THOMPSON RIVERS UNIVERSITY

Assessing methods of suppressing invasive smallmouth bass (*Micropterus dolomieu*) and characterizing smallmouth bass diet overlap with walleye (*Sander vitreus*) in Clear Lake, Manitoba

by

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I respectfully acknowledge that Thompson Rivers University campuses are on the traditional lands of the Tk'emlúps te Secwépemc (Kamloops campus) and the T'exelc (Williams Lake campus) within Secwépemc'ulucw, the traditional and unceded territory of the Secwépemc. I would also like to acknowledge that Riding Mountain National Park, where the fieldwork for this study was completed, is located in Treaty 2 Territory and is considered part of the traditional and present homeland of the Anishinaabe peoples.

Thesis Supervisor: Associate Professor Brian Heise

ABSTRACT

Smallmouth bass (*Micropterus dolomieu*) is among North America's most popular game fish and has been introduced to freshwater systems across the continent through stocking programs, illegal introductions, and live bait release. Invasive smallmouth bass are aggressive top predators associated with changes in trophic energy flow and reduced abundance and diversity of native fish and invertebrates. In June 2021, non-native smallmouth bass were found in Clear Lake, Riding Mountain National Park. Clear Lake has important ecological, economic, social, and cultural values. Local Anishinaabe people believe its water is sacred and Keeseekoowenin Ojibway First Nation holds fish harvesting rights. The objectives of this research was to identify an effective strategy to suppress smallmouth bass and characterize the potential impacts of the species invasion in Clear Lake.

Spawning males exhibit parental care, which contributes to the species' ability to establish new populations. Nest-guarding males are aggressive and can be easier to capture; removal leaves eggs and fry vulnerable to predation. Angling males off their nests can induce nest failures but is labour-intensive and inefficient for suppressing bass invasions. Electrofishing is efficient in targeting juveniles but requires specialized equipment. Spearfishing is popular for targeting invasive fish in marine waters but has not been assessed for smallmouth bass control.

In this study, we assessed the efficacy of spearfishing for invasive smallmouth bass by (1) comparing catch rates and size structure to angling and boat electrofishing, (2) evaluating spearfishers' skills and progress, and (3) examining bycatch, costs, and safety considerations involved. Spearfishing and boat electrofishing were conducted in Clear Lake, Manitoba, while angling data was obtained from a separate study in Cultus Lake, British Columbia. This study found that catch rates for spearfishing in Clear Lake were more than triple those for angling in Cultus Lake. The length distribution among mature males was also different; spearfishers captured a wider variety of sizes compared to angling in Cultus Lake and boat electrofishing in Clear Lake. Spearfishers' skills improved as the study progressed, resulting in fewer missed shots and total shots taken. Our results suggest that spearfishing was effective for capturing mature males in Clear Lake; we recommend that regulators consider the method as part of a multi-pronged approach to managing invasive smallmouth bass.

We also examined the dietary overlap between invasive smallmouth bass and walleye (*Sander vitreus*) in Clear Lake, Manitoba by (1) quantifying their diets, (2) assessing feeding behaviour, and (3) comparing dietary overlap. The study revealed that bony fishes were the most frequently consumed prey for both species, followed by leeches for walleye and crayfish for smallmouth bass. Schoener's overlap index indicated there was no significant overlap ($\alpha = 0.477$), suggesting that the two species might not be in direct competition for food resources. Differences in diet were primarily driven by walleye larger than 300 mm eating more leeches and fewer fish. Identifying food web impacts, studying population dynamics of crayfish, and exploring the use of non-destructive diet analysis techniques would be beneficial for guiding management decisions and supporting the long-term health of the Clear Lake ecosystem.

Keywords: aquatic invasive species, smallmouth bass, *Micropterus dolomieu*, suppression, spearfishing, angling, fisheries management, infestations, walleye, *Sander vitreus*

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CHAPTER 1 INTRODUCTION

Aquatic invasive species are non-native aquatic organisms introduced to a new ecosystem such as a river, lake, wetland, or ocean and have negative impacts on the environment, economy, or human health (Pimentel et al. 2005, Sanderson et al. 2009, Simberloff et al. 2013). Aquatic invasive species alter aquatic ecosystems, threaten biodiversity, disrupt trophic structure, and reduce populations of native species (Havel et al. 2015, Britton et al. 2023). Invasive populations can establish rapidly due to the lack of natural predators in their new environment and the species' invasive characteristics (Thomaz et al. 2015). Introduction rates are increasing globally and if populations establish, impacts on freshwater biodiversity can be severe (Jackson and Mandrak 2002, Britton et al. 2023). The prevalence of invasions in Canada is increasing as suitable habitats expand northward due to climate change (Jackson and Mandrak 2002).

Once an invasive species has been introduced to a system, a rapid response is critical to limit the impacts on the ecosystem's biodiversity and to reduce management costs (Ahmed et al. 2022). The invasion curve (Figure 1.1), describes the establishment of invasive species in relation to stages of management; from pre-arrival (prevention) to long-term control (Fleming et al. 2017). If management strategies are delayed, costs increase while the probability of eradication is reduced (Ahmed et al. 2022). Prevention is the most cost-effective method for managing an invasive species. Investing in public outreach and communication about the impacts of invasive species raises awareness and increases economic returns compared to managing invasions. Eradication may be possible if a population is localized, but as invasive populations increase in size, management priorities shift to prevent and reduce further spread through containment. Lastly, long-term control is aimed at limiting the establishment of the population and reducing potential impacts on native species and ecosystem processes (Fleming et al. 2017).

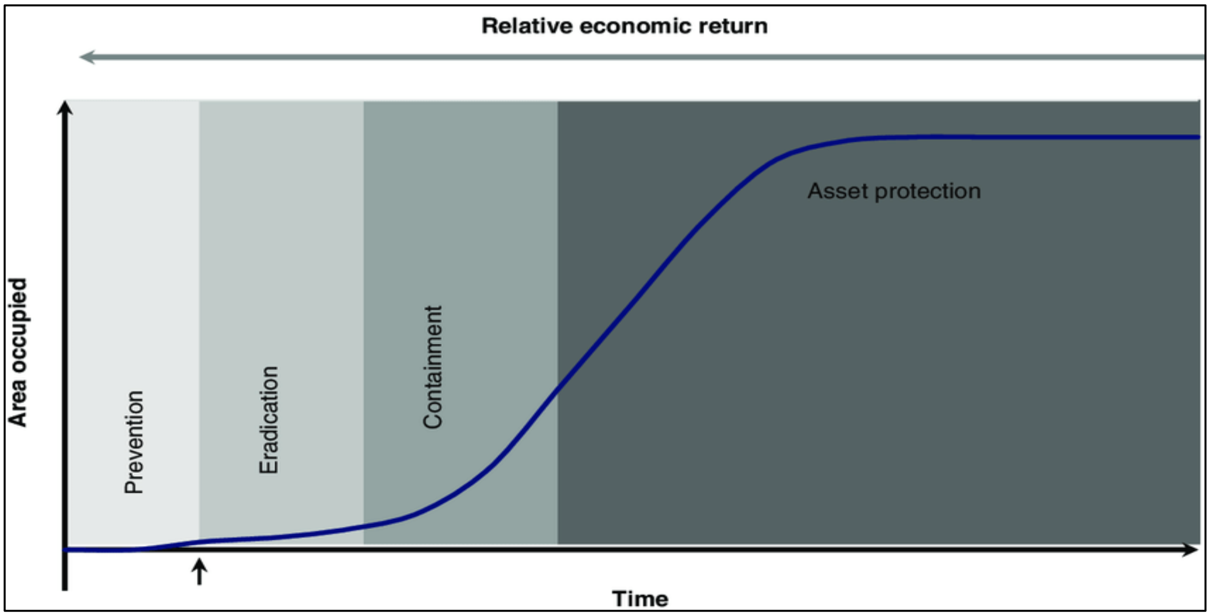

Figure 1.1. Generalised invasion curve showing the four phases of invasion, management actions, and returns on investment. The up arrow on the x-axis represents the point of invasion. From Fleming et al. (2017) adapted from the Department of Environment and Primary Industries Victoria (2017).

SMALLMOUTH BASS ECOLOGY

Smallmouth bass are a cool-warm water centrarchid, with a laterally compressed body and emarginated caudal fin (Brown et al. 2009). Adults typically measure less than 50 cm and weigh under 2 kg (Brown et al. 2009, Fisheries and Oceans Canada 2010). Their colouration varies with size, condition, and habitat. The back and top of the head range from brown to green, while the sides are lighter and marked by 8 to 15 vertical stripes (Brown et al. 2009). Their eyes are often red in colour, and they have two joined dorsal fins that may appear as one. Young-of-the-year (YOY) typically have a banded, tricolour tail (Brown et al. 2009). Largemouth bass (*Micropterus salmoides*) and smallmouth bass are both members of the sunfish family but smallmouth bass can be distinguished by the shorter upper jaw, which does not extend beyond the back edge of the eye (Tovey et al. 2008, Brown et al. 2009, Fisheries and Oceans Canada 2010) (Figure 1.2).

Figure 1.2. Smallmouth bass captured in Clear Lake, Manitoba (Parks Canada 2022).

Canadian Range and Introductions

Smallmouth bass' native distribution extends from the Great Lakes to the southern United States (Scott and Crossman 1973) (Figure 1.3). The species is among North America's most popular game fish and has been introduced to freshwater systems across the continent (Tovey et al. 2008) through stocking programs, illegal introductions, and live bait release (MacRae and Jackson 2001). In Canada, smallmouth bass can be found in southern Nova Scotia, southern and western New Brunswick, southern Quebec, throughout Ontario, and central Saskatchewan (Scott and Crossman 1973). Although not native to Manitoba, smallmouth bass populations have been introduced in numerous locations (Stewart and Watkinson 2004). Similarly, smallmouth bass have been introduced to multiple regions in British Columbia (Tovey et al. 2008), causing significant concern due to their impacts on salmon populations (Fisheries and Oceans Canada 2010). Several studies have documented smallmouth bass predation on juvenile salmon, particularly during smolt outmigration when habitats overlap (Tabor et al. 2007, Emingway et al. 2019).

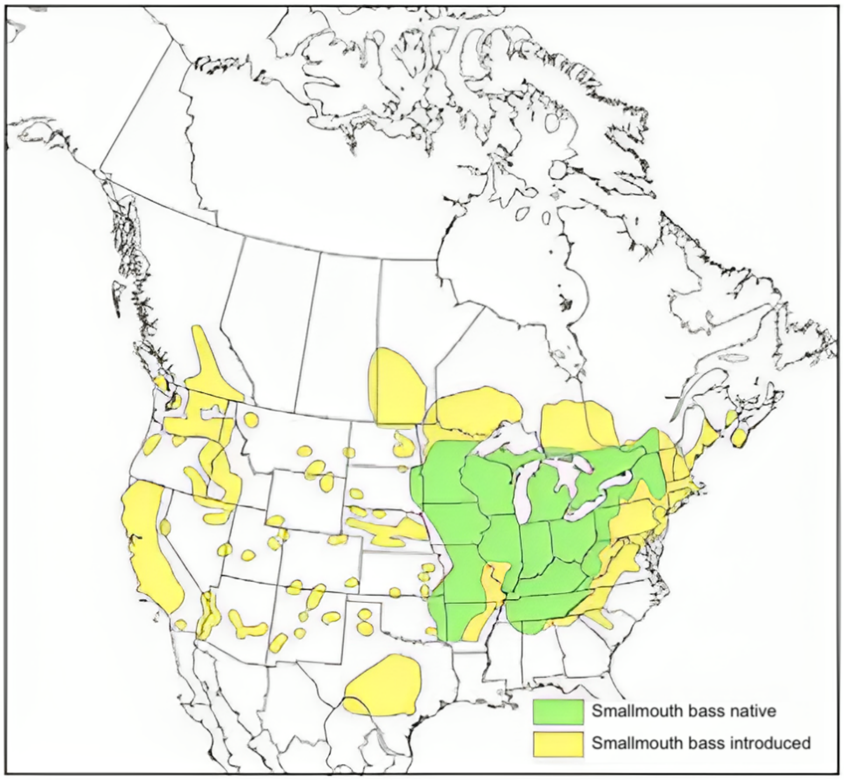

Figure 1.3. Native and non-native distribution of smallmouth bass in North America, from Tovey et al. (2008).

Feeding and Diet Shifts

Smallmouth bass can feed on a wide range of species. Important diet items include invertebrates, juvenile fish, and amphibians (Sweka and Hartman 2003). During their larval stage smallmouth bass predominantly feed on zooplankton, including copepods and water fleas. After hatching, young fry (~6 mm in length) will emerge from their nest and feed on zooplankton while still being guarded by the male (Moyle 2002). Their diets gradually shift from zooplankton to aquatic insects as they grow. Once they reach a total length greater than 50 mm, crayfish and fish become important and these prey items dominate their diet once they reach a length of 100 – 150 mm (Moyle 2002).

Reproduction and Behaviour

One of the most studied aspects of smallmouth bass is its reproductive behaviour. Once introduced, populations grow rapidly as females can lay thousands of eggs at each spawning event (Brown et al. 2009). Age-at-maturity varies based on location and temperature (Dunlop et al. 2005), but females usually reach sexual maturity at six years of age, while males can reach maturity one year earlier (Brown et al. 2009). Spawning times vary annually and geographically. Smallmouth bass spawn later in northern latitudes than they do in southern environments (Scott and Crossman 1973). Bass move to shallower, warmer waters in the spring for spawning and typically remain at depths ranging from 1.5 – 4 m (Suski and Ridgway 2009). The onset of spawning begins when water temperatures reach 15°C (Kaemingk et al. 2011) and continues through early summer until water warms to 20°C (Brown et al. 2009). In Ontario lakes, Scott and Crossman (1973) have documented nest-building when water temperatures reached 12.5°C, and spawning when the water warms to 16°C. The preferred habitat for nest-building and spawning is along shorelines on substrate consisting of gravel or rock (Kerr and Grant 2000). Preferred depth for spawning is between 0.6 – 1.8 m and nests are typically located near cover such as large rocks or fallen trees (Moyle 2002).

