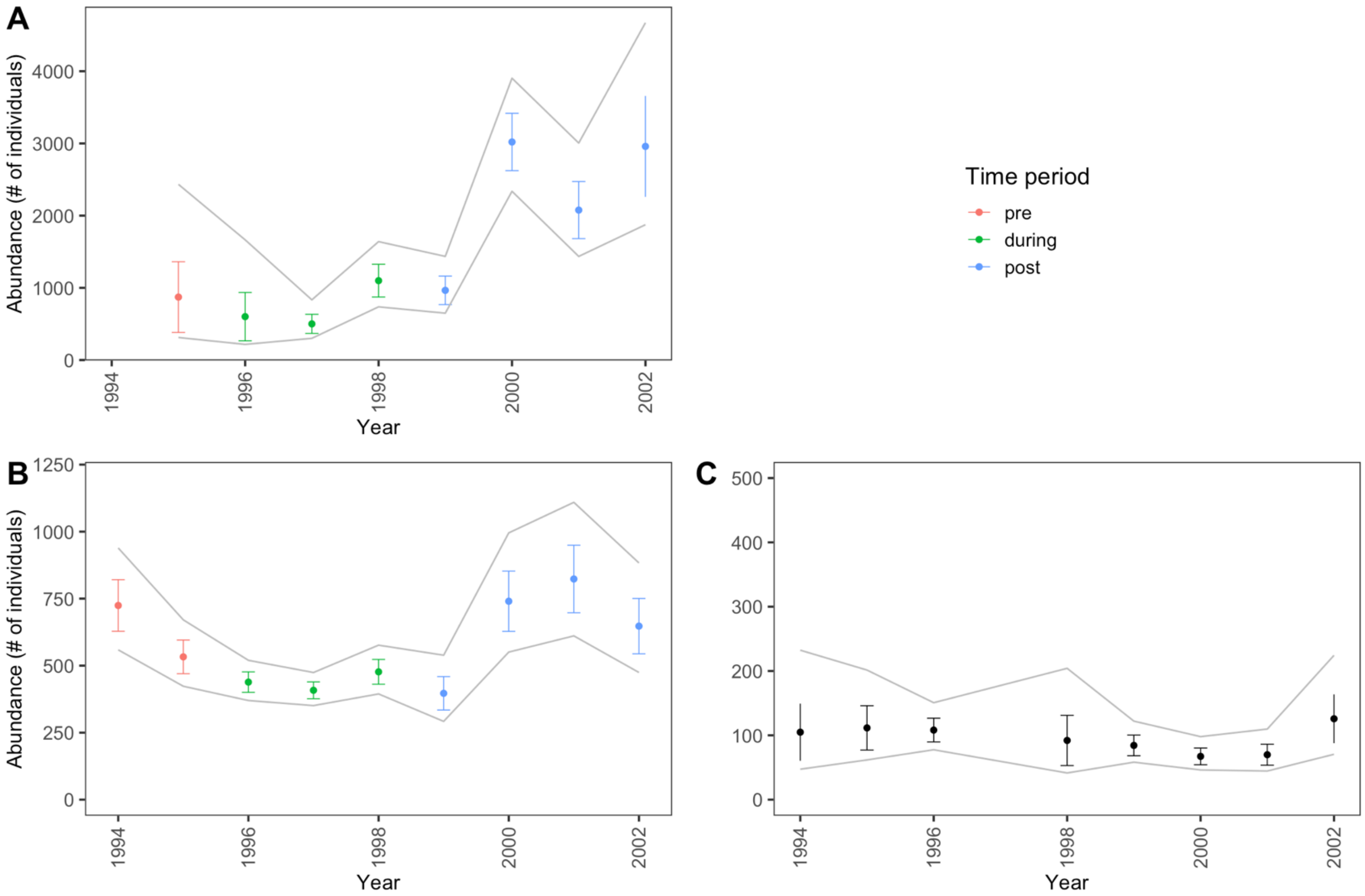

Figure 3.7. Annual population abundance estimates for A) Lake 191 yellow perch > 100 mm; B) Lake 191 northern pike; and C) Lake 239 northern pike. Standard error bars and 95% confidence intervals (grey lines) are plotted, along with the 3 time periods as follows: pre-experimental monitoring in pink, macrophyte cutting in green, and post-experimental monitoring in blue. Note for Lake 191 northern pike (B), top two models were not averaged and only the highest ranking model is represented here (time-dependent survival, experimental dependent capture probability, and time dependent probability of entry). Note differences in scale between panels.

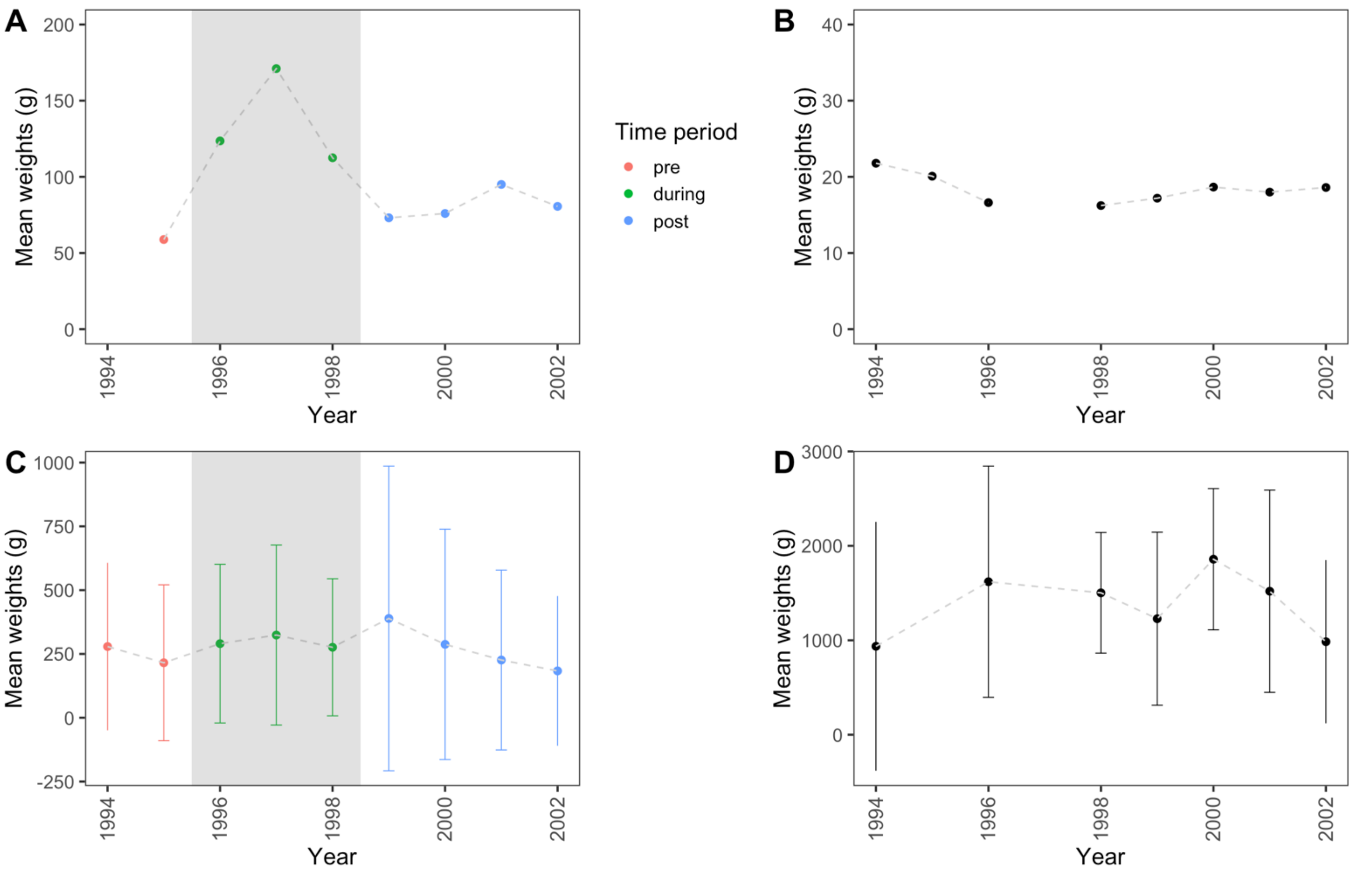

Figure 3.8. Mean weights (g) for A) Lake 191 yellow perch >100mm; B) Lake 239 yellow perch >100mm; and C) Lake 191 northern pike, and D) Lake 239 northern pike with the 3 time periods are as follows: pre-experimental monitoring in blue, macrophyte cutting in green, and post-experimental monitoring in pink. Note differences in scales between panels.