During the spawning period, males tend to excavate small, saucer-shaped nests with substrates such as sand, gravel, and pebbles in the centre (Scott and Crossman 1973, Cooke et al. 2002, Fisheries and Oceans Canada 2010). Mating occurs when males have attracted females to lay their eggs (Scott and Crossman 1973). Females can lay ~2,000 eggs at each spawning event, with some females spawning in the nest of one male while others may spawn in multiple nests (Scott and Crossman 1973, Moyle 2002). The duration of spawning periods ranges from 6 to 60 days (Scott and Crossman 1973). Females can produce 2,000 to 21,000 eggs in a spawning season (Moyle 2002), with an average between 5,000 and 14,000 eggs (Scott and Crossman 1973). Males are responsible for parental care (Cooke et al. 2002). To prevent predation on eggs and fry, smallmouth bass males will aggressively guard their nests throughout the duration of the spawning period (Scott and Crossman 1973, Cooke et al. 2002). A successful nest may produce upwards of 2,000 fry (Scott and Crossman 1973) but if nest-guarding males are removed, eggs and fry become vulnerable to predation (Ridgway and Friesen 1992, Lewin et al. 2006).

ECOLOGICAL IMPACTS AND INVASIONS

Impacts on Native Species

Smallmouth bass have several characteristics that make them successful invaders: their small size at the onset of piscivory, use of cover, low dietary and spatial overlap with other predators, high fecundity, and parental care (Weidel et al. 2000). Smallmouth bass are considered top predators that can impact native fish by reducing population sizes, changing behaviour patterns, and competing for habitat and food resources. Studies have shown that smallmouth bass introductions in North America have led to declines and local extirpations of small-bodied fish (MacRae and Jackson 2001). Introductions in Ontario lakes have reduced abundance, altered habitat use, and locally extirpated many small-bodied species such as brook stickleback (*Culaea inconstans*), fathead minnow (*Pimephales promelas*), and pearl dace (*Margariscus margarita*) (MacRae and Jackson 2001). Smallmouth bass introductions may also reduce crayfish abundance (Mather and Stein 1993), which could indirectly alter habitat complexity and cause changes in the benthic invertebrate community (Kerr and Grant 2000).

Suppression and Control Strategies

Many unsuccessful attempts have been made to control smallmouth bass invasions (Loppnow et al. 2013, Breton et al. 2014). Previous research indicates that the most effective strategies for controlling invasive freshwater fish populations focus on removing adults and reducing reproductive success (Rytwinski et al. 2019, Sorensen 2021). Spawning male smallmouth bass exhibit parental care and aggressive, nest-guarding males can be easier to capture (Boucher 2006). In the eastern basin of Lake Ontario, which is within the native range of smallmouth bass, Tufts et al. (2019) demonstrated that once a guarding male was removed, eggs and fry became vulnerable to predation. Catch-and-keep angling can induce nest failure when males are caught but it is labour-intensive and inefficient for suppressing smallmouth bass invasions (Loppnow et al. 2013). Electrofishing is efficient in capturing juveniles due to their habitat preferences and vulnerability to electric shock (Loppnow et al. 2013); however, the method requires specialized equipment, which can be prohibitively expensive. Gillnetting is generally ineffective for capturing smallmouth bass and is considered controversial for invasion management due to the technique being non-selective and lethal (Loppnow et al. 2013).

Spearfishing is popular for targeting invasive fish in marine environments (Harris et al. 2019), but has seldom been used in freshwater. Spearfishers in Texas successfully suppressed invasive armoured catfish (family Loricariidae) by nearly doubling the species' natural mortality rate (Blanton et al. 2020). In 2021, the Oregon Department of Fish and

Wildlife (ODFW) approved spearfishing for invasive smallmouth bass in the Coquille River but the efficacy was not assessed (Vonderhoe 2021). In a previous study assessing changes in bass physiology across repeated captures, spearfishing was used to collect adults at the final stage of brood development (Hanson and Cooke 2009). Other research focused on inducing nest failure for smallmouth bass control has also documented that adult removal using spearfishing was sometimes the only viable option (Loppnow 2017), but the technique's efficacy has never been directly assessed for this species.

STUDY SITES

In Chapter 2, data were collected from two different sites; spearfishing was conducted in Clear Lake, Manitoba (MB), while angling data were obtained from a separate study in Cultus Lake, British Columbia (BC) (Margetts unpublished data) (Appendix C). In Chapter 3, all data were collected from Clear Lake, MB.

Riding Mountain National Park (RMNP) is located in southwestern Manitoba (Figure 1.4), in Treaty 2 Territory and is considered part of the traditional and present homeland of the Anishinaabe peoples. Within the park, Clear Lake (50°46'N, 99°59'W) holds significant ecological, economic, social, and cultural value. Local Anishinaabe communities believe its water is sacred, and Keeseekoowenin Ojibway First Nation (KOFN) holds subsistence fish harvesting rights. Smallmouth bass observations in Clear Lake were first reported to park staff by anglers in August 2020. The presence was confirmed when an adult bass was turned in to officials on June 3, 2021. Parks Canada and KOFN decided to manage the population using electrofishing and 354 smallmouth bass were removed in 2021. In 2022, another electrofishing operation was conducted, along with this research project, aimed at developing a long-term bass management strategy for Clear Lake and characterizing potential impacts on native species.

Figure 1.4. Location of Manitoba within Canada (shown in red). Riding Mountain National Park is represented by the yellow star (MapGrid 2020).

Clear Lake has a surface area of approximately 29 km^2, a maximum depth of 34.2 m, and an average depth of 11.5 m (Glufka 1992). Clear Lake is oligotrophic and supports native fish species such as lake whitefish (*Coregonus clupeaformis*) and northern pike (*Esox lucius*), and has a high diversity of phytoplankton, zooplankton, benthic fauna, and aquatic vegetation (Glufka 1992). Following the smallmouth bass observation in August 2020, suitable spawning habitat was identified based on substrate characteristics and depth (Figure 1.5). Habitat mapping indicated which areas were suitable for spawning; however, as of 2022, most spawning bass were isolated to the northern side of the lake.

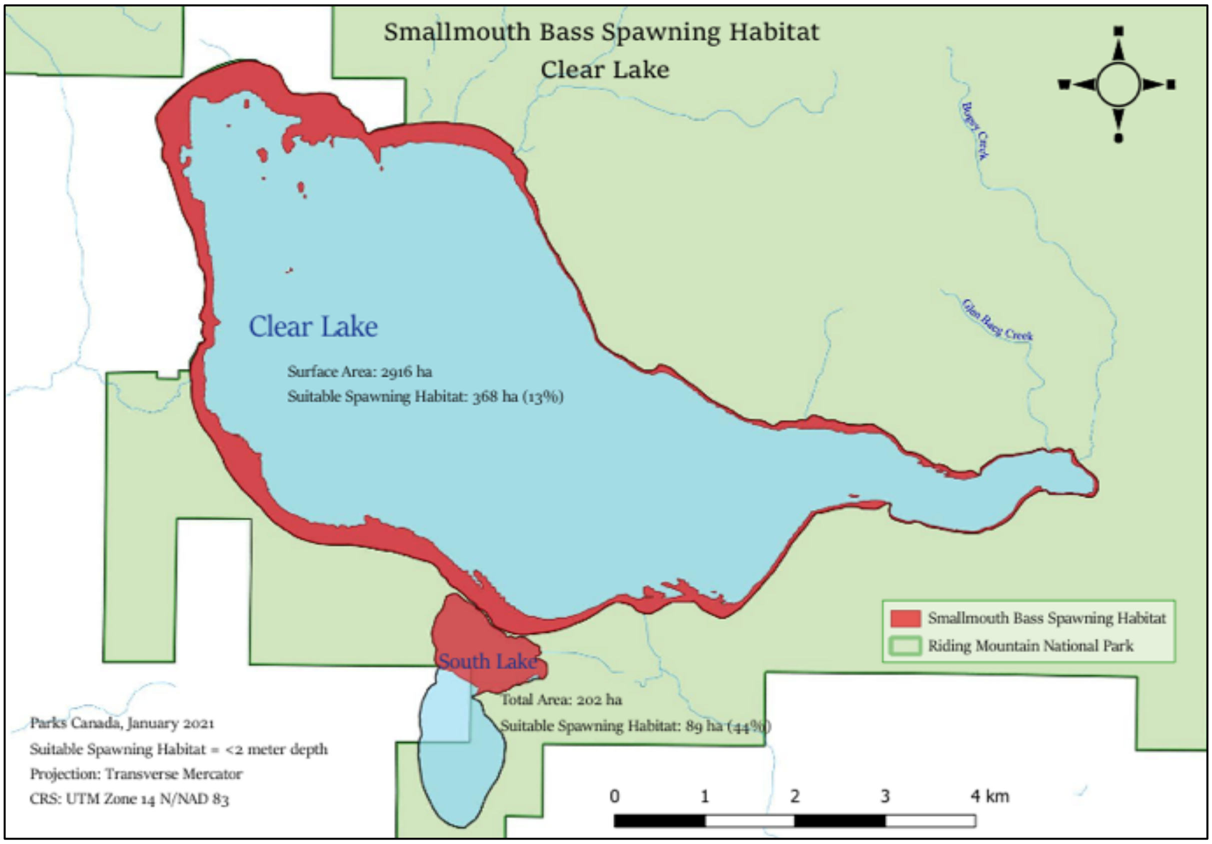

Figure 1.5. Suitable spawning habitat for smallmouth bass in Clear Lake, Manitoba (Parks Canada 2021).

Cultus Lake (49°03’00” N, 121°53’52” W) is located in southwestern British Columbia (Figure 1.6), on the ancestral territory of the Soowahlie (The’wá:lí) First Nation. Cultus Lake is a mesotrophic, monomictic lake (Shortreed 2007) with an area of 6.3 km^2 and a maximum depth of 42 m. Smallmouth bass were detected in Cultus Lake in 2017, the species' first confirmed establishment within British Columbia's lower mainland (Margetts 2022). From 2020 – 2021, Margetts (2022) conducted research on the invasive smallmouth bass population in Cultus Lake. Through a diet analysis and spatial distribution study, Margetts (2022) documented the species' impacts, identified spawning patterns, and established a framework for developing an effective suppression plan.

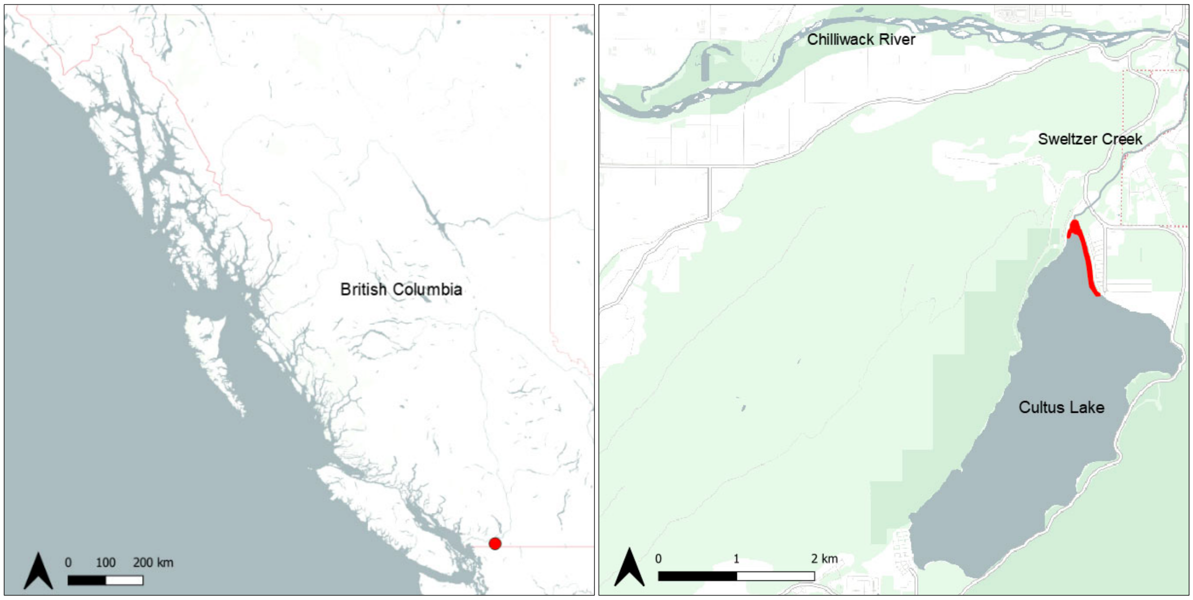

Figure 1.6. Location of Cultus Lake within British Columbia, Canada (red dot) (left). The smallmouth bass spawning area is shown in red with outflow into the Chilliwack River via Sweltzer Creek (right). From Margetts (2022).

THESIS OBJECTIVES

The objectives of this research was to identify an effective strategy to suppress smallmouth bass and characterize the potential impacts of the species invasion in Clear Lake. In Chapter 2, we assessed the efficacy of spearfishing for invasive smallmouth bass in Clear Lake by (1) comparing catch rates and size structure to angling in Cultus Lake and boat electrofishing in Clear Lake, (2) assessing captures by evaluating spearfishers' skills and progress, and (3) examining bycatch, costs, and safety considerations involved. In Chapter 3, we characterized the impact of invasive smallmouth bass on walleye in Clear Lake by (1) quantifying their diets using morphological identification, (2) assessing feeding behaviour and diet composition, and (3) comparing the degree of diet overlap using mean proportional abundances and Schoener's similarity index.

This project was co-developed in the spirit of Reconciliation with Thompson Rivers University, Parks Canada, Keeseekoowenin Ojibway First Nation, and the Coalition of First Nations with Interests in Riding Mountain National Park. This research was supported by Parks Canada's 2022-2023 Nature Legacy Applied Science Fund and Indigenous Leadership in Conservation Fund. A Research and Collection Permit was approved through Parks

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CHAPTER 2 ASSESSING THE EFFICACY OF SPEARFISHING AS A NOVEL METHOD OF SUPPRESSING INVASIVE SMALLMOUTH BASS (*MICROPTERUS DOLOMIEU*) IN CLEAR LAKE, RIDING MOUNTAIN NATIONAL PARK, MANITOBA

INTRODUCTION

Aquatic invasive species alter aquatic ecosystems, threaten biodiversity, disrupt trophic structure, and reduce populations of native species (Havel et al. 2015). Invasive populations can establish rapidly due to the lack of natural predators in their new environment and the species' invasive characteristics (Thomaz et al. 2015). The prevalence of invasions in Canada are increasing as suitable habitats expand northward due to climate change (Jackson and Mandrak 2002). Once an invasive species has been introduced to a system, a rapid response is critical to limit impacts on the ecosystem's biodiversity and to reduce management costs (Ahmed et al. 2022).

Smallmouth bass' (*Micropterus dolomieu*) native distribution extends from the Great Lakes to the southern United States (Scott and Crossman 1973). The species is among North America's most popular game fish and has been introduced to freshwater systems across the continent (Tovey et al. 2008) through stocking programs, illegal introductions, and live bait release (MacRae and Jackson 2001). In Canada, smallmouth bass can be found in southern Nova Scotia, southern and western New Brunswick, southern Quebec, throughout Ontario, and central Saskatchewan (Scott and Crossman 1973). Smallmouth bass have been introduced to multiple regions in British Columbia (Tovey et al. 2008), raising concerns about their impact on salmon populations (Fisheries and Oceans Canada 2010). Several studies have documented smallmouth bass predation on juvenile salmon, particularly when habitats overlap during smolt outmigration (Tabor et al. 2007, Emingway et al. 2019). In Manitoba, smallmouth bass populations have also been introduced in numerous locations (Stewart and Watkinson 2004). The current smallmouth bass distribution in Manitoba is considered to be at the northern limit of their range (Brown et al. 2009), extending from Lake Winnipeg and its tributaries to the east, Riding Mountain National Park (RMNP) to the west, and Rocky Lake, near The Pas, to the north (Stewart and Watkinson 2004).

Invasive smallmouth bass are aggressive top predators, associated with changes in trophic energy flow and reduced abundance and diversity of fish and invertebrates (MacRae and Jackson 2001, Brown et al. 2009, Wuellner et al. 2011). Smallmouth bass have several characteristics that make them successful invaders: their small size at the onset of piscivory, use of cover, low overlap with other predators, high fecundity, and parental care (Weidel et al. 2000). Adding to its adaptability, the species exhibits physiological tolerance to a wide range of temperatures (Cooke et al. 2003), opportunistic feeding habits (Weidel et al. 2000), and spiny rays, which act as a defence mechanism against predators (Tovey et al. 2008).

Many unsuccessful attempts have been made to control smallmouth bass invasions (Loppnow et al. 2013). Previous research indicates that the most effective strategies for controlling invasive freshwater fish populations focus on removing adults and reducing reproductive success (Rytwinski et al. 2019, Sorensen 2021). Spawning male smallmouth bass exhibit parental care and aggressive nest-guarding males can be easier to capture (Boucher 2006). Once a guarding male is removed, eggs and fry are vulnerable to predation (Tufts et al. 2019).

Catch-and-keep angling can induce nest failure when males are caught but it is labour-intensive and inefficient for suppressing smallmouth bass invasions (Loppnow et al. 2013). Angling can also become less effective over time if it drives selection for lure avoidance (Hessenauer et al. 2016). Philipp et al. (2015) found that the catchability of nesting males is highly dependent on fisheries-induced evolution, causing smallmouth bass to become less aggressive during parental care. As angling pressure increases, the selection against aggressive individuals in the population becomes more pronounced, leading to an evolutionary shift. In lakes with minimal angling, the vulnerability of nesting males remains higher, indicating that the process of fisheries-induced evolution is influenced by the intensity of fishing activity and its impact on bass behaviour (Philipp et al. 2015).

Electrofishing is efficient for capturing adult and juvenile smallmouth bass (Loppnow et al. 2013) but requires specialized equipment, which can be prohibitively expensive. While electrofishing is a common method in fisheries management, its effectiveness is limited in controlling invasive smallmouth bass (Loppnow et al. 2013) and can even lead to an increase in recruitment (Weidel et al. 2007, Hawkins et al. 2009). For instance, after the partial removal of smallmouth bass from an Adirondack lake in New York state, Weidel et al.

(2007) observed an increase in smallmouth bass abundance, particularly among juveniles. The removal of adult smallmouth bass likely accelerated recruitment (Ridgway et al. 2002) and increased offspring survival (Zipkin et al. 2008). Although electrofishing is often effective in shallow, isolated systems lacking complex habitat, the method is labour-intensive, non-selective, and requires repeated, long-term application (Loppnow et al. 2013).

Spearfishing is popular for targeting invasive fish in marine environments (Harris et al. 2019), but has seldom been used in freshwater. Spearfishers in Texas successfully suppressed invasive armoured catfish (family Loricariidae) by nearly doubling the species' natural mortality rate (Blanton et al. 2020). In 2021, the Oregon Department of Fish and Wildlife (ODFW) approved spearfishing for invasive smallmouth bass in the Coquille River but the efficacy was not assessed (Vonderhoe 2021). Spearfishing has been used to remove nest-guarding adult male bass in previous research (Hanson and Cooke 2009, Loppnow 2017), but the technique's efficacy has never been assessed for this species.

In this study, we assessed the efficacy of spearfishing for invasive smallmouth bass by (1) comparing catch rates and size structure to angling and boat electrofishing, (2) evaluating spearfishers' skills and progress, and (3) examining bycatch, costs, and safety considerations involved. While this study focused on targeting nest-guarding males, all life stages were compared to provide greater context on gear efficiency and selectivity for multiple life stages. The results of our study will provide guidance for fisheries managers who seek to control invasive bass using a multi-pronged approach.

METHODS

Study Sites

Data obtained for this study were collected from two different sites. Spearfishing was conducted in Clear Lake, Riding Mountain National Park (RMNP), Manitoba (MB), while angling data was obtained from a separate study in Cultus Lake, British Columbia (BC) (Margetts unpublished data) (Appendix C).

RMNP is located in southwestern Manitoba, in Treaty 2 Territory and is considered part of the traditional and present homeland of the Anishinaabe peoples. Within the park, Clear Lake (50°46'N, 99°59'W) holds significant ecological, economic, social, and cultural value. Local Anishinaabe communities believe its water is sacred, and Keeseekoowenin

Ojibway First Nation (KOFN) holds subsistence fish harvesting rights. In August 2020, anglers reported catching invasive smallmouth bass in Clear Lake. Sightings were later confirmed, and the first bass was captured on June 3, 2021 (Parks Canada 2023). This was of great concern because smallmouth bass are not native to Clear Lake and may outcompete native species for habitat and food resources (MacRae and Jackson 2001).

Clear Lake has a surface area of approximately 29 km^2, a maximum depth of 34.2 m, and an average depth of 11.5 m (Glufka 1992). Clear Lake is oligotrophic and supports native fish species such as lake whitefish (*Coregonus clupeaformis*) and northern pike (*Esox lucius*), and has a high diversity of phytoplankton, zooplankton, benthic fauna, and aquatic vegetation (Glufka 1992). Habitat mapping in Figure 2.1 indicated which areas were suitable for spawning; however, as of 2022, most spawning bass were located on the northern side of the lake.

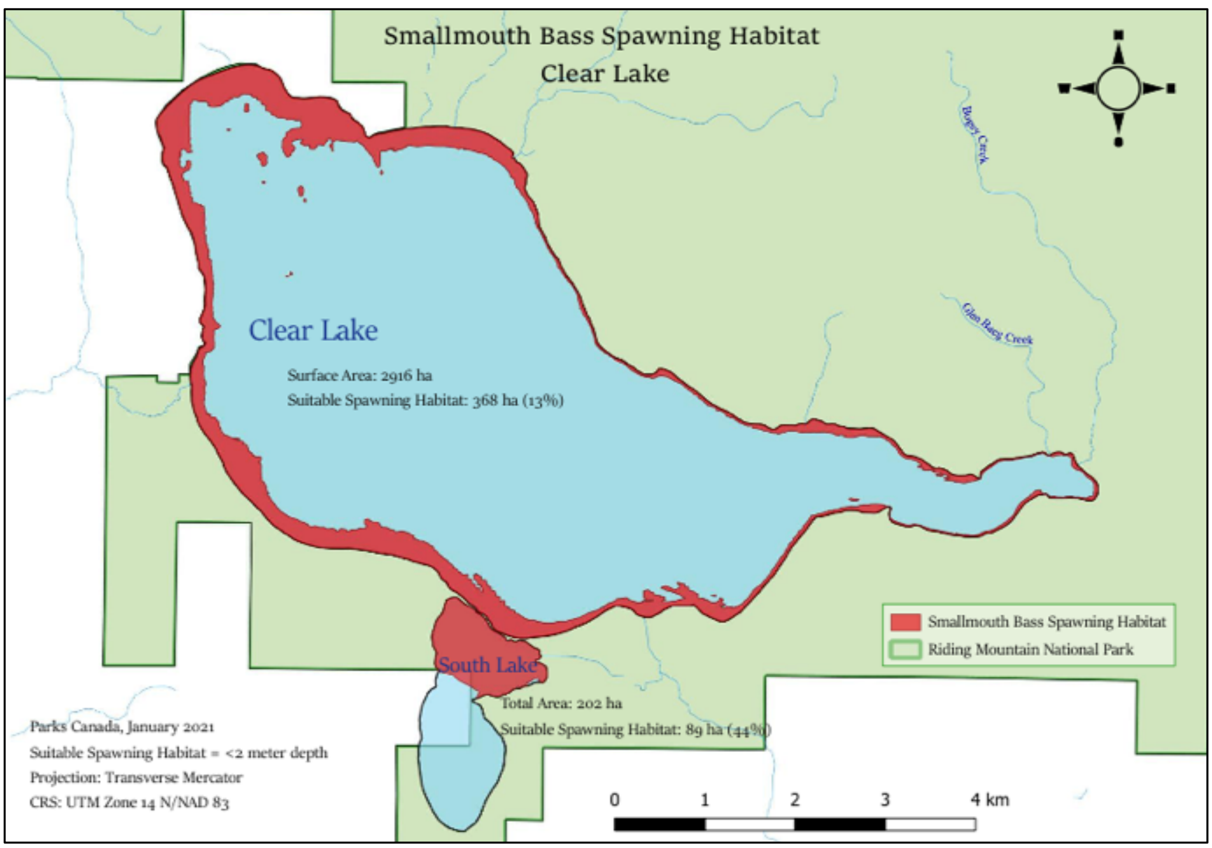

Figure 2.1. Suitable spawning habitat for smallmouth bass in Clear Lake, Manitoba (Parks Canada 2021).

Cultus Lake (49°03’00” N, 121°53’52” W) is located in southwestern British Columbia (Figure 2.2), on the ancestral territory of the Soowahlie (The’wá:lí) First Nation. Cultus Lake is a mesotrophic, monomictic lake (Shortreed 2007) with an area of 6.3 km^2 and a maximum depth of 42 m. Smallmouth bass were detected in Cultus Lake in 2017, the species' first confirmed establishment within British Columbia's lower mainland (Margetts 2022). From 2020 – 2021, Margetts (2022) conducted research on the invasive smallmouth bass population in Cultus Lake. Through a diet analysis and spatial distribution study, Margetts (2022) documented the species' impacts, identified spawning patterns, and established a framework for developing an effective suppression plan.

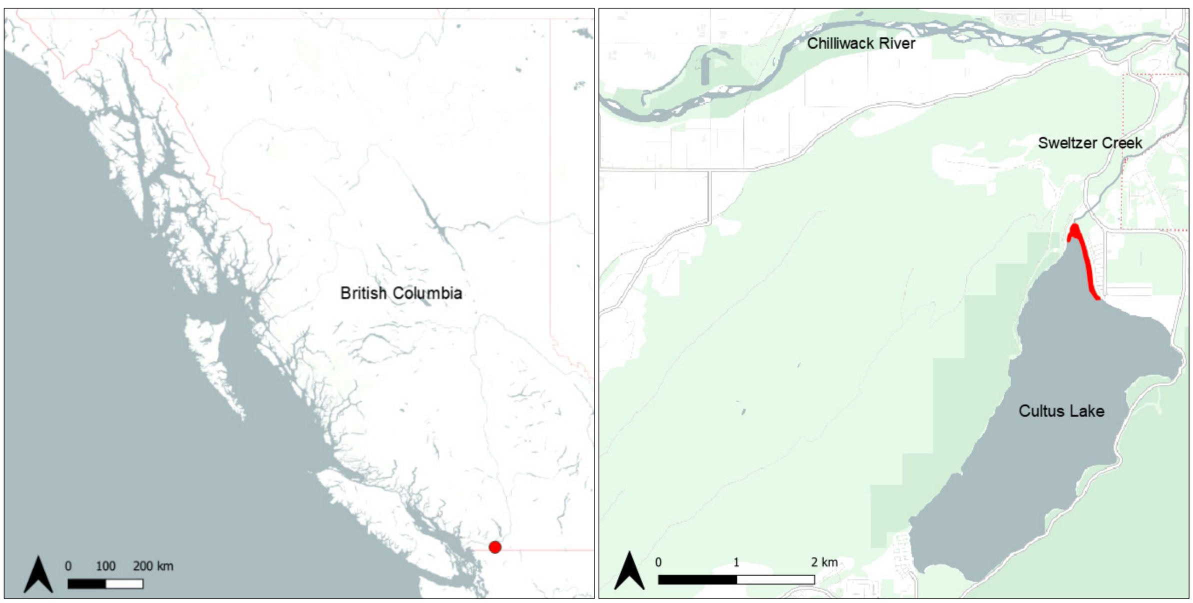

Figure 2.2. Location of Cultus Lake within British Columbia, Canada (red dot) (left). The smallmouth bass spawning area is shown in red with outflow into the Chilliwack River via Sweltzer Creek (right). From Margetts (2022).