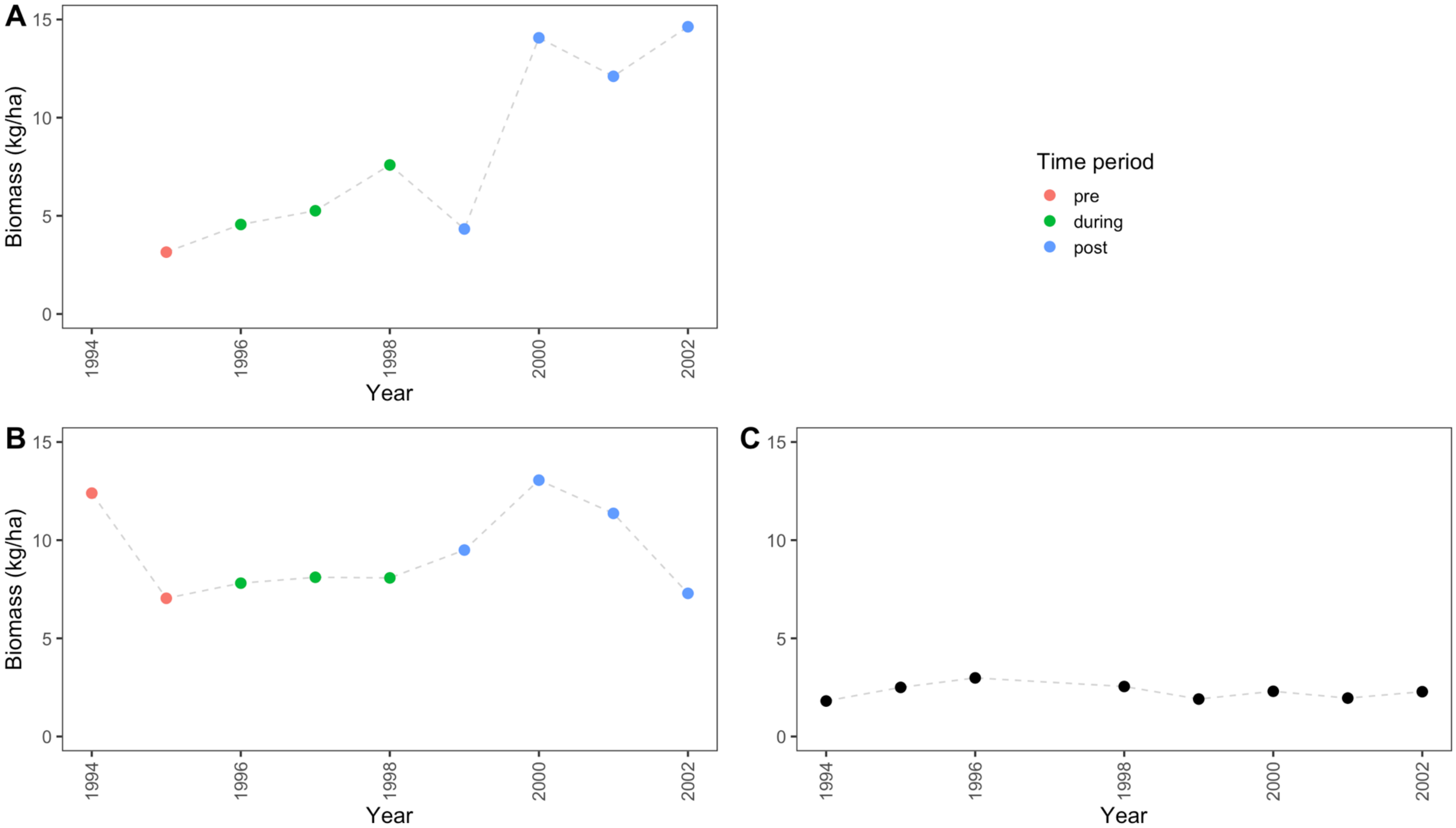

Figure 3.9. Annual biomass estimates (kg/ha) for A) Lake 191 yellow perch > 100 mm; B) Lake 191 northern pike; and C) Lake 239 northern pike, with the 3 time periods as follows: pre-experimental monitoring in pink, macrophyte cutting in green, and post-experimental monitoring in blue. Note differences in scale between Panel B vs. A, C, but that in each panel the range shown is similar (10 kg/ha) facilitating relative comparisons between panels.

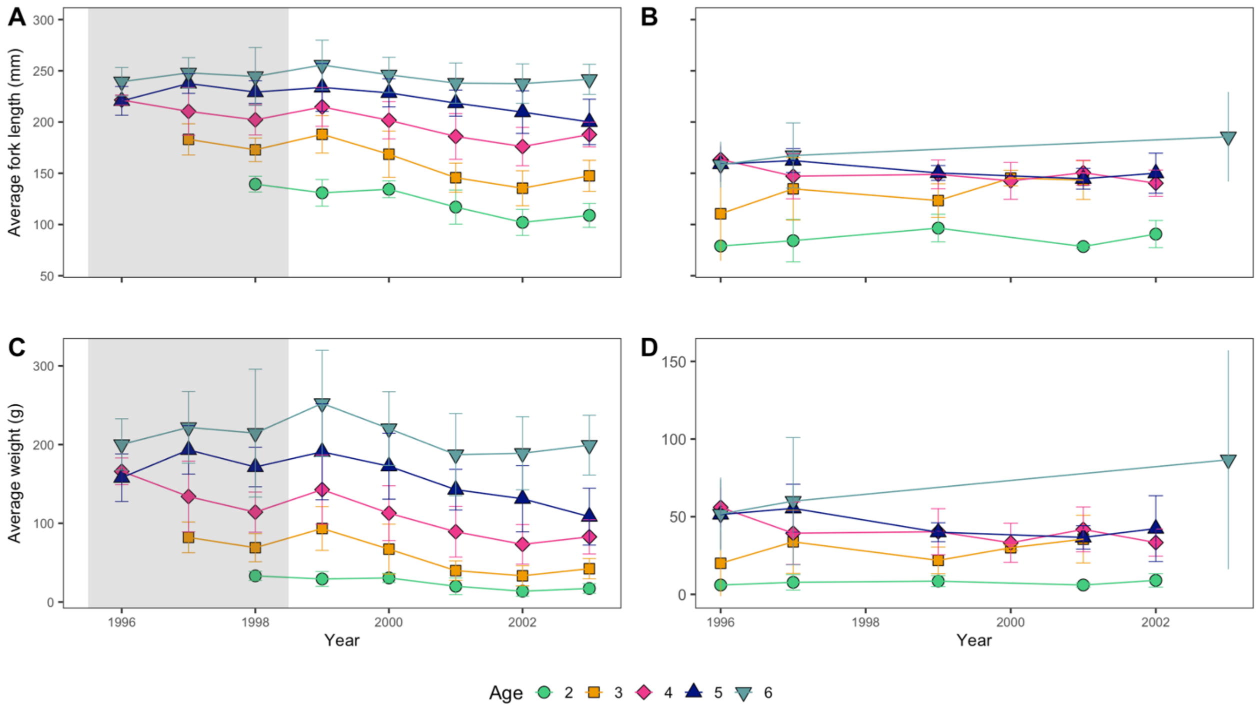

Figure 3.10. Plots A-B: Average annual fork length (mm) for yellow perch for ages 2-6 for A) Lake 191 and B) Reference Lake 468. Plots C-D: Average annual weight (g) for yellow perch for ages 2-6 for A) Lake 191 and B) Reference Lake 468. Ages are colour coded (age 2 = green circle, age 3 = orange square, age 4 = pink diamond, age 5 = navy blue triangle, age 6 = blue-gray upside-down triangle) with standard deviation error bars. Experimental macrophyte cutting period has been shown using a grey window. Note the difference in scaling of y-axes for C and D.