Reconnaissance

Reconnaissance surveys in Clear Lake started in mid-June 2022 as the water reached temperatures of 12°C. Reconnaissance was focused on locating smallmouth bass nesting sites and efforts totalled 98 hours of combined snorkel, boat, and aerial drone surveys over the course of 18 non-consecutive days. Aerial drone surveys were the primary method used for identifying nesting sites. The drone operator confirmed the presence/absence of males before directing boats toward the nests.

In Cultus Lake, smallmouth bass spawning areas were identified through snorkel surveys conducted every 2 – 3 weeks from April – June, 2021 (Margetts 2022). Snorkelers swam a 400-m meandering transect and repeated this process over the course of three days. These surveys were used to visually identify and quantify nesting sites, and to document timing of nesting behaviour. Although additional exploratory snorkel surveys were conducted in similar habitats throughout the lake, nesting activities were exclusively observed and documented along the northeast shore of Cultus Lake (Margetts 2022).

Suppression

Spearfishing

From June 21 – 23, 2022, spearfishing training was completed by Parks Canada staff and a crew of community members from local First Nations. The three-day workshop was delivered by a certified Performance Freediving International (PFI) instructor from Bottom Dwellers Freediving Ltd. The training focused on safe snorkeling techniques, risk management, and spearfishing skills. The program totalled 24 hours of training on theory and practical skills in confined water, open water, and band-powered device handling. Given that catch rates may be influenced by skill, the ability of spearfishers was standardized by selecting four individuals who recently completed the spearfishing training program.

Spearfishing sessions were conducted from June 29 – July 28, 2022, over the course of 12 days, representing eight full days and four half-day sessions. As smallmouth nesting sites were located in Clear Lake, spearfishing was applied twice a week on different days (depending on weather) between 0600 – 1300 hours. All captured smallmouth bass were humanely handled and euthanized according to Parks Canada Research and Collection Permit (No. RMNP-2022-42359) and Thompson Rivers University Animal Use Protocol (No. 8452). After measurement and sample collection, edible portions were distributed among local First Nations communities.

Crews consisted of at least two spearfishers accompanied by support teams on a workboat and a safety patrol boat. To mitigate bias associated with crew ability, targeted nests and pairs of snorkelers were randomly assigned every dive session. Following protocols established by PFI's buddy system, one spearfisher would actively "hunt" the bass while the other acted as a safety watch and relayed information to the data collector. Spearfishers used pole spears (© JBL International; Abaco Composite – 6′ (183 cm) length, Barbed Paralyzer Tip – 12″ (30 cm) length, and Slip Tip Spectra – 14″ (35 cm) length).

Once an occupied nest was located, the workboat was anchored as close as possible without disturbing the fish. The effort was recorded when spearfishers had visual confirmation of the targeted bass and were actively "hunting." Attempts that resulted in failed captures were also recorded. A stopwatch was used to record effort, which included the sum of the spearfisher's time for capture, euthanizing the fish, and swimming back to the workboat. While every attempt was made to standardize the distance between captures and the workboat, environmental conditions (*e.g.*, wind shift) resulted in some variability. The distance between the workboat and the capture sites reduced as the study progressed. Overall, captures were an average of 46 m away from the workboat.

Angling

Angling was chosen as a control to which spearfishing could be compared, but the method was found to be labour-intensive and ineffective for capturing nest-guarding males in Clear Lake. Scientific angling in Clear Lake was attempted on six days from July 14 – July 29, 2022 during the spawning period. Due to the stage of the invasion (*i.e.*, limited number of nests), less time was allocated to angling than spearfishing. Additional details on the scientific angling protocol can be found in Appendix A, Table A 1.

Because angling was unsuccessful in Clear Lake, we used an auxiliary angling dataset obtained from targeted smallmouth bass removal in Cultus Lake, BC (Margetts unpublished data). See Margetts (2022) and Appendix C for details on study design and raw data, respectively. Expert anglers were contracted to fish at Cultus Lake from 0730 – 1300 hours from July 20 – September 10 in 2020, and from May 12 – September 11 in 2021 (Margetts 2022). Anglers targeted bass on the northeast shore using a mixture of crank baits and worms. Angling occurred from onboard a boat and most captures were near docks within the spawning area. The duration of angling efforts was determined by measuring the time elapsed between the first recorded cast and the successful landing of a fish onto the boat. Time expended on unsuccessful attempts, where fish were not landed, was not included. Thus, only efforts resulting in actual fish captures were recorded. Any additional time spent fishing beyond this period was not included in the calculation of angling effort. Cultus Lake anglers did not have a visual confirmation of bass before recording effort; however, they were knowledgeable of areas with higher bass density due to prior snorkel surveys.

Electrofishing

From August 8 – 11, 2022, boat electrofishing was conducted by Parks Canada staff and KOFN community members. Electrofishing occurred between 2200 – 0600 hours and crews consisted of a boat operator and three to four netters. Weighted transects (n = 14) were standardized along the shoreline in 100-m lengths. However, most efforts were focused on targeted spot control in pre-determined areas (n = 20). Targeted spot control involved removing as many bass as possible and therefore varied in length of time and area covered (see Appendix A, Table A 2 for details on boat electrofishing). All live bycatch was released, except for selectively retained walleye, which were kept for a feeding study.

Citizen Science

Submissions from members of the public (anglers) were collected throughout the summer. Recreational anglers in Clear Lake were encouraged to report and submit samples of smallmouth bass to Parks Canada.

Data Collection

For each fish collected (in both lakes), location, depth of capture, time spent (effort), and suppression method were recorded. The number and biomass of captured bass (during each attempt) were divided by the amount of time spent fishing, resulting in units of fish h^{-1} or kg h^{-1} (per fisher). Catch rates were indexed by CPUE and were calculated as

$$C/f \tag{1}$$

where C represents the number of fish caught and f is the unit of effort expended (Hubert and Fabrizio 2007). All smallmouth bass captured were euthanized and kept for analysis of age, diet, sex, and maturity. Fish maturity was estimated based on the developmental stage of the gonads as described in RISC (1997). All captures were categorized by life stage: mature males (total), mature males nesting, mature males non-nesting, mature females, and juveniles (including young-of-the-year). Because it was unknown whether mature males caught by electrofishing in Clear Lake or angling in Cultus Lake were actively guarding a nest, these fish were characterized only as mature males, without categorization by nesting status.

Aging structures including otoliths (*n* = 139) and dorsal spines (*n* = 5) were collected to estimate fish age in Clear Lake. Otoliths were the preferred aging structure (Maceina et al. 2007, Starks and Rodger 2020) and dorsal spines were only collected when otoliths were either damaged or not located. AAE Tech Services Inc. was contracted to determine the estimated age from the structures. In Cultus Lake, otoliths and scales were removed from smallmouth bass, and aging was done at the BC Provincial Aging Lab after the 2020 (*n* = 50) and 2021 (*n* = 26) field seasons (Margetts 2022). Scales were removed from below the lateral line, posterior to the operculum and collected as a secondary means of aging (Blackwell et al. 2019).

Spearfishing captures were assessed based on the total number of shots, shot type (surface or underwater), and shot result. Surface shots were defined as shots taken from the top of the water (no breath-holding) while underwater shots occurred when spearfishers dove down. Shot results were categorized into five groups: (1) single-shot success = one shot that successfully hit the target, (2) multiple-shot success = more than one shot was needed to successfully hit the target, (3) fish nicked = the spear tip made contact with the fish but did not result in a successful capture, (4) fish lost = the fish was missed and subsequently escaped unharmed (*i.e.*, no spear-induced injuries), (5) missed shots = shots that failed to hit the target, resulting in no contact with the fish.

Nest coordinates and developmental stage were recorded immediately after male removal in Clear Lake. Nest developmental stage was based on methods used in Ridgway and Friesen (1992) and Tufts et al. (2019). Stages were defined as follows: stage 0 – nest built with male present but no eggs, stage 1 – eggs present on nest, stage 2 – eggs hatched into embryos that remain on the bottom (*i.e.*, bottom fry), stage 3 – fry elevated off the bottom and still associated with the nest (*i.e.*, swim-up fry) (Ridgway and Friesen 1992, Tufts et al. 2019).

Lastly, we assessed the suitability of spearfishing by examining factors such as bycatch, project expenses, logistics, and safety considerations involved. Although this evaluation considered the findings of the present study, we broadly discuss the practical application of spearfishing to inform fisheries management in western North America. Our aim is to assist water managers and regulators in making evidence-based decisions by identifying feasible, cost-effective strategies for suppressing smallmouth bass populations.

Statistical Analysis

Statistical analyses were performed using R software 4.2.2 (R Core Team 2022). Relevant assumptions were checked before each test and a significant difference was considered if $p < 0.05$ (Zar 2010). Normality assumptions were checked using Shapiro-Wilk tests which revealed if the data were not normally distributed. A non-parametric Mann-Whitney U test was used to compare mean CPUEs of spearfishing (Clear Lake) and angling (Cultus Lake). Mixed effects models were used to account for potential variation due to both fixed and random effects (Zuur et al. 2009). In the model, fishing method and experience were treated as fixed effects, while individual fishers (herein referred to as fisher ID) were considered as a random effect. The experience gained per fisher (by method) was standardized (Harrison et al. 2018) and calculated as

(2) $$Z = \frac{(X - \mu)}{\sigma}$$

where Z is the standardized experience, X is the sum of their experience (hours) gained up until that fishing effort (cumulative), μ is the fishing method mean experience (across all fishers), and σ is the fishing method standard deviation (across all fishers). Standardizing variables gives standard units (Schielzeth 2010, Harrison et al. 2018) that consider each fisher's individual experience relative to the average across all fishers. This allows for measuring fishers' effects on CPUE, despite having different levels of experience. Variables used in the model and their units are presented in Table 2.1.

Table 2.1. Summary table of fixed (explanatory variable) and random effects (grouping factor) used for mixed effects model.

Fixed effect	Random effect
Method – spearfishing, angling	Fisher – ID
Experience – standardized (per fisher/method)	

A generalized linear mixed model (GLMM) was fitted using the *glmer* function of R package 'lme4' (Bates et al. 2015). To handle zero catches, a positive constant (0.15) was added to each catch (Butterworth 1966). A Gamma distribution and log-link function were used to account for the positive and right-skewed distribution of the CPUE data (Maunder and Punt 2004). First, a global model was constructed which included all explanatory variables. Then, variations were created with all possible combinations of uncorrelated explanatory variables. Models were ranked by lowest Akaike Information Criterion value (AICc) and all models within a ΔAICc <2 were considered equivalent (Burnham et al. 2011). The goodness of fit was checked using the function *check_model* in the ‘performance’ R package (Lüdecke et al. 2021), and included visualisation of residuals in quantile-quantile plots and correlations between residual and fitted values. If significant patterns or deviations were observed, preference was given to models which satisfied assumptions and included random effects. Finally, we used the R package ‘ggplot2’ (Wickham 2016) to create boxplots comparing the CPUE between methods (raw data, not model predictions). Catch rates for all fish were also compared across capture methods, lakes, and life stages.

A Mann-Whitney U test was used to compare the length and weight of mature males captured by spearfishing in Clear Lake and angling in Cultus Lake. Length-frequency distributions of mature males and all life stages were analyzed using a Kolmogorov-Smirnov test (Zar 2010). Citizen science submissions were only compared in terms of size structure.

Spearman’s rank correlation tests were used to evaluate spearfishers’ skills and progress. The cumulative sum of effort was calculated for each fisher and a correlation matrix was created to identify trends in improvement. The capture assessment variables examined were cumulative effort (hours), total shots, missed shots, and fish nicked. Multiple comparisons were adjusted for familywise error rate using a Holm correction (Holm 1979).

RESULTS

Catch Per Unit Effort

Spearfishing for mature males in Clear Lake was three times faster than angling in Cultus Lake (Mann-Whitney U = 1183.00, $p < 0.001$; Figure 2.3). The fishing method was the most important determinant of CPUE (GLMM fixed effect Method: spearfishing, estimate = 37.86, SE = 12.48, $t_{(102)} = 11.03$, $p < 0.001$; Appendix A, Table A 3). Fishers’ experience level did not explain variability (estimate = 0.99, SE = 0.03, $t_{(101)} = -0.22$, $p = 0.826$), while fisher ID accounted for some (variance = 0.12, SD = 0.35). See Appendix A, Table A 4 for model selection tables and Figure A 1 for diagnostics. The total catch is summarized in Table 2.2 and the average CPUEs grouped by life stage, method, and lake are provided in Appendix A, Table A 5.