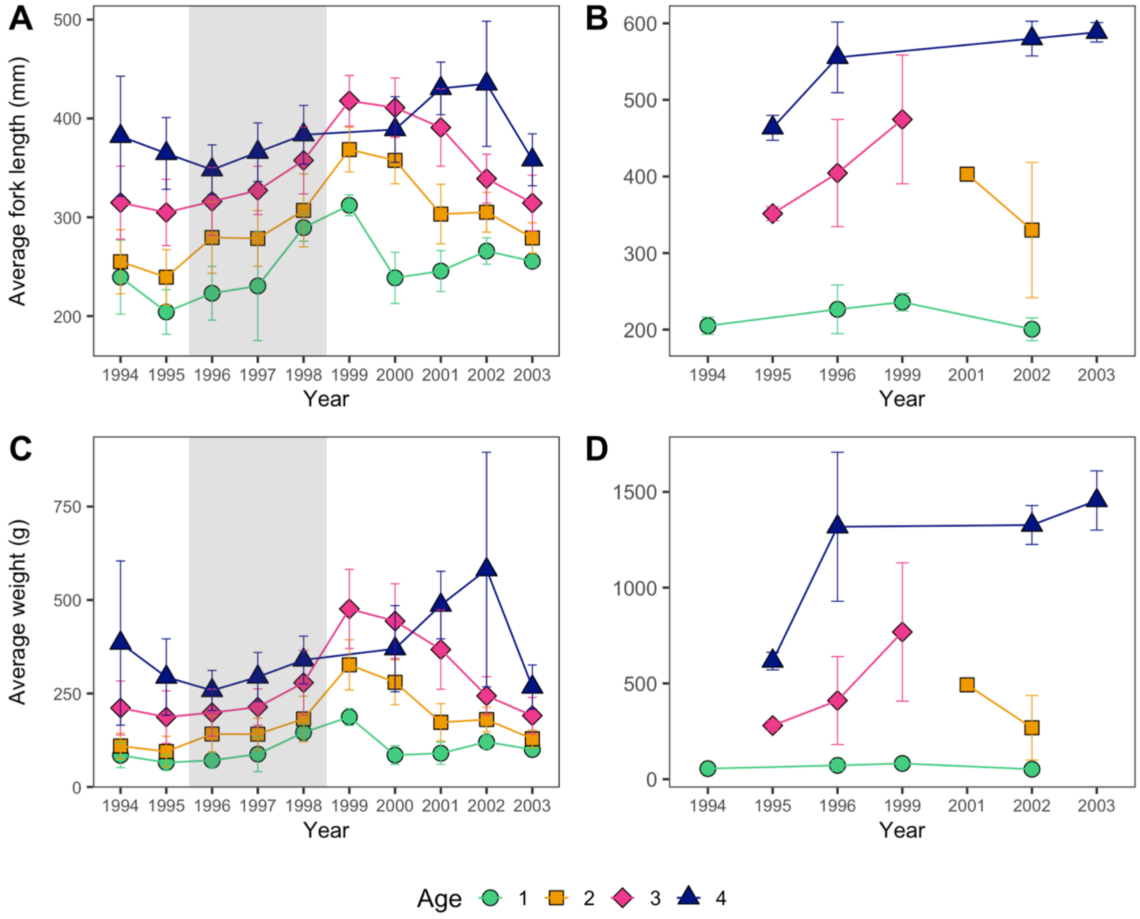

Figure 3.11. Plots A-B: Average annual fork length (mm) for northern pike for ages 1-4 for A) Lake 191 and B) Reference Lake 239. Plots C-D: Average annual weight (g) for northern pike for ages 1-4 for A) Lake 191 and B) Reference Lake 239. Ages are colour coded (age 1 = green circle, age 2 = orange square, age 3 = pink diamond, age 4 = navy blue triangle) with standard deviation error bars. Experimental macrophyte cutting period has been shown using a grey window.

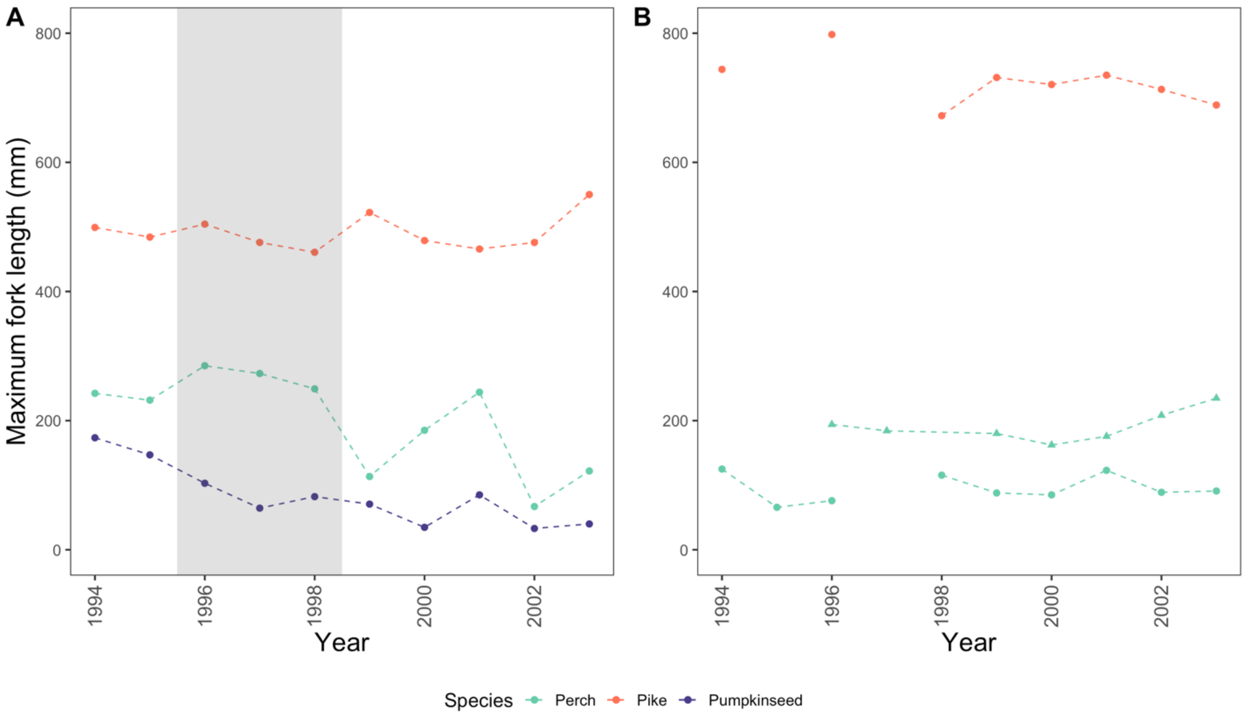

Figure 3.12. Maximum annual fork lengths (mm) for northern pike (pink), perch (light blue), and pumpkinseed (dark blue) in A) Lake 191 and B) Lake 239 pike and perch (circles) and Lake 468 perch (triangles). Experimental macrophyte cutting period has been shown using a grey window.

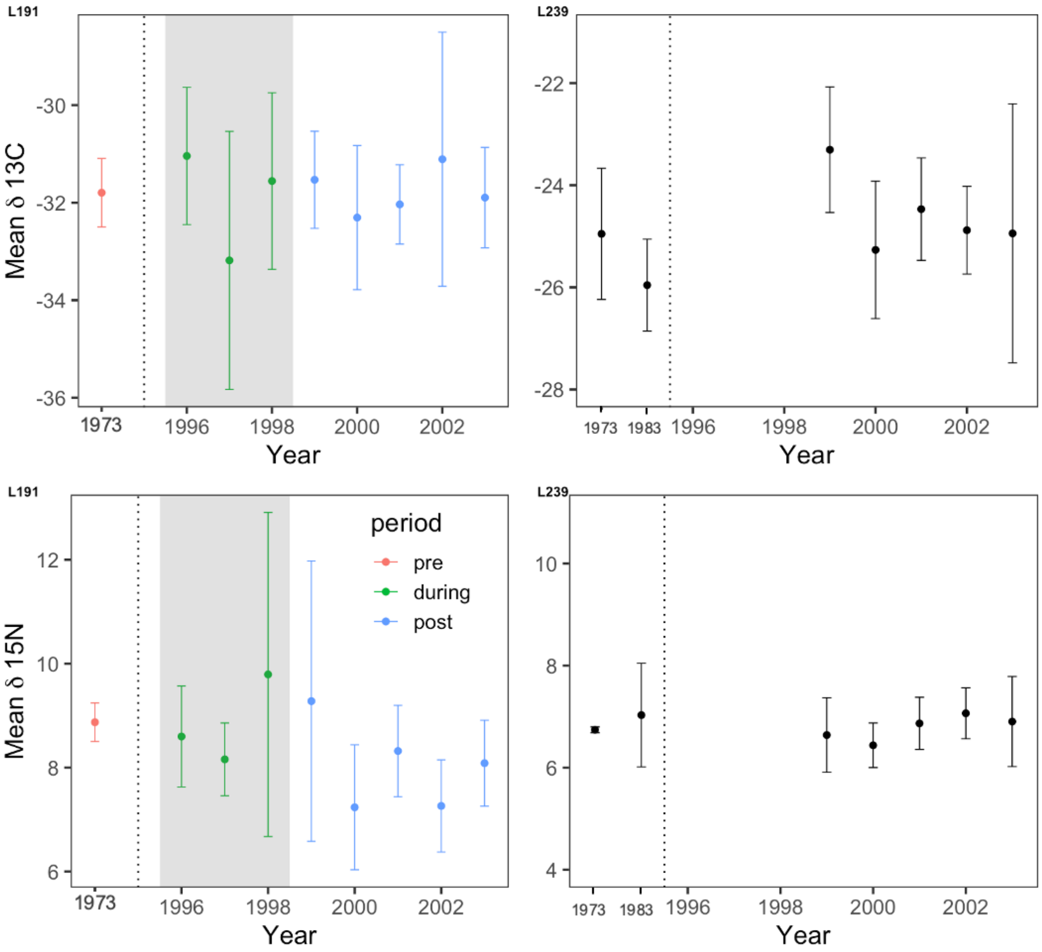

Figure 3.13. Annual $\delta^{13}C$ (top) and annual $\delta^{15}N$ (bottom) for yellow perch in Lake 191 (left) and Lake 239 (right) with standard deviation error bars. For Lake 191, time periods are colour-coded with pre-experimental monitoring in pink, macrophyte cutting period in green, and post-experimental monitoring in blue. The macrophyte removal period has been shown using a grey window. A horizontal dotted line depicts a break in the x-axis where the years jump from 1983 – 1996. Y-axis scales have been manipulated to show the same range.

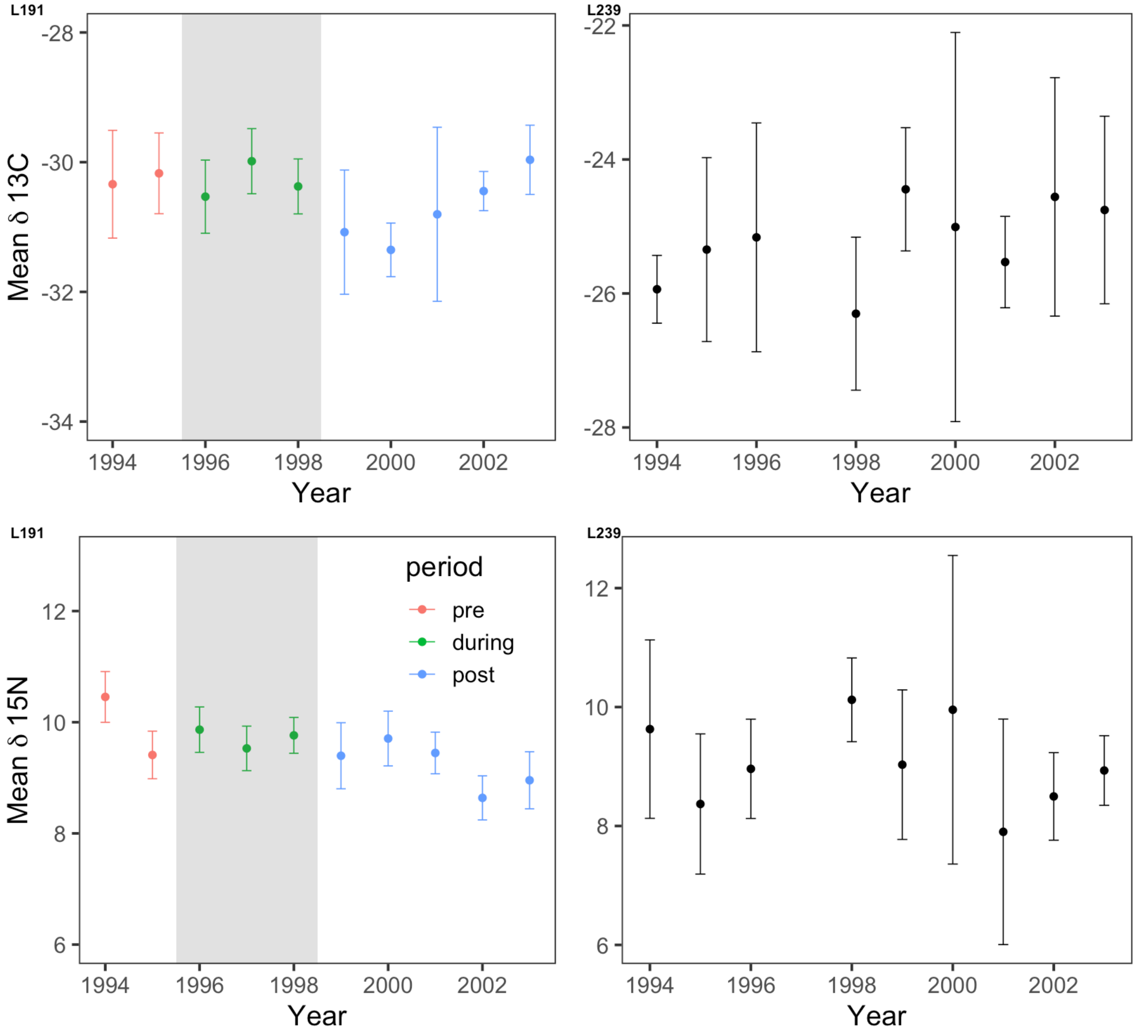

Figure 3.14. Annual δ^{13}C (top) and annual δ^{15}N (bottom) for northern pike in Lake 191 (left) and Lake 239 (right) with standard deviation error bars. For Lake 191, time periods are colour-coded with pre-experimental monitoring in pink, macrophyte cutting period in green, and post-experimental monitoring in blue. The macrophyte removal period has been shown using a grey window. Y-axis scales have been manipulated to show the same range.

Chapter 4: Synthesis

In this thesis, I evaluated the impacts of macrophyte cutting on a whole lake ecosystem. Overall, I found that macrophyte cutting increased phytoplankton biomass immediately following manipulation, decreased zooplankton biomass in 1997, and had profound impacts on the fish community. As such, biomass of several key parts of the ecosystem in Lake 191 were affected by the cutting of 50% of vegetation. Perhaps most surprisingly, total relative biomass of macrophytes at 0.5m (e.g., the total biomass of the region of the lake suitable for supporting macrophytes) increased during the cutting period, despite cutting from 50% of macrophytes by area. This was mainly due to a large increase by (2-3 times) in biomass in uncut regions of the lake. Ultimately, total relative macrophyte biomass did not decrease below pre-manipulation levels until 2000 (2 years after cutting was ceased), which coincided with the observed decrease in water clarity, declines in fish growth, and changes in northern pike trophic levels. In this same year when relative macrophyte biomass was at its lowest, light penetration in Lake 191 was also at its lowest. This was expected as macrophytes are known to decrease sediment resuspension, so as they reduced in biomass it is plausible water clarity would decrease in response (Madsen et al., 2001; Marinho et al., 2010; Zhu et al., 2015). Total annual phytoplankton biomass increased during the first two years of the manipulation period, while offshore and pelagic total zooplankton biomass decreased. However, the pre-experimental monitoring years for these two populations were variable, making it difficult to say definitively if the changes in biomass observed were due to macrophyte cutting.