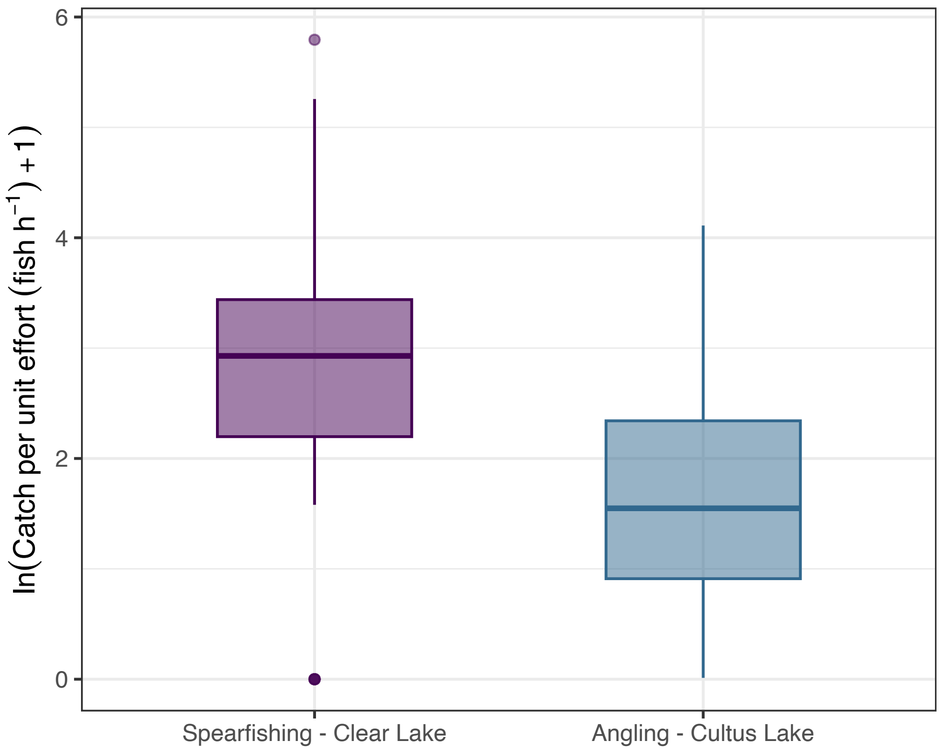

Figure 2.3. Boxplots comparing the catch per unit effort (CPUE) of smallmouth bass mature males by fishing method and lake. The box represents the interquartile range (IQR), with the median indicated by the horizontal line inside each box. The whiskers extend 1.5 times the IQR from lower and upper quartiles, respectively. Spearfishing (n = 18) represents all attempts (failed efforts included) while angling in Cultus Lake (n = 88) represents captures only (failed efforts excluded). The response data were ln-transformed (CPUE + 1) with an added constant value of 1 to address spearfishing records with zero catch.

Table 2.2. Comparison of fishing effort (hours), catches, and catch per unit effort (CPUE) of smallmouth bass (life stages combined) by fishing method in Clear Lake, 2022 and Cultus Lake, 2020 to 2021. Catch for mature males are shown in parenthesis. Citizen science submissions (n = 13) for Clear Lake are excluded. Data for Cultus Lake are from Margetts (2022).

	Clear Lake			Cultus Lake
	Spearfishing	Angling[1]	E-fishing[2]	Angling[3]
Total effort	3.6	2.4	6.5	51.7
Total catch	33 (14)	2 (2)	693 (7)	172 (88)
CPUE (fish h^{-1}) ± SE	40.7 ± 9.7	2.8 ± 1.8	81.2 ± 17.3	15.3 ± 1.4

[1] Scientific angling.
[2] Electrofishing bycatch excluded from CPUE calculation.
[3] Expert anglers.

Size Structure

In Clear Lake, all bass larger than 299 mm (total length) were exclusively caught by spearfishing (Figure 2.4). Angling and electrofishing were unsuccessful in capturing larger fish. There was no difference in the length of mature males captured by spearfishing in Clear Lake and angling in Cultus Lake (Mann-Whitney U = 910.50, p = 0.06; Figure 2.5). Similarly, the mean weight of mature males did not differ between spearfishing in Clear Lake and angling in Cultus Lake (Mann-Whitney U = 905.50, p = 0.07; Figure 2.5). Length-frequency distributions of mature males captured by spearfishing were different than electrofishing in Clear Lake (Kolmogorov-Smirnov, $Z_{(21)} = 0.73$, p = 0.003) and angling in Cultus Lake (Kolmogorov-Smirnov, $Z_{(102)} = 0.36$, p = 0.037). See Figure 2.5 for total lengths and weights, and Figure 2.6 for the age distribution of all captured fish.

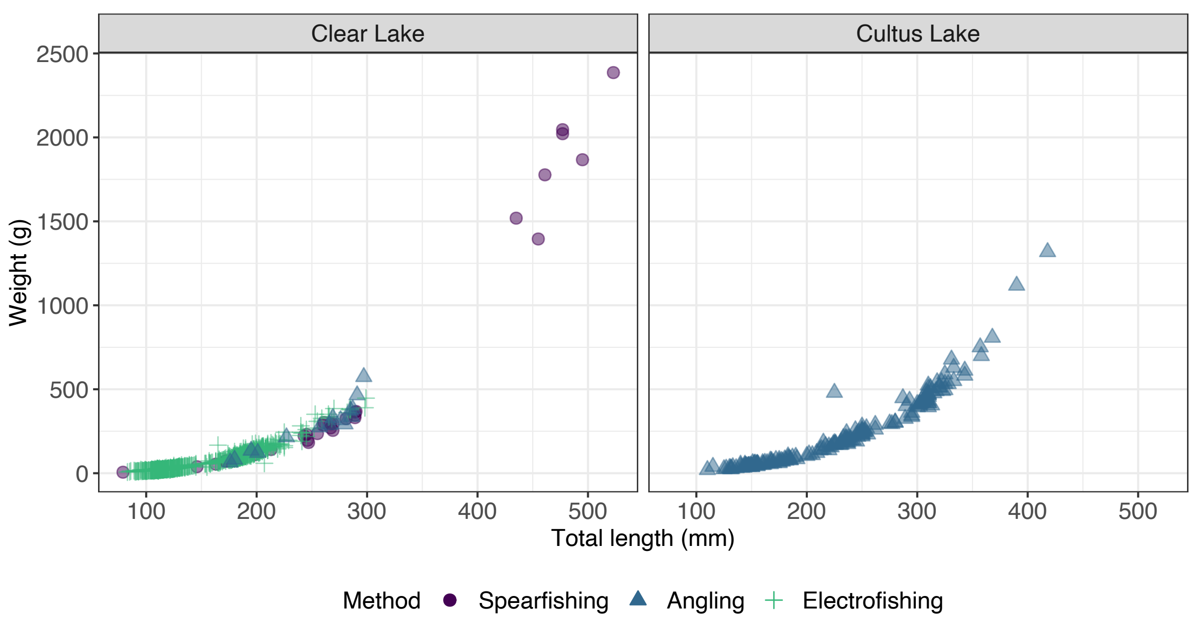

Figure 2.4. Total length (mm) versus weight (g) of smallmouth bass captured across all life stages and fishing methods used in Clear Lake, Manitoba (left) and Cultus Lake, British Columbia (right). Points represent fishing methods: spearfishing (purple circles), angling (blue triangles), and electrofishing (green plus). Angling submissions from members of the public (*n* = 13) were combined with scientific angling catch (*n* = 2) from Clear Lake.

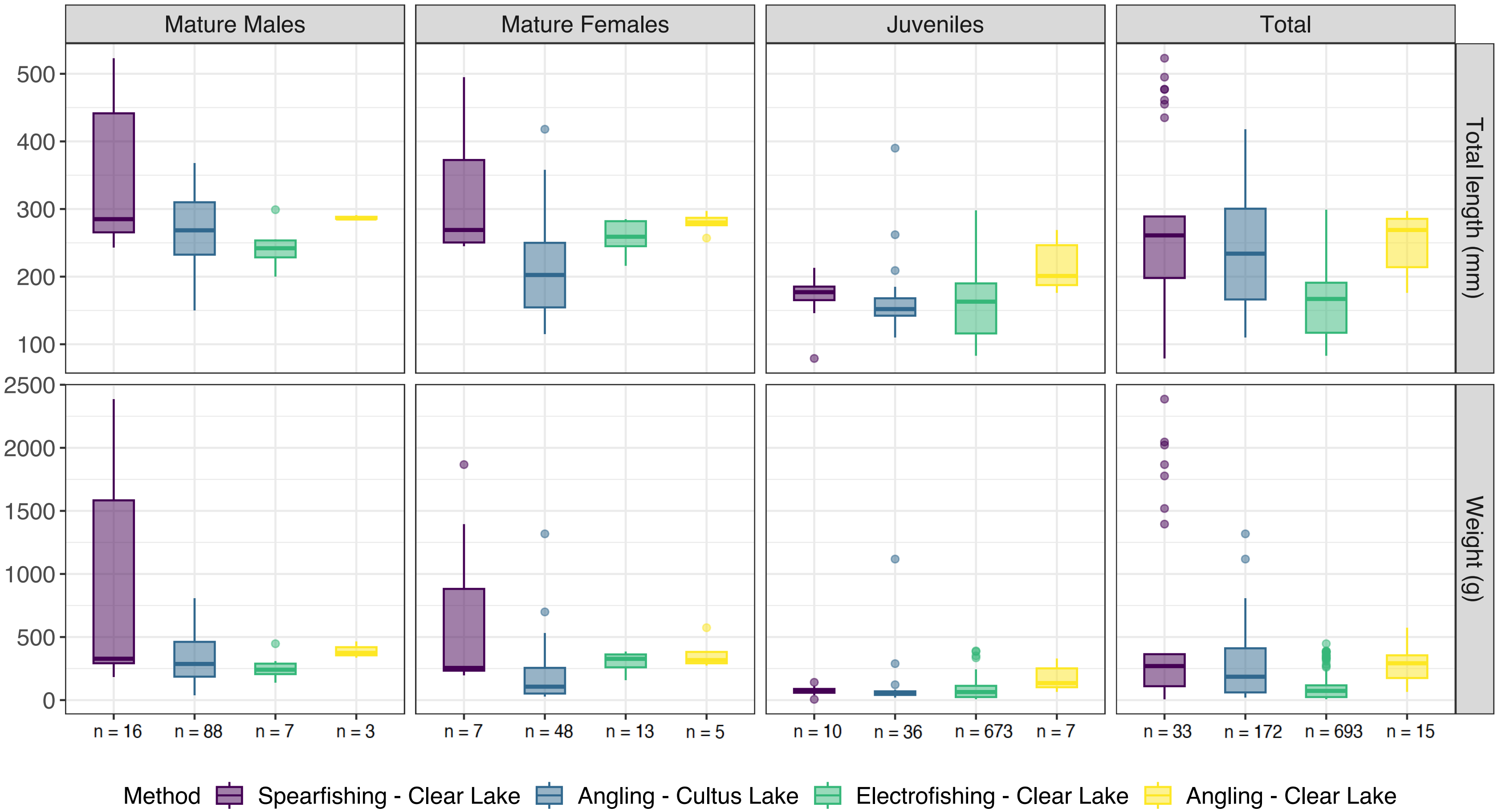

Figure 2.5. Boxplots comparing the total length (mm; top panels) and weight (g; bottom panels) of smallmouth bass captured in Clear Lake, Manitoba (spearfishing, electrofishing, angling), and Cultus Lake, British Columbia (angling). Cultus Lake data from Margetts (2022). Catches are categorized by life stage and fishing technique used. Juveniles are inclusive of young-of-the-year captures. Clear Lake scientific angling and angling submissions from members of the public combined. The sample sizes (n) represent captured fish within a given life stage. The box represents the interquartile range (IQR), with the median indicated by the horizontal line inside each box (raw data). The whiskers extend 1.5 times the IQR from lower and upper quartiles, respectively.

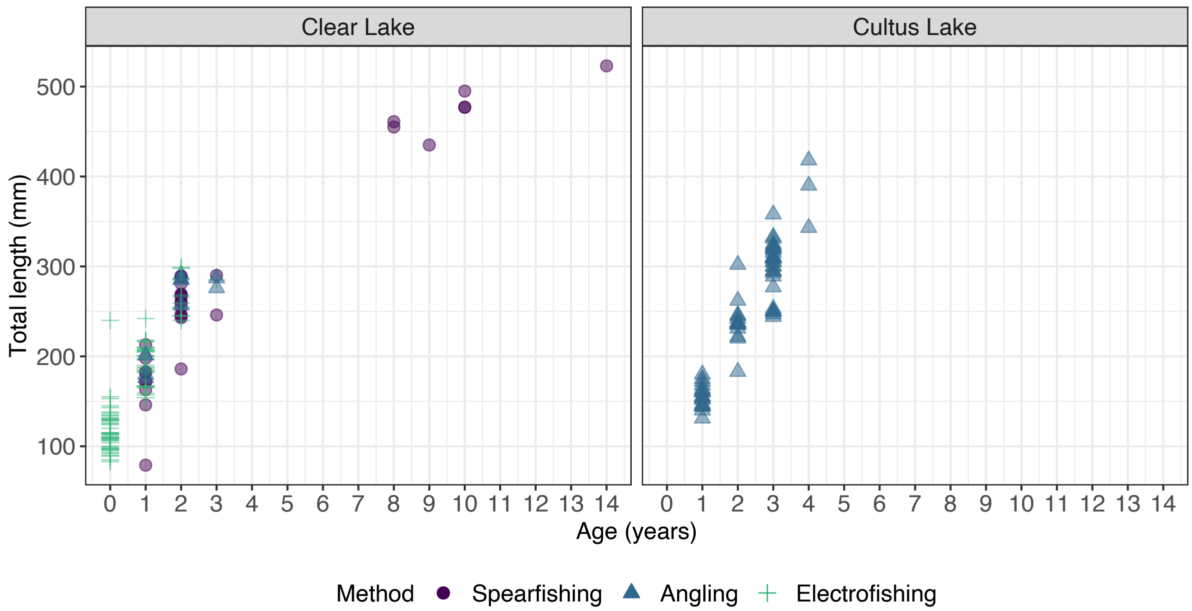

Figure 2.6. Total length (mm) versus age (years) of smallmouth bass (*n* = 144) caught in Clear Lake, Manitoba. Aging structures used were otoliths (*n* = 135) and dorsal spines (*n* = 5). Clear Lake scientific angling and angling submissions from members of the public combined. An age-length key was created using otoliths (*n* = 76) and total lengths (*n* = 128) for smallmouth bass in Cultus Lake (*n* = 172), British Columbia (Margetts 2022). Points represent fishing methods: spearfishing (purple circles), angling (blue triangles), and electrofishing (green plus).