Biomass of yellow perch >100 mm and biomass and abundance of northern pike also decreased during macrophyte cutting. While I expected biomass and abundance of northern pike to decline, I also expected abundance and biomass of larger yellow perch to follow in suit, which was not observed. This could be due to the increase in smaller sized yellow perch after macrophyte cutting began, which was displayed in the size-frequency distributions. While this would not be expected since macrophytes are important to yellow perch as nursery habitat, relative macrophyte biomass at 0.5 m actually increased during the macrophyte cutting period, which may have allowed for survival of juvenile yellow perch. Further, while biomass of yellow perch increased gradually over the cutting period, it declined in 1999 before increasing in the following years. This gradual increase over the manipulation period may be a result of delayed impacts on the yellow perch populations following manipulation, which has previously been observed at the Experimental Lakes Area (M. Rennie, pers. comm.). Growth of northern pike increased, however, this was likely due to increased resource availability and not density dependence as I predicted. In 2000, northern pike displayed a switch to pelagic food sources and in 2002, as well as a shift towards lower trophic levels, which is supported by the explosion of population in yellow perch <100 mm seen in the length-frequency distributions. As macrophytes are primary producers in the littoral zone and provide structure, food and habitat to numerous organisms (Nõges et al., 2009; O’Brien et al., 2014; Tamire & Mengistou, 2014), the results of this work demonstrates the negative impacts cutting of vegetation can have on northern pike abundance and biomass in particular.

I observed a number of concurrent changes in that appear to have culminated in the year 2000 that, together, may aid in understanding further the outcome of this experiment at the whole-ecosystem scale. In 2000, total relative macrophyte biomass was at its lowest, as was light penetration. Thiemer et al. (2021) suggested that growth rates of macrophytes can increase following macrophyte removal, which was reported in several species like *Sparganium erectum* (L), *Myriophyllum spicatum* (L), and *Lagarosiphon* major. This supports our result of increased relative biomass during cutting (driven primarily by increased biomass in uncut regions of the lake). Also in the year 2000, the abundance of large yellow perch and both abundance and biomass of northern pike increased. Both yellow perch and northern pike utilize macrophytes for survival. Yellow perch use macrophytes in the presence of predators for refuge (Jacobsen & Perrow, 1998), while northern pike use macrophytes extensively for habitat, reproduction, and foraging for food (Casselman & Lewis, 1996; Kobler et al., 2008). While the increase in abundance observed following cutting for both species does not agree with the decrease observed in relative macrophyte biomass given their reliance on macrophytes for survival, it may help to explain results observed for northern pike diet and trophic levels. In 2000, a shift to feeding on pelagic sources was observed for northern pike based on the $\delta^{13}C$ values, and a shift to lower trophic levels was observed based on $\delta^{15}N$ values. This could be due to northern pike switching from feeding on larger, benthivorous prey fish to smaller, more abundant zooplanktivorous prey (as maximum size of yellow perch decreased). Yellow perch feed on zooplankton when they are smaller sizes and tend to migrate between the littoral zone and the pelagic zone to feed (Thorpe 1977; Paszkowski

& Tonn, 1994; Wang & Eckmann, 1994), and if northern pike utilized smaller yellow perch as a diet source, this would explain the changes in both trophic level and diet.

While we saw no clear changes in phytoplankton and zooplankton community composition that could be clearly attributed to macrophyte cutting, total biomass did change. When phytoplankton biomass increased at the beginning of cutting, zooplankton subsequently decreased. This would not be expected given that zooplankton feed on phytoplankton, however, it is possible that zooplankton were disturbed in that zooplankton species living amongst the macrophytes were displaced and easier to feed on for fish when macrophyte harvesting occurred, causing a decrease in biomass. Phytoplankton rely on sunlight and nutrients to thrive (Baker & Newman, 2014), so an increase in nutrients in the water column could be what was driving this shift from macrophyte dominance to phytoplankton dominance, which was observed in total phosphorus at the beginning of cutting in Lake 191. Scheffer et al. (1993) showed that in more turbid water with higher nutrients, phytoplankton were able to colonize and thrive. This could be what was happening in Lake 191 at the start of macrophyte cutting. In 1997, we know that zooplankton biomass decreased. Since zooplankton feed on phytoplankton, a decrease in zooplankton biomass (and therefore zooplankton grazing rates) could allow phytoplankton biomass to increase. Yellow perch use zooplankton as a primary food source at smaller sizes, incorporating macroinvertebrates once they reach a larger size. As such, this decline in zooplankton biomass in 1997 may be driven by the increase in smaller sized yellow perch during the first year of cutting, which could be further driving the increase in phytoplankton biomass at the same time. Once zooplankton biomass declined, it is possible that smaller yellow perch were forced alter their feeding habitats, feeding in the littoral zone instead of the pelagic zone, relieving pressure on the zooplankton communities and allowing biomass to increase in 1998. The decline in phytoplankton biomass during this year could then be due to increased grazing by the high biomass of zooplankton in 1998. After 1998, it appears the populations of phytoplankton, zooplankton, and yellow perch found some sort of equilibrium where all three were able to stabilize. Subsequently, the increase in large yellow perch abundance following cutting could tie into the increase in zooplankton biomass observed at the same time as larger perch rely more on benthivores than zooplankton.

Some of the results of this study were unexpected. I expected change in both zooplankton and phytoplankton community composition as a consequence of reduced macrophyte cover; however, the correspondence analyses did not show much of a change over the three time periods. It is possible that by separating the data into different groupings, (versus over experimental periods) like we did with the fish communities, we may be able to different results. However, one limitation in doing this is whether there is sufficient data. For pre-experimental monitoring years (1994 and 1995) and 1999, sampling was not done as frequently as in 1996 and 1998, and 2000-2003. Along with this, data exploration of the correspondence analysis showed grouping based on season caused variation in the data, so summer sampling dates were chosen to eliminate this variation. Both of these aspects of the analysis made it difficult to separate zooplankton and phytoplankton groupings any other way, which is the reason we stuck with summer sampling dates for the lower trophic levels. For fish, there was no pre-experimental monitoring years for yellow perch fin samples for isotopes or age determinations or for seine netting data. Additionally, pumpkinseed had no fins available for age data or stable isotopes until 1997, as well as no corresponding reference system with which to compare to, which is why they were not included in the stable isotope analysis. If there was more consistency in sampling for the years mentioned above, this may have produced more consistent results.

One group that was not sampled at all were macroinvertebrates, which I propose is a key piece missing from my analysis of the lower trophic levels. Macroinvertebrates are an extremely important part of the ecosystem. Given their prevalence in macrophyte dominated areas for refuge and habitat (Cyr & Downing 1988a; Cyr & Downing 1988b; Jeppesen et al. 1997; Schramm et al., 1987), this group would be important look to in regards to macrophyte cutting. It is possible that, while we did not see strong changes in the smaller invertebrate community, assessing the impacts on macroinvertebrates may have given stronger insight into what was happening to the lower trophic levels. Misteli et al., (2023) found that macroinvertebrates associated with macrophytes decreased after macrophyte removal, which may be directly related to the loss of substrates as a consequence of removal of macrophytes. Although plant matter was not removed from Lake 191, habitat of macrophyte-associated macroinvertebrates was still disturbed, which could have led to increased predation due to loss of habitat. This would explain yellow perch abundance remaining high, as prey fish, like yellow perch, rely on macroinvertebrates along with zooplankton as a food source, so the increased accessibility of macroinvertebrates could have enabled yellow perch survival (Thorpe 1977; Paszkowski & Tonn, 1994).