Capture Assessments

Crews showed improvements in spearfishing techniques and confidence as the study progressed, leading to better capture results. Accuracy improved over the study, resulting in fewer missed shots and total shots taken (Spearman rank correlation coefficients, $\rho_{missed\ (75)} = -0.47$, p = 0.01; $\rho_{total\ (75)} = -0.29$, p < 0.01; Figure 2.7). Spearfishers retained 87.5% of nest-guarding males they attempted to catch, 62.5% of which were captured in one shot. Counts of spearfishing shots can be found in Table 2.3.

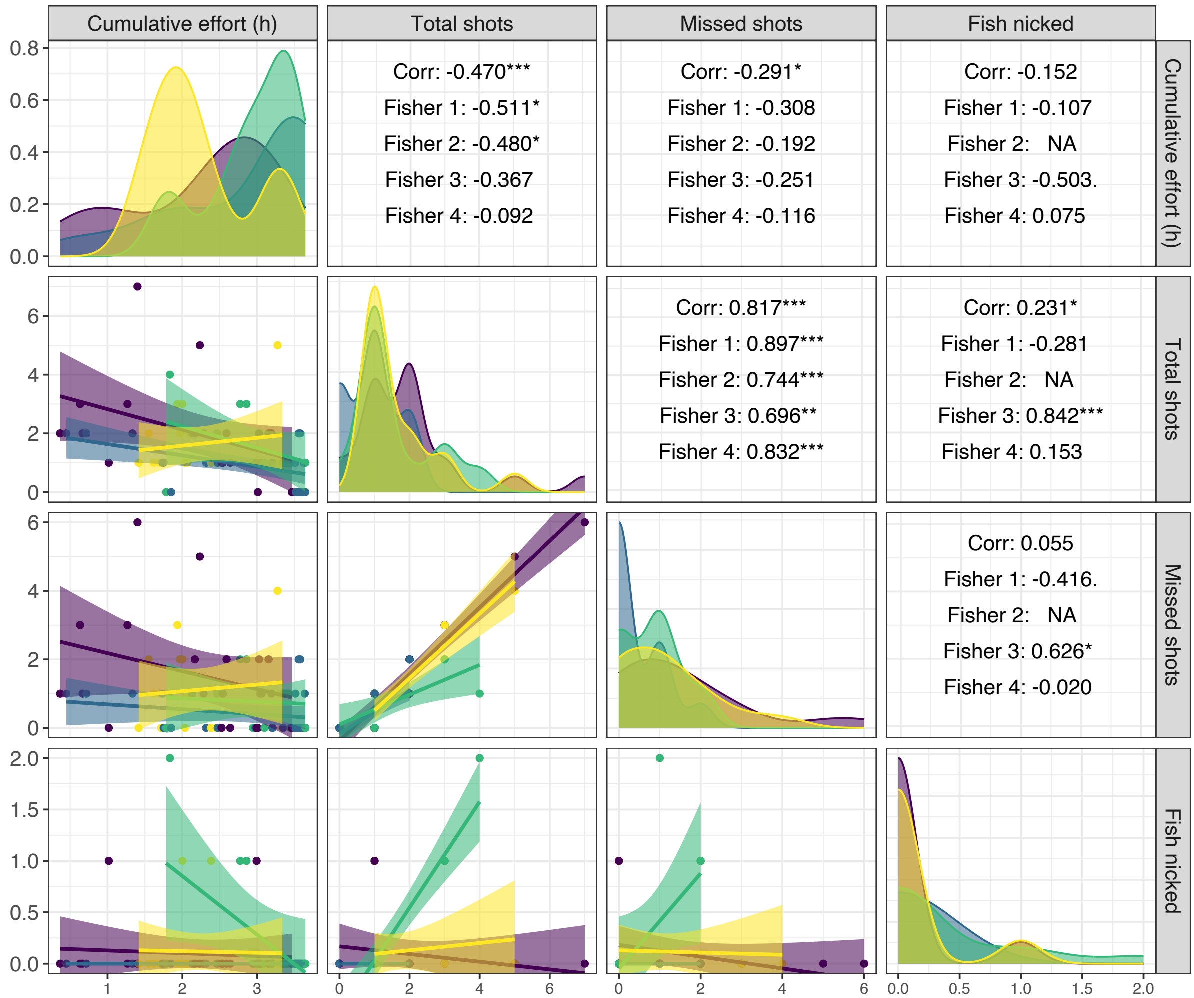

Figure 2.7. Correlation between spearfishers' cumulative effort (hours) and capture assessment variables (total shots, missed shots, and fish nicked) in Clear Lake, Manitoba. Correlation across all fishers is shown in grey, while colours represent individual fishers. Levels of significance are denoted by asterisks (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Table 2.3. Summary table of spearfishing shots taken, shot type (surface or underwater), result (fish nicked or missed shot). Efforts are categorized by attempts on nesting and non-nesting smallmouth bass. Nesting refers to adult smallmouth bass associated with a nest. Non-nesting refers to smallmouth bass not associated with a nest (*i.e.*, juveniles, females, and non-spawning males).

	Total shots	Surface shot	Underwater shot	Fish nicked	Missed shots
Nesting	28	15	13	3	11
Non-Nesting	85	70	15	5	61
Total	113	85	28	8	72

A total of 15 nest assessments (Appendix A, Table A 6) were performed in Clear Lake after male removal (*n* = 13) or nest abandonment (*n* = 2). One nest had eggs (stage 1), and one had fry (stage 3). The remaining 13 did not have any eggs (stage 0), meaning that 87% of the males captured by spearfishing were removed before spawning.

There was no bycatch of native species from spearfishing in Clear Lake. Electrofishing resulted in the total capture of 1399 fish, representing nine different species (Appendix A, Table A 7). Among these, smallmouth bass (*n* = 693) and walleye (*n* = 49) (kept for a feeding study) were retained, while 657 were released as bycatch. Anglers in Cultus Lake reported bycatch of two northern pikeminnow (*Ptychocheilus oregonensis*).

DISCUSSION

Catch rates for spearfishing in Clear Lake (43.9 ± 17.5 fish h^{-1}, ±SE) were more than triple those for angling in Cultus Lake (13.0 ± 1.7 fish h^{-1}, ±SE). The length distribution among mature males also differed among methods; spearfishing was able to capture both smaller and larger adult males compared to angling in Cultus Lake and electrofishing in Clear Lake. We scanned the literature for results of other studies to which we could compare our findings, but the existing body of literature on spearfishing in freshwater systems remains sparse. Nonetheless, the technique is gaining traction and finding practical applications in such freshwater environments (Blanton et al. 2020). In Texas, spearfishers successfully suppressed invasive armored catfish (family Loricariidae) and increased mortality 1.50- to 1.75-fold relative to natural mortality (Blanton et al. 2020). In contrast, spearfishing is a well-established method for managing invasive fish in marine environments (Harris et al. 2019), demonstrating its effectiveness for invasive fish control. In a study on the Great Barrier Reef, Frisch et al. (2008) found that spearfishing yielded a 41% higher biomass (2.22 ± 0.23 kg h^{-1}, ±SE) compared to line-fishing (1.57 ± 0.20 kg h^{-1}, ±SE). Frisch et al. (2008) also found that spearfishing captured a wider variety of sizes than line-fishing. These findings correspond with our results, suggesting that spearfishing is able to improve catch rates and biomass yields, thereby highlighting its potential as an effective method for invasive smallmouth bass control.

Angling achieved the lowest CPUE of the methods compared in this study, proving to be the least effective method for capturing smallmouth bass. Other studies also found that angling performed poorly for controlling smallmouth bass. For example, in Oxford County, Maine, anglers targeting smallmouth bass achieved a CPUE of 0.31 fish h^{-1} (Boucher 2006). While angling is probably accessible to a wider audience, due to the availability and relatively low cost of basic gear, it is not considered a practical method for smallmouth bass control (Moore et al. 2005, Gomez and Wilkinson 2008) and is likely only effective in smaller systems with higher fishing pressure (Loppnow et al. 2013).

In Clear Lake, electrofishing was effective at capturing juvenile smallmouth bass but not adults. While studies have reported mixed results, electrofishing is not always effective for targeting both life stages. In Miramichi Lake, New Brunswick, Biron et al. (2014) reported higher CPUE for young-of-the-year (YOY) smallmouth bass compared to juveniles and adults. In contrast, control efforts in New York state initially reduced smallmouth bass abundance by 90%, resulting in decreased competition and accelerated maturation, ultimately leading to an increased abundance (Ridgway et al. 2002, Weidel et al. 2007, Zipkin et al. 2008). This phenomenon, termed overcompensation, has been well documented in previous research (Zipkin et al. 2008, Abrams 2009, Strevens and Bonsall 2011).

Because strategies that only target adults can lead to overcompensation (Loppnow et al. 2013), a multi-pronged approach may be needed to capture both juveniles and adults. Strategies that target eggs and fry (via adult removal) combined with YOY removal are most effective (Loppnow 2017). In Clear Lake, we found that spearfishing was effective for capturing adult smallmouth bass and electrofishing was effective for capturing juveniles, so combining these methods may be beneficial for controlling invasive bass and preventing overcompensation.

Spearfishing has been dismissed as a technique for smallmouth bass control because it is relatively labour-intensive and requires specialized skill (Loppnow 2017). However, the spearfishers in this study rapidly developed skills to effectively capture mature males and there was no bycatch. As the study progressed, the number of missed shots decreased, indicating that accuracy improved. The total number of shots taken to capture a fish also decreased, indicating that skills improved with time and experience.

Our results suggest that spearfishing is a viable strategy for suppressing smallmouth bass, offering distinct advantages. Crews can get started with small initial investments, with the cost per person ranging from $500 to $2000 CAD. Different gear types are available for spearfishing; however, we chose pole spears for this study. Compared to spearguns, pole spears are a simpler, safer alternative as they lack mechanical parts, thereby reducing the risk of accidental discharge and potential harm to divers, swimmers, and the public (Christopher Adair (Bottom Dwellers Ltd., Spearfishing Canada Ltd.), personal communication, February 8, 2022). In comparison to alternative methods such as boat electrofishing, spearfishing is a low-cost, low-tech suppression technique.

Several factors affected the suitability of using spearfishing for controlling smallmouth bass in Clear Lake. True to its name, the water is very clear (Secchi disk depth 5.06 m; Butcher 2017), which is required for a visual technique like spearfishing. Smallmouth bass also tend to nest in shallow water and exhibit parental care, making it easier for spearfishers to find and capture nesting males. Spearfishing is a highly selective technique, reducing the likelihood of bycatch. More broadly, spearfishing may be suitable for a wide variety of systems and species that exhibit similar characteristics.

While this study demonstrated the effectiveness of spearfishing for capturing nest-guarding males in Clear Lake, our sample size was limited to 15 nests. Our sample size was impacted by several factors. Clear Lake's smallmouth bass population was still in the early stages of invasion, resulting in few spawners and a limited number of nests. In addition, suppression activities were constrained by the spawning period, when males could be found on nests. Finally, spearfishing sessions were primarily dependent on weather, which further reduced the number of days available for spearfishing. Ultimately, these factors resulted in a relatively small sample size.

Because angling was unsuccessful in Clear Lake, angling data from Cultus Lake were chosen as an auxiliary dataset for comparison. However, comparing fishing methods between lakes introduces limitations related to differences in lake ecology, fishing pressure, sampling bias, and study design. Angling was used for fish collection for the study in Cultus Lake, but efforts reflected capture times only; time spent which yielded no captures was not recorded. As a result, the recorded effort may have led to an overestimation of the CPUE. In contrast, spearfishing efforts in Clear Lake included failed captures. Time spent swimming from the capture site to the workboat was also included, which would have further reduced the CPUE, possibly resulting in an underestimation. Further, while spearfishing efforts resulted in more than three times the CPUE (fish h^{-1}), a potential overestimation in angling CPUE and underestimation in spearfishing CPUE may mean that spearfishing outperformed angling to an even greater degree than reported. While this swimming distance reduced over the course of the study, future studies may wish to exclude time spent swimming when calculating spearfishing CPUE (see Harris et al. 2019).

This study explored the use of spearfishing for suppressing invasive smallmouth bass, but there are several avenues for further research and refinement. When assessing gear efficiency, future studies could benefit from comparing removal methods in systems with established populations and abundant nests, allowing for larger sample sizes. Research focused on rapidly locating nests could reduce reconnaissance time and improve efficiency. In our study on Clear Lake, while spearfishing proved effective for quickly capturing fish, substantial time was spent on reconnaissance (totalling 98 hours; Appendix A, Table A 8). Aerial drone surveys were the most effective method for locating nesting sites, aligning with established practices for detecting invasive plants (Martinez et al. 2020). Recent advances in machine and deep learning for detecting invasive species are becoming more popular and widely used as an environmental management tool (Jensen et al. 2020, Huelsman et al. 2023, Valicharla et al. 2023). By automating drone flights during spawning seasons and using the footage as training data, AI algorithms could identify potential nesting sites based on predefined patterns. However, different ecosystems may require different approaches, as drones might not be suitable for turbid waters or smaller systems with many nests.

In addition to refining nest location methods, there is a need to develop strategies for selectively targeting productive females to reduce population growth rates. Though not the focus of this study, spearfishing successfully captured four mature females. Larger females can spawn in multiple nests (Scott and Crossman 1973, Moyle 2002) and contribute disproportionally more to fecundity (Barneche et al. 2018). Consequently, exploring methods that selectively target larger females could be beneficial.