Given the negative impacts on the ecosystem in Lake 191, it is apparent that 50% of macrophyte cutting harmed the fish communities, as reflected by northern pike decline in abundance and biomass and yellow perch decreased growth. It has been suggested that limited macrophyte cutting causes less disturbance (Trebitz & Nibbelink, 1996), suggesting that limited but targeted macrophyte cutting can be a technique that is acceptable to make aquatic activities for humans more enjoyable (ie, cottages, swimming, boating, fishing, etc) while reducing impacts on native ecosystems. Some studies propose that around 50% macrophyte cutting is the "sweet spot", allowing for potentially positive impacts on communities (Choi et al., 2014; Olson et al., 1998; Trebitz & Nibbelink, 1996). From the results of the study on Lake 191, water clarity decreased, but only after harvest manipulations were stopped, which could be observed as a positive impact in regards to cottagers looking to partake in aquatic activities without altering local water quality, if harvest could be effectively coordinated among all property owners to keep overall levels of cutting at or below 50%. Further, macrophyte cutting in Lake 191 did increase biomass and abundance of fish post-manipulation, so it is possible that alternating between periods of cutting and allowing for recovery in between could benefit the fish community, while keeping macrophyte biomass low. Perhaps 50% of macrophytes being cut is too much to see positive impacts on the fish communities. Keeping cutting to less than 50% may then mitigate the negative impacts on northern pike abundance and biomass, and yellow perch biomass.

The results found in my thesis are still very prevalent today as macrophyte cutting is still commonly used to improve quality of human activities. There are still guidelines being released regarding macrophyte cutting in areas across Ontario, for example, in 2019 an advisory report was released regarding aquatic macrophyte removal on spotted gar in Burlington, Ontario (Canadian Science Advisory Secretariat Science Response, 2020). In this report, it was suggested that based on available evidence, and since spotted gar rely heavily on macrophytes, macrophyte removal should not be pursued in regions where this species is present as it is unlikely to benefit the population and instead will likely jeopardize the survival and recovery of spotted gar. This is similar to the results seen for northern pike in Lake 191 in that northern pike rely heavily on macrophytes for various aspects of their lives, and we observed a decline in abundance and biomass during macrophyte cutting. Northern pike is a popular sport fish, so it is understandable that knowing the impacts of macrophyte cutting on this species is pertinent to the health of northern pike populations. I propose that future research focuses on finding the ‘right’ percentage of cutting that is acceptable and may possibly benefit the fish population. This could be done using the results from models produced by Trebitz and Nibbelink (1996), from which it would be possible to see if predicted “sweet spots”, or cutting levels, result in the predicted outcomes. Applying the same methods to both small and large lakes may help in understanding if different approaches need to be used depending on the lake size.

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Appendix

Table A1. Dates that differed between chemistry variables (total phosphorus ($\mu g \cdot L^{-1}$) and chlorophyll a ($\mu g \cdot L^{-1}$)) and light extinction coefficients. These dates were kept as they were less than 7 days apart.

	Chemistry variables	Light extinction coefficients
Date (DD/MM/YYYY)	19/07/1994	18/07/1994
	17/07/2000	18/07/2000
	09/08/2000	08/08/2000
	16/09/2002	17/09/2002

Table A2. Dates that differed between chemistry variables (total phosphorus ($\mu g \cdot L^{-1}$) and chlorophyll a ($\mu g \cdot L^{-1}$)) and light extinction coefficients, and zooplankton correspondence analysis row scores. These dates were kept as they were less than 7 days apart.

	Chemistry variables & light extinction coefficients	Zooplankton row scores
Date (DD/MM/YYYY)	17/07/1995	24/07/1995
	14/08/1995	19/08/1995
	11/08/1997	12/08/1997

Table A3. Seasonal fin nicks for northern pike in Lake 191 and 239.

Lake	*Season*	*Fin nicks*									
		1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
191	SPR	D1/D14	D6	A12	A15	A17	-	-	-	-	-
	SUM	-	-	A13	-	-	-	-	-	-	-
	FALL	D3	D8	A14	A16	A18	A19	A110	A111	D13	D14
239	SPR	D29	D211	D35	-	D37	-	-	-	D45	-
	FALL	D210	D34	D36	-	D38	D39	D310	D311	D46	D47

Table A4. Season fin nicks for yellow perch in Lake 191.

Lake	Season	Fin nicks									
		1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
191	SPR	2D1/2D14	2D3/D6	-	A15	A17	-	-	-	-	-
	SUM	D14	-	-	-	-	-	-	-	-	-
	FALL	2D2	D3	A14	A16	A18	A19	D1	D2	D3	D4

Table A5. Annual percent of fall fish samples used for stable isotope analysis for northern pike and yellow perch in Lake 191 and 239.

Lake	Species	Percent fall samples											
		1973	1983	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
191	Perch	0	-	-	-	100	100	100	100	100	100	0	100
	Pike	-	-	100	100	100	100	100	100	100	100	100	100
239	Perch	0	100	-	-	-	-	-	100	100	100	100	100
	Pike	-	-	66.67	66.67	50	-	0	100	100	100	83.33	100

Table A6. Annual mean fork length (mm) for northern pike and yellow perch in Lake 191 and 239.

Lake	*Species*	*Average fork length (mm)*											
		1973	1983	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
191	Perch	273.67	-	-	-	279	256.33	217.17	240.5	195.83	219.17	171.67	234.17
	Pike	-	-	436.5	330.5	407.17	406	368	381.17	420.33	411	354.67	356.67
239	Perch	175.67	135.67	-	-	-	-	-	152	117.83	158.67	148.67	128
	Pike	-	-	577.5	457.17	510.5	-	657.17	580.33	600.2	509.33	630.83	606.33

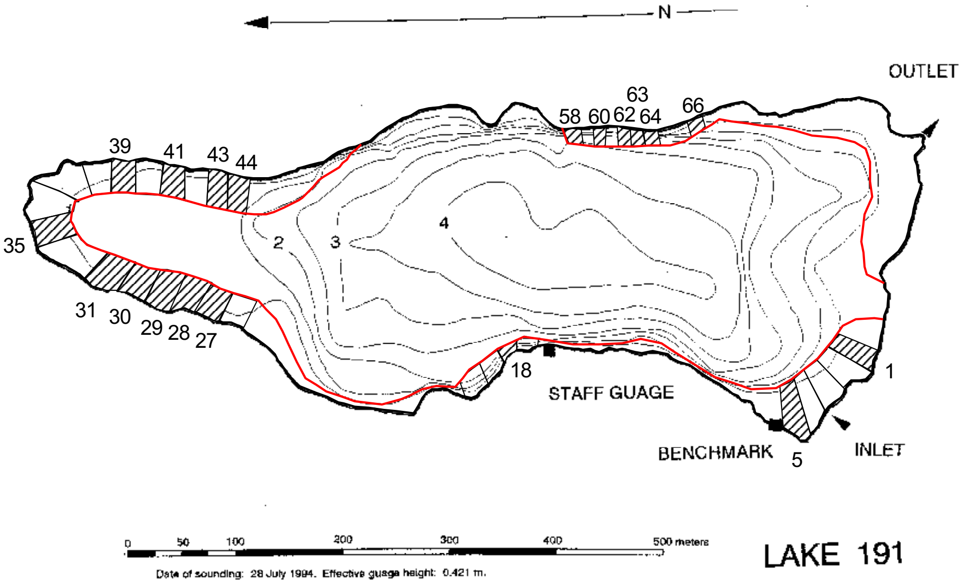

Figure A1. Map of Lake 191 showing the sections of macrophyte cutting. The littoral zone of the lake is outlined in red and depicts the area of the lake where macrophyte cover is present. Hatched regions indicate regions of macrophyte removal and open regions indicate areas that were uncut.

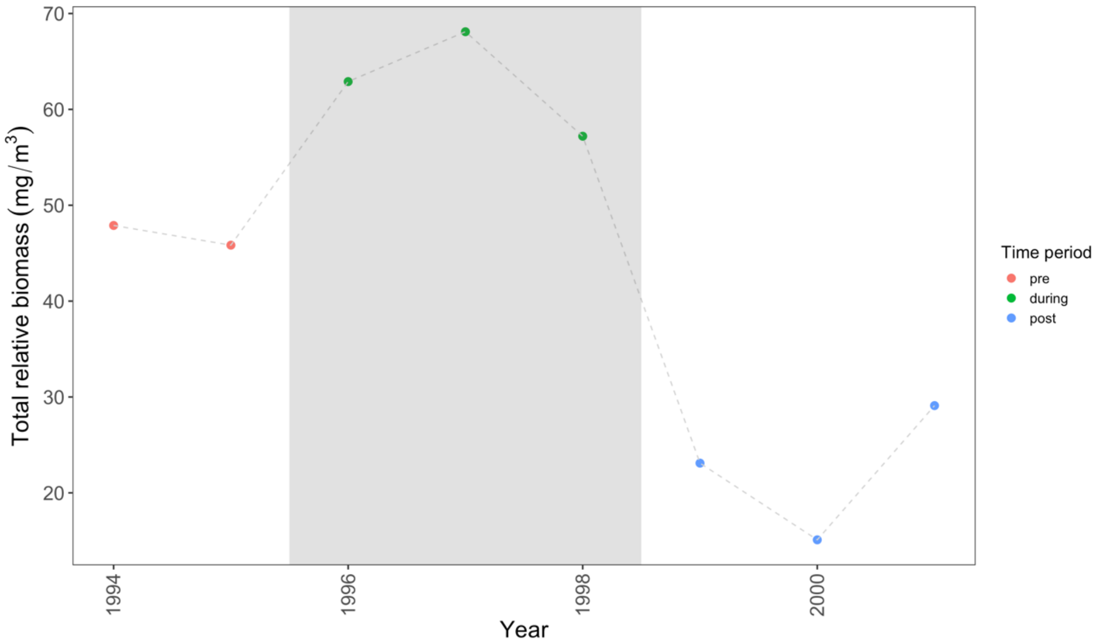

Figure A2. Relative macrophyte biomass, calculated from percent cover and biomass of cut and uncut areas, for Lake 191 over the duration of the experiment. Time periods are colour-coded with pre-experimental monitoring in blue, macrophyte removal period in green, and post-experimental monitoring in pink. The macrophyte removal period has been shown using a grey window.

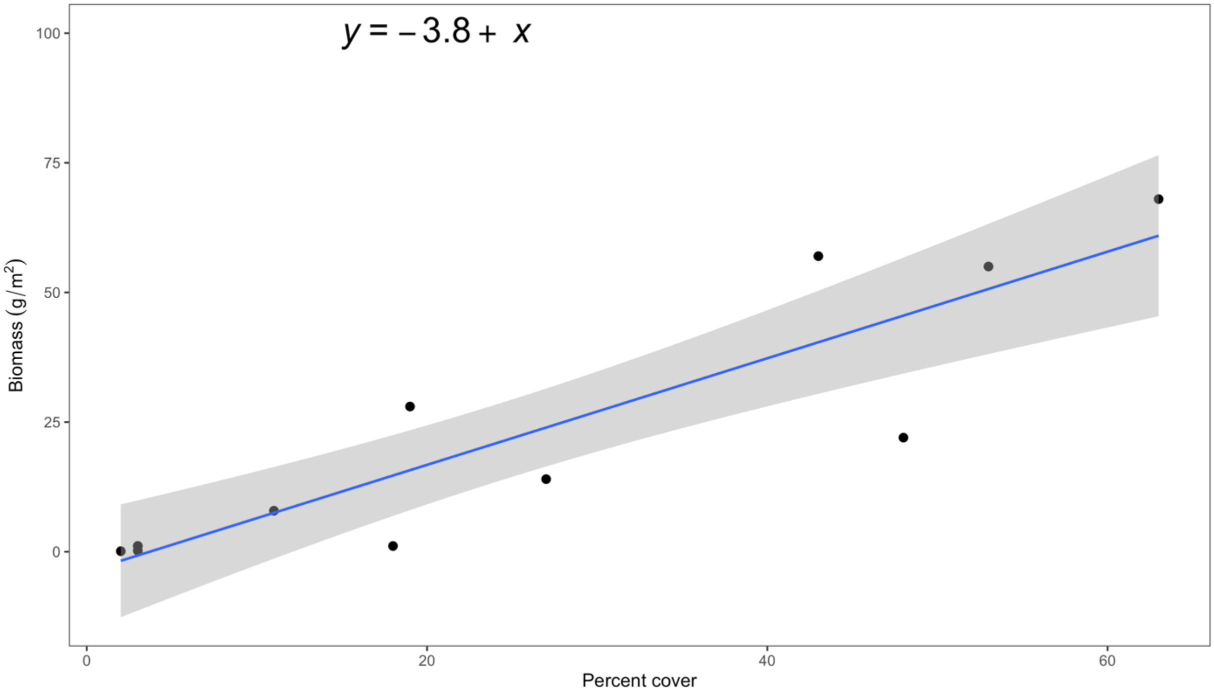

Figure A3. Relationship between percent cover and biomass of macrophytes in Lake 191. Line of best fit is plotted in a dotted line and the equation of this line is in the top left corner (y = – 3.8047 + x).

Note regarding Figure A2 and A3: Total relative macrophyte biomass at 0.5m (i.e., biomass in the region of macrophyte cover prior to cutting, as the sum of cut and un-cut regions) was calculated using the estimated average percent cover and biomass estimates for each region (g/m^2; Figure A2). For 1994 and 1995, no biomass data were available. To estimate biomass of macrophytes for these years, a relationship between biomass (y) and percent cover (x) was determined using linear regression from existing data across annual estimates from both cut and uncut regions of the lake (Figure A3). From the resulting regression ($F_{1,10} = 50$, $p < 0.05$), percent cover for 1994 and 1995 was used to estimate macrophyte biomass for these years. To facilitate comparisons of the lake-wide macrophyte biomass across both cut and uncut areas of the lake across all years, relative biomass was estimated as the sum of cut and uncut areas in the lake for all years (assuming cut regions were equivalent to uncut regions of the lake in 1994 and 1995). While macrophyte biomass in previous reports (Huebert Unpublished 1995, 1996, 1997) was measured from 0 – 1m, for the purpose of this study 0.5 m was chosen as the measurement point as this is the area most likely inhabited by phytoplankton, zooplankton, and fish.

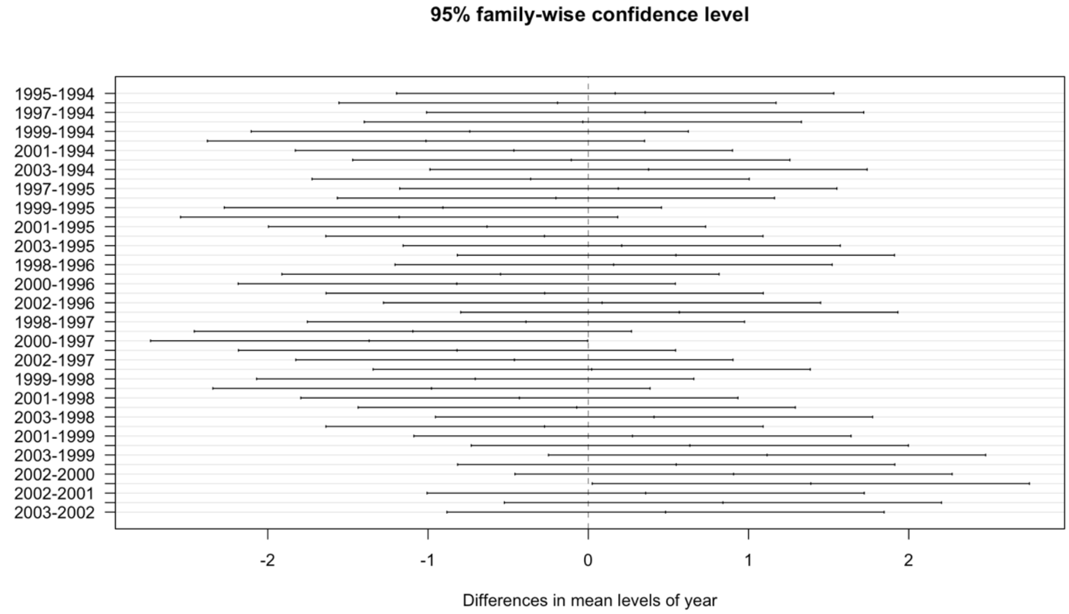

Figure A4. Tukey's pairwise comparison results for single-factor ANOVA on years for Lake 191 $\delta^{13}C$ isotopic signatures.