Further, quantifying reproductive success following male removal could inform strategies that ensure nest failure. After the removal of nest-guarding males, Loppnow (2017) found that the rate of nest failure increased from the natural background rate of 42% to 94%, primarily due to predation of eggs and fry (79%). Since natural predation may vary by system, destroying nests (*e.g.*, by burying eggs) may be necessary to ensure nest failure.

If bass predation successfully reduces crayfish densities, this could positively impact bass reproductive success by mitigating the significant consumption of bass eggs by crayfish (Baldridge and Lodge 2013). Lower crayfish densities may lead to fewer instances of nest failure, potentially reducing nest abandonment rates and increasing overall nest success for smallmouth bass (Baldridge and Lodge 2013). Given the predatory capabilities of smallmouth bass, it would be beneficial to identify thresholds or critical densities of crayfish that could lead to high impacts on bass nests. In Clear Lake, monitoring surveys conducted in the summers of 2021 and 2022 showed a decline in crayfish abundance during this period (Parks Canada unpublished data), but the population should be monitored going forward as it may have an effect on bass egg predation. Understanding the levels at which crayfish densities become problematic for bass reproduction may provide valuable insights for effective management and conservation strategies in ecosystems where these interactions occur.

Finally, spearfishing may also be appropriate for controlling other invasive fish species that have similar behaviours and vulnerable life stages. There are 41 bony fish families that display nest-guarding behaviour (Blumer 1982). Among these are cichlids and gobies (Ridgway and Shuter 1997, Steinhart et al. 2005), for which spearfishing may be useful for inducing nest failure in systems where they are invasive. While this study focused on invasive smallmouth bass, spearfishing may be a useful tool for invasive fish control in Canada and other locations across the globe.

Management Recommendations

Different systems may require different techniques to enhance removal methods, improve catchability, and achieve control. The outcomes from this study provide informative general management recommendations for smallmouth bass control.

1. *Use spearfishing for adult removal where appropriate*.

Where feasible, fisheries managers should consider the method as part of a multi-pronged approach to managing invasive smallmouth bass. To determine whether spearfishing is appropriate for their program, managers would want to consider the following: bycatch, costs, local regulations, safety, water quality, training, and system-specific information about the gear types that are most effective for adult removal. As regulations on spearfishing vary by jurisdiction, it is important to be aware of local regulations and apply for permits if required. Fisheries managers should also consider specialized training, evacuation plans, boat traffic, and logistics. Spearfishing requires a specific set of skills. Training in first aid, oxygen administration, and completing routine dive rescue drills can help ensure the safety of crews. Professional training is not essential but may be beneficial. Using a certified trainer could teach proper techniques, expedite skill development, and ensure safe practices are followed. A certified trainer can also help alleviate some of the stress and anxiety that comes with learning a new skill. By combining safety measures and strategic planning, spearfishing could be an effective supplementary control strategy for managing invasive smallmouth bass.

2. *Determine size and structure of the invasive smallmouth bass population*.

Mark-recapture studies provide insights into population dynamics, reproductive success, and survival rates of invasive smallmouth bass (Restif et al. 2012, van Poorten and Beck 2021). Based on population estimates, a simulation model could be developed to project the potential population dynamics of invasive smallmouth bass over time and under different control treatments (*i.e.*, spearfishing and electrofishing). For instance, Loppnow and Venturelli (2014) developed an individual-based model to simulate options for smallmouth bass control via induced nest failure. Their research suggested there are many feasible combinations of YOY removal and supplemental removal that could achieve control in less than 10 years. Estimating the optimal duration and frequency of treatments can contribute to evidence-based decision-making for implementing effective control strategies.

3. *Study movement and spatial distribution of the smallmouth bass*.

Acoustic telemetry can be used to track the bass' movements and spatial distribution, which may provide insights into habitat use and movement patterns (Gutowsky et al. 2020). This information could be used to enhance removal methods and improve catchability (Loppnow et al. 2013). This information may also help locate aggregations of smallmouth bass during spawning or winter shoaling and inform targeted control (Bajer et al. 2011).

Acoustic telemetry could be suitable for large systems such as Clear Lake as it provides an opportunity to improve targeted removal. Since increased fishing pressure has been shown to help control invasive fish (Moore et al. 2005), Parks Canada could leverage assistance from members of the public to spearfish and angle for bass in Clear Lake. Sharing location data would help citizen scientists in locating bass, enabling effective targeting for removal. This approach provides an additional method of control while engaging the community in removal efforts.

Conclusion

To conclude, spearfishing showed potential as a viable technique for suppressing invasive smallmouth bass in Clear Lake. Spearfishing may be suitable in a wide variety of systems; the technique shows promise for inducing nest failure while minimizing non-target effects. The method may be applicable for controlling other populations of invasive smallmouth bass and other large-bodied, nest-guarding, invasive, freshwater fish in Canada and beyond.

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CHAPTER 3 DIET OVERLAP BETWEEN INVASIVE SMALLMOUTH BASS (*MICROPTERUS DOLOMIEU*) AND WALLEYE (*SANDER VITREUS*) IN CLEAR LAKE, RIDING MOUNTAIN NATIONAL PARK, MANITOBA

INTRODUCTION

Aquatic invasive species are non-native aquatic organisms that are introduced to a new ecosystem, such as a river, lake, wetland, or ocean, and have negative impacts on the environment, economy, or human health (Pimentel et al. 2005, Sanderson et al. 2009, Simberloff et al. 2013). Aquatic invasive species pose significant threats to the biodiversity of aquatic ecosystems by disrupting the trophic structure and reducing populations of native species (Havel et al. 2015). One of the key factors that contribute to the rapid establishment of invasive populations is the lack of natural predators in their new habitat (Thomaz et al. 2015). Understanding invasive characteristics and impacts of these species is key to effectively managing and controlling their spread (Thomaz et al. 2015). The prevalence of invasions in Canada are increasing as suitable habitats expand north due to climatic trends associated with global warming (Jackson and Mandrak 2002).

Native to eastern Canada and the southern United States (Scott and Crossman 1973), smallmouth bass (*Micropterus dolomieu*) now have established populations in both western North America, and internationally (Loppnow et al. 2013). Smallmouth bass is among North America's most popular game fish and has been introduced to freshwater systems across the continent (Tovey et al. 2008) through stocking programs, illegal introductions, and live bait release (MacRae and Jackson 2001). Its Canadian presence extends from southern Nova Scotia, southern and western New Brunswick, southern Quebec, across Ontario to central Saskatchewan and Manitoba, and British Columbia (Scott and Crossman 1973). Although not native to Manitoba, the species has been introduced in many water bodies (Stewart and Watkinson 2004). Their distribution in Manitoba is considered to be at the northern limit of their range (Brown et al. 2009), extending from Lake Winnipeg and its tributaries to the east, Riding Mountain National Park (RMNP) to the west, and Rocky Lake, near The Pas, to the north (Stewart and Watkinson 2004).

Invasive smallmouth bass are aggressive top predators, associated with changes in trophic energy flow and reduced abundance and diversity of fish and invertebrates (MacRae and Jackson 2001, Brown et al. 2009, Wuellner et al. 2011). Smallmouth bass' success as an invader stems from its early onset of piscivory, adept use of cover, minimal overlap with other predators, high fecundity, and parental care behaviour (Weidel et al. 2000). Adding to its adaptability, the species exhibits physiological tolerance to a wide range of temperatures (Cooke et al. 2003), opportunistic feeding habits (Weidel et al. 2000), and spiny rays, which act as a defence mechanism against predators (Tovey et al. 2008).

Smallmouth bass feed on a wide range of prey species, including aquatic invertebrates, small fish, and amphibians (Sweka and Hartman 2003). During their larval stage smallmouth bass predominantly feed on zooplankton, including copepods and water fleas. After hatching, young fry (~6 mm in length) will emerge from their nest and feed on zooplankton while still being guarded by the male (Moyle 2002). Their diets gradually shift from zooplankton to aquatic insects as they grow. Once bass surpass 50 mm in length, crayfish and fish become prominent components in their diet and dominate intake in fish larger than 150 mm (Pflugr and Pauley 1984).

Fayram et al. (2005) found that predatory interactions and habitat suitability may contribute to the inverse relationship observed between walleye (*Sander vitreus*) and smallmouth bass populations. Walleye thrive in sandy, gravelly, or detritus-laden substrates, while smallmouth bass dominate areas with rocky or boulder substrates, sheltered bays suitable for spawning, and scarce forage fish (Kerr and Grant 2000). In some northern Wisconsin lakes, Frey et al. (2003) found that the introduction of either smallmouth bass or walleye resulted in the reduction or elimination of the other species. However, in eastern Canada, walleye and smallmouth bass coexist. In a review of nearly 1,000 lakes in Ontario, northern pike (*Esox lucius*), walleye, and smallmouth bass were a common association and coexisted in 17.8% of the lakes (Johnson and Hale 1977). Coexistence has been documented in both lakes where smallmouth bass are native (Kempinger and Carline 1977) and introduced (Galster et al. 2012), and the two species appear to coexist well in larger lakes with a diversity of habitats. However, the impacts of introduced smallmouth bass on walleye are varied and difficult to predict, resulting in recommendations that smallmouth bass are not introduced into lakes with walleye (Wuellner et al. 2011). Smallmouth bass prey on walleye fry (Colby et al. 1979, Liao et al. 2004) and are believed to decrease walleye year-class strength (Johnson and Hale 1977).

Visual analysis of gut contents is a typical method for studying diet overlap, predator-prey dynamics, and competition between species (Sampson et al. 2009). A widely used metric in diet analysis is frequency of occurrence (*FO*), which indicates the percentage of individuals that have consumed a prey item (Baker et al. 2014). This metric is robust to challenges such as the presence of unidentifiable tissues (Buckland et al. 2017) and provides a comprehensive measure of diet composition (Baker et al. 2014). In addition, Schoener's similarity index quantifies the degree of dietary overlap between species, facilitating the prediction of invasive impacts on native fish species (Pilger et al. 2010).

In this study, we examined the dietary overlap between invasive smallmouth bass and walleye in Clear Lake, Manitoba by (1) quantifying their diets using morphological identification and frequency of occurrence (*FO*), (2) assessing feeding behaviour and diet composition using mean prey abundances (*Ni*), and (3) comparing the degree of diet overlap using mean proportional abundances and Schoener's similarity index.

METHODS

Study Site

Sampling was conducted in Clear Lake, Riding Mountain National Park (RMNP) (50°46'N, 99°59'W), in southwestern Manitoba (MB), Canada (Figure 3.1, Figure 3.2). Clear Lake has important ecological, economic, social, and cultural values. Local Anishinaabe people believe its water is sacred and Keeseekoowenin Ojibway First Nation (KOFN) holds subsistence fish harvesting rights. In June 2021, RMNP confirmed that smallmouth bass were present in Clear Lake (Parks Canada 2023). This was of great concern because smallmouth bass are not native to Clear Lake and could outcompete native species for habitat and food resources (MacRae and Jackson 2001).

Clear Lake has a surface area of approximately 29 km^2, a maximum depth of 34.2 m, and an average depth of 11.5 m (Glufka 1992). Clear Lake is oligotrophic and supports native fish species such as lake whitefish (*Coregonus clupeaformis*) and northern pike, and has a high diversity of phytoplankton, zooplankton, benthic fauna, and aquatic vegetation (Glufka 1992).

Figure 3.1. Location of Manitoba within Canada (shown in red). Riding Mountain National Park is represented by the yellow star (MapGrid 2020).

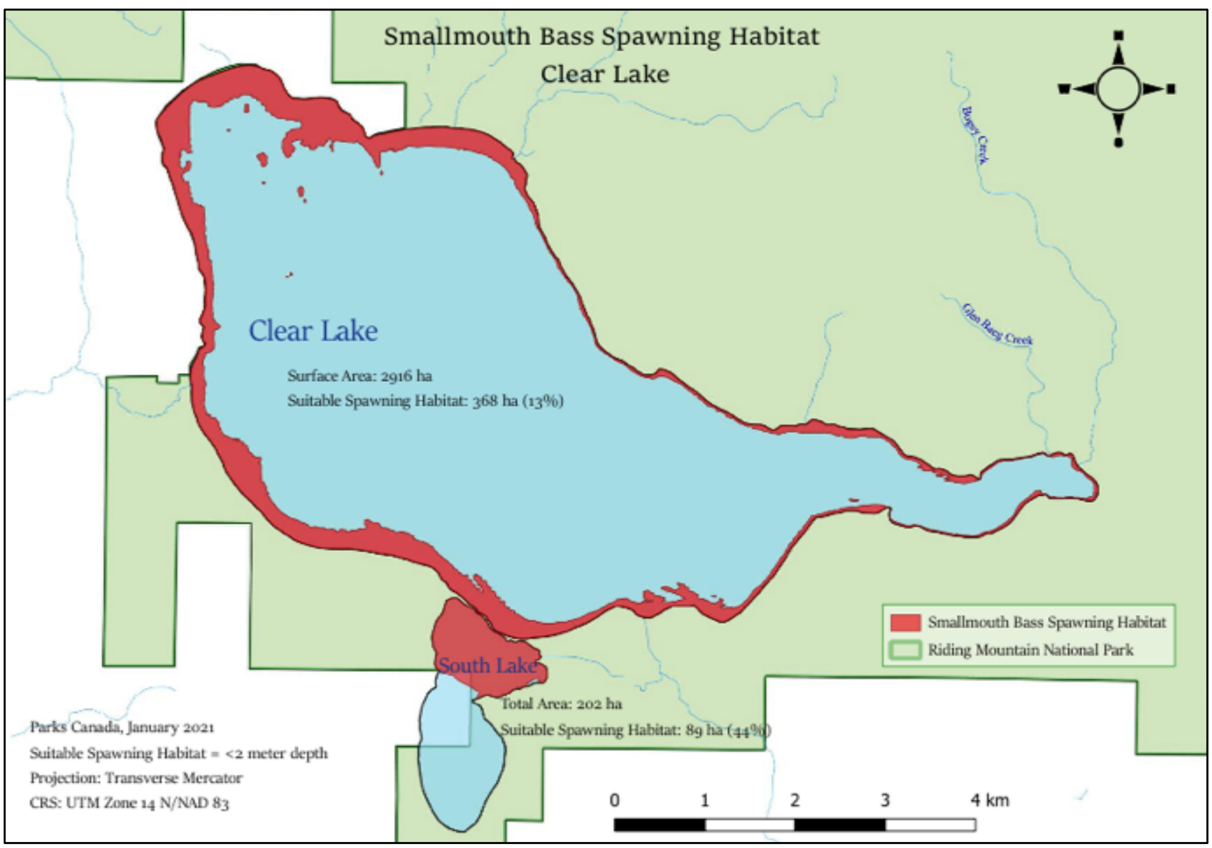

Figure 3.2. Suitable spawning habitat for smallmouth bass in Clear Lake, Manitoba (Parks Canada 2021).