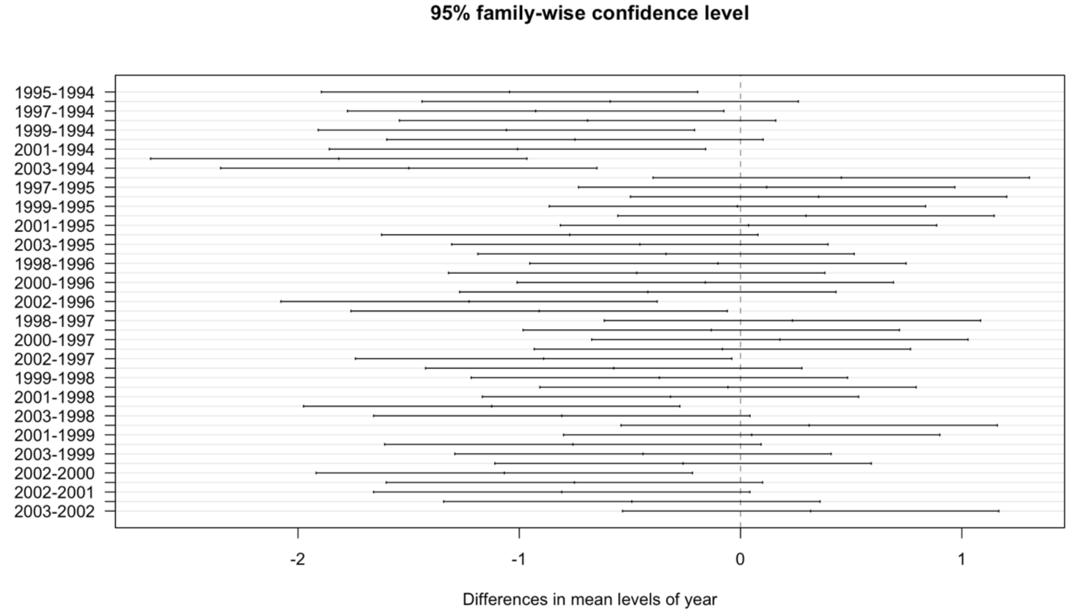

Figure A5. Tukey's pairwise comparison results for single-factor ANOVA on years for Lake 191 $\delta^{15}N$ isotopic signatures.

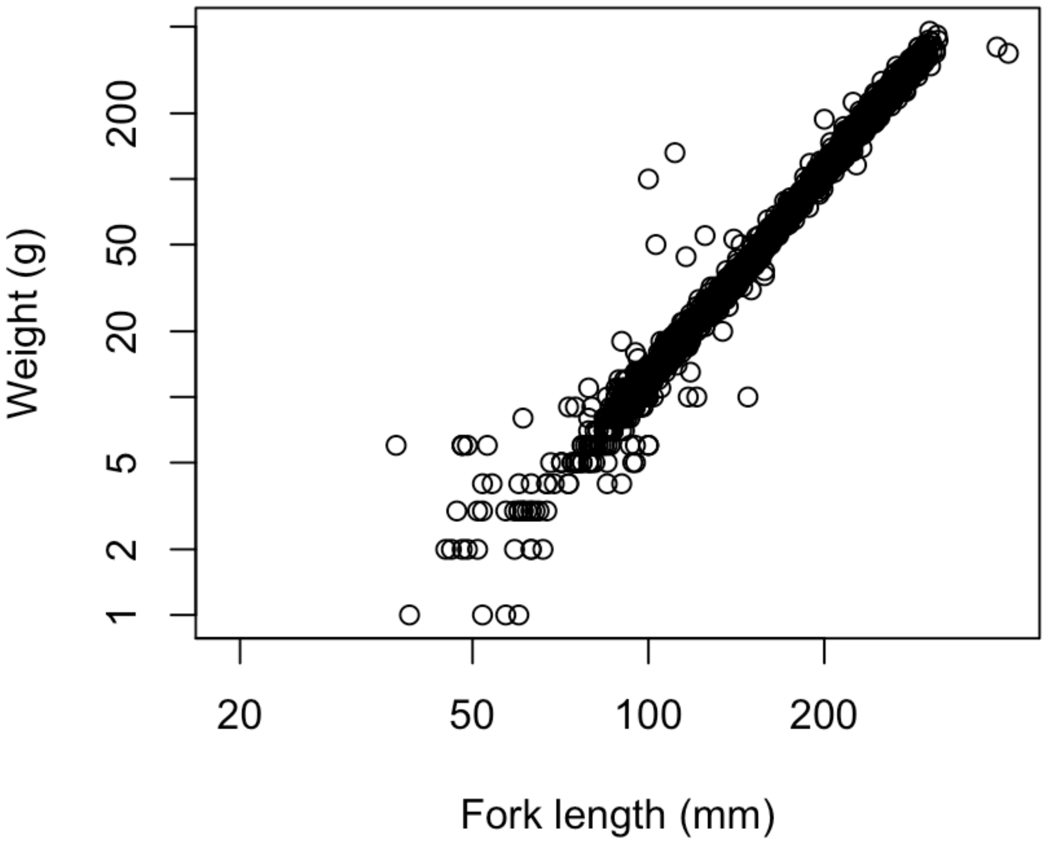

Figure A6. Weight-length regression used to calculate mean weights for yellow perch in Lake 191.

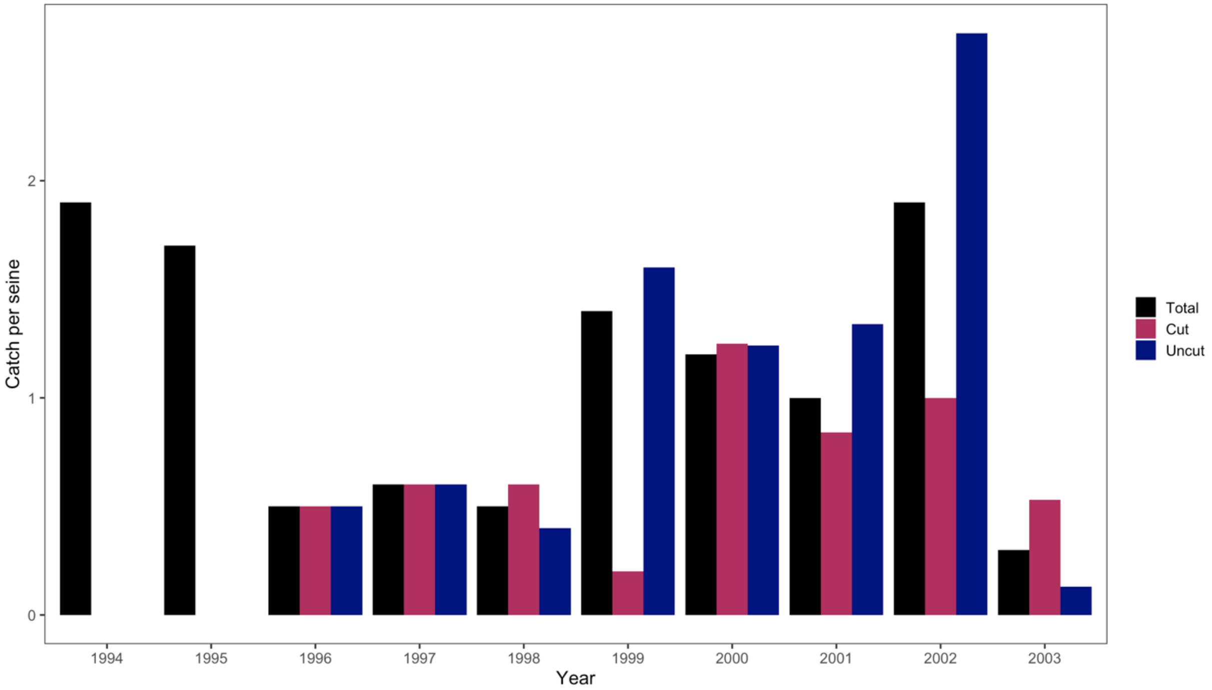

Figure A7. Catch per unit effort of northern pike young of year from 2000 – 2003 in cut (blue) and uncut (red) areas of Lake 191.