Fish Collection

Fish were collected using a range of methods: spearfishing, electrofishing, gillnetting, angling, and submissions by members of the public. Different sampling methods were used to collect a variety of length classes of each species. Fish were euthanized and stored in the on ice and dissected in the RMNP laboratory or at a mobile workstation set up at the Keeseekoowenin 61A day-use area. Total length (mm), weight (g), sex, and maturity were recorded for each fish and the entire gut was removed and preserved in 95% ethanol. Smallmouth bass and walleye were categorized into five size categories based on their total lengths (mm), with intervals of 50 mm. Otoliths and dorsal spines were collected to estimate fish age for smallmouth bass (n =103) and walleye (n = 109). Otoliths were the preferred aging structure (Maceina et al. 2007, Starks and Rodger 2020) and dorsal spines were only collected when otoliths were either damaged or not located. AAE Tech Services Inc. was contracted to estimate ages from the structures.

Captured bass, walleye, and gillnetting bycatch were humanely handled and euthanized according to Parks Canada Research and Collection Permit (No. RMNP-2022-42359), and Thompson Rivers University Animal Use Protocol (No. 8452). After measurement and sample collection, edible portions were distributed among local First Nations communities. All live bycatch was released.

Diet Analysis

Guts were emptied and contents were analyzed using a Leica MZ 6 stereo microscope. Prey items were identified and separated into their lowest operational taxonomic units (OTU). Items were identified to family using taxonomic keys from Merritt et al. (2019) for insects and Thorp and Covich (2001) for non-insects. Frequency of occurrence (*FO)* was estimated by calculating the percentage of stomachs in which each OTU was present, based on all stomachs (excluding empty ones). Diets were characterized using percent composition (Chipps and Garvey 2007) and different length classes for each species. Percent composition represents the frequency of a diet item in relation to the total count of food items (Chipps and Garvey 2007).

Frequency of occurrence (*FO*) and mean prey abundance (N_i) were calculated and used to quantify the diets of individual fishes. *FO* is the occurrence of a prey item F_i divided by the number of nonempty guts (P). This is the percentage of individuals that have consumed a specific food item (1).

$$FO = \left[\frac{F_i}{P}\right] \times 100. \quad (1)$$

Mean prey abundance (N_i) was used to compare feeding behaviour and diet composition among fishes (Macdonald and Green 1983). N_i is the mean number of prey i consumed, P is the number of nonempty guts, N_{ij} is the number of prey i in a single predator j, and ΣN_{ij} is the sum of all the prey in a single predator gut j (2).

$$N_i = \frac{1}{P} \times \left(\Sigma\left[\frac{N_{ij}}{\Sigma N_{ij}}\right]\right). \quad (2)$$

The degree of diet overlap between both species was calculated using numerical gut content abundances. Mean proportional abundances were compared using Schoener's similarity index, where C is Schoener's similarity index metric, and $P_{x,i}$ and $P_{y,i}$ are the proportions of diet item i in the gut of species x and y (Schoener 1970) (3). The index ranges from 0 to 1 with values of 0 indicating no diet overlap and values of 1 indicating a complete overlap. Values less than 0.4 and greater than 0.6 are considered ecologically relevant (Childs et al. 1998).

$$C = 1 - \frac{1}{2}\left(\Sigma \left|P_{x,i} - P_{y,i}\right|\right). \quad (3)$$

Statistical Analysis

Statistical analyses were performed using R software 4.2.2 (R Core Team 2022). Relevant assumptions were checked before each test and a significant difference was considered if $p < 0.05$ (Zar 2010). To compare fish gut contents between the species, we used permutational multivariate analysis of variance (PERMANOVA) (Anderson 2017) with the R package *vegan* (Oksanen et al. 2022). We examined the dissimilarity between gut contents of both fish using the Chao-Jaccard index (999 permutations, $\alpha = 0.05$). PERMANOVA is robust to heterogeneity and has been shown to provide greater statistical power than ANOSIM (Anderson 2017). To ensure collection methods did not have undue influence on the results, we also tested for differences in gut contents within species by each sampling method. Post-hoc tests were used to identify pairwise differences in gut contents and examine the influence of different sampling methods on each species' diet.

Then, non-metric multidimensional scaling (NMDS) with Chao-Jaccard distance was used to examine relationships among fish gut contents by species. NMDS generates an ordination and attempts to meet the conditions of a rank similarity matrix (Clarke 1993). NMDS produces stress values to assess the fit of the ordination to the data, with values below 0.2 indicating a good fit (Clarke 1993). This method uses ranked distances and is useful for data that fail to meet the assumptions of normality (McCune et al. 2002, Clarke et al. 2014).

Finally, to identify the diet items responsible for the differences identified in the steps above, Spearman's correlations were conducted using NMDS scores derived from prey abundances. These correlations were used to assess the degree of association between fish species and diet items (West et al. 2003). Multiple comparisons were adjusted for familywise error rate using a Bonferroni correction (Zar 2010).

RESULTS

A total of 103 smallmouth bass and 109 walleye guts were processed for diet analysis (Table 3.1). Of the 212 bass and walleye processed for diet, about 11% (*n* = 23) had empty stomachs, with a more common occurrence in walleye (*n* = 17; 74%) than bass (*n* = 6; 26%).

Table 3.1. The number of fish analyzed for diet, categorized by fishing technique. Numbers in parentheses represent individuals with empty guts.

Species	Electrofishing	Spearfishing	Gillnetting	Angling	Total
Smallmouth bass	55	32	1	9	103 (6)
Walleye	39	0	52	1	109 (17)

Capture methods provided a variety of size and age classes (Figure 3.3, Figure 3.4, respectively) for comparison, particularly for walleye. Bass were primarily captured using electrofishing (*n* = 55), while walleye captures were mostly from gillnetting (*n* = 52). Electrofishing led to the capture of 1399 fish, with nine species identified in the capture-keep (*n* = 742) and released bycatch (*n* = 657) categories (Appendix B,

Table B 1). Gillnetting yielded a total catch of 181 fish, representing six different species (Appendix B, Table B 2).

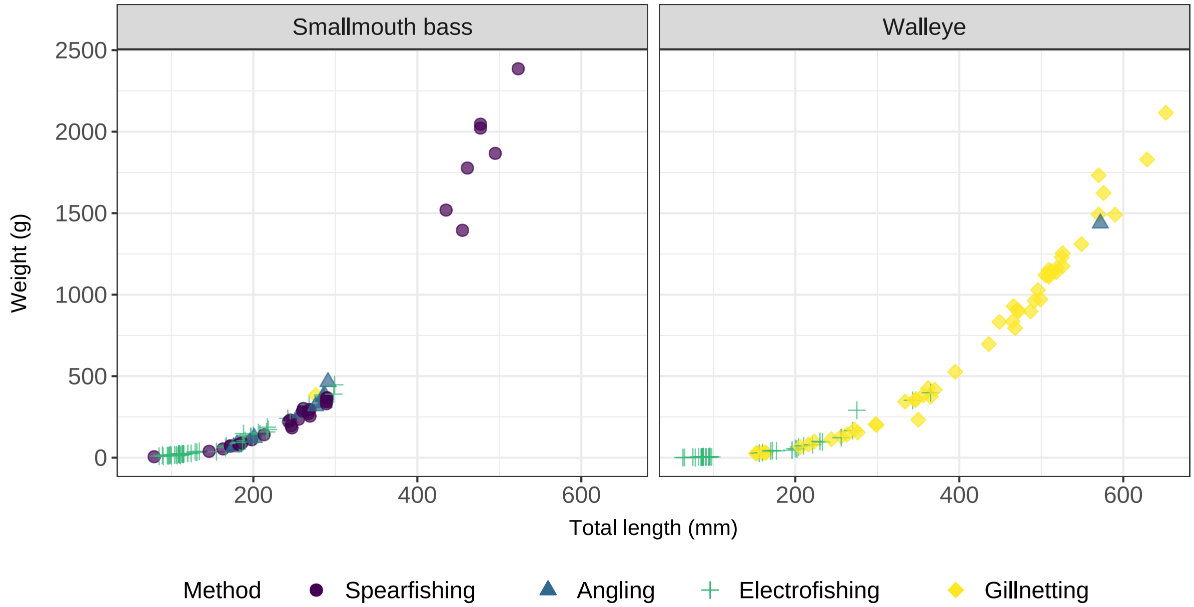

Figure 3.3. Total length (mm) versus weight (g) of smallmouth bass (n = 97; left panel) and walleye (n = 92; right panel) captured from Clear Lake, Manitoba and visually analyzed for diet. Captures were plotted by fishing method.

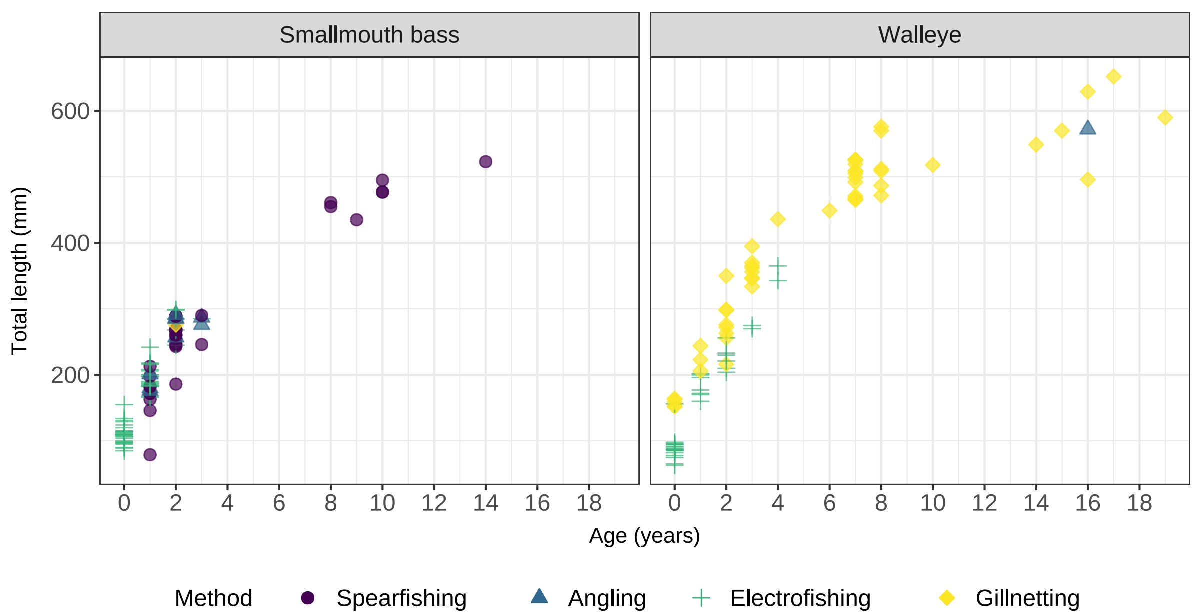

Figure 3.4. Total length (mm) versus age (years) of smallmouth bass (n = 97; left panel) and walleye (n = 92; right panel) captured from Clear Lake, Manitoba and visually analyzed for diet. Captures were plotted by fishing method.

Diet Contents

The visual analysis identified 19 orders, 17 invertebrate families, and 4 fish species. Several insect families were detected in both walleye and smallmouth bass guts, with many families being rare or limited to the diets of a few fish. Smallmouth bass mainly ate bony fishes and crayfish all summer (Table 3.2). The *FO* decreased in July for all taxa apart from crayfish and leeches. Shifts in seasonal diet were less clear for walleye due to insufficient data for June. Regardless, for walleye, bony fishes and leeches were the most important diet items throughout the sampling period. In July, walleye primarily consumed leeches and fish, but in August, their diet shifted towards a greater consumption of fish, with a decrease in their reliance on leeches (Table 3.2).

Table 3.2. Frequency of prey occurrence of stomachs collected from smallmouth bass and walleye captured by month in Clear Lake, Manitoba. Group totals include unidentified and identified species.

Month	Bony fishes	Crayfish	Mayflies	True flies	Leeches	Roundworms
Smallmouth bass						
June (*n* = 4)	75%	75%	50%	25%	25%	50%
July (*n* = 38	52%	53%	32%	13%	32%	45%
August (*n* = 55)	87%	29%	24%	22%	13%	25%
Walleye						
June (*n* = 1)	100%	0%	0%	0%	0%	100%
July (*n* = 52)	42%	19%	29%	29%	67%	29%
August (*n* = 39)	74%	18%	10%	3%	5%	3%

Bony fishes were the primary prey for smallmouth bass (74%) and walleye (56%). Among the bony fishes identified, yellow perch (*Perca flavescens*) were the dominant prey for smallmouth bass (24%) and walleye (16%), followed by crayfish for smallmouth bass (40%) and leeches for walleye (40%) (Figure 3.5). See Appendix B, Table B 3 for scientific order names and Figure B 1 for the frequency of occurrence (*FO*) of prey items grouped by order.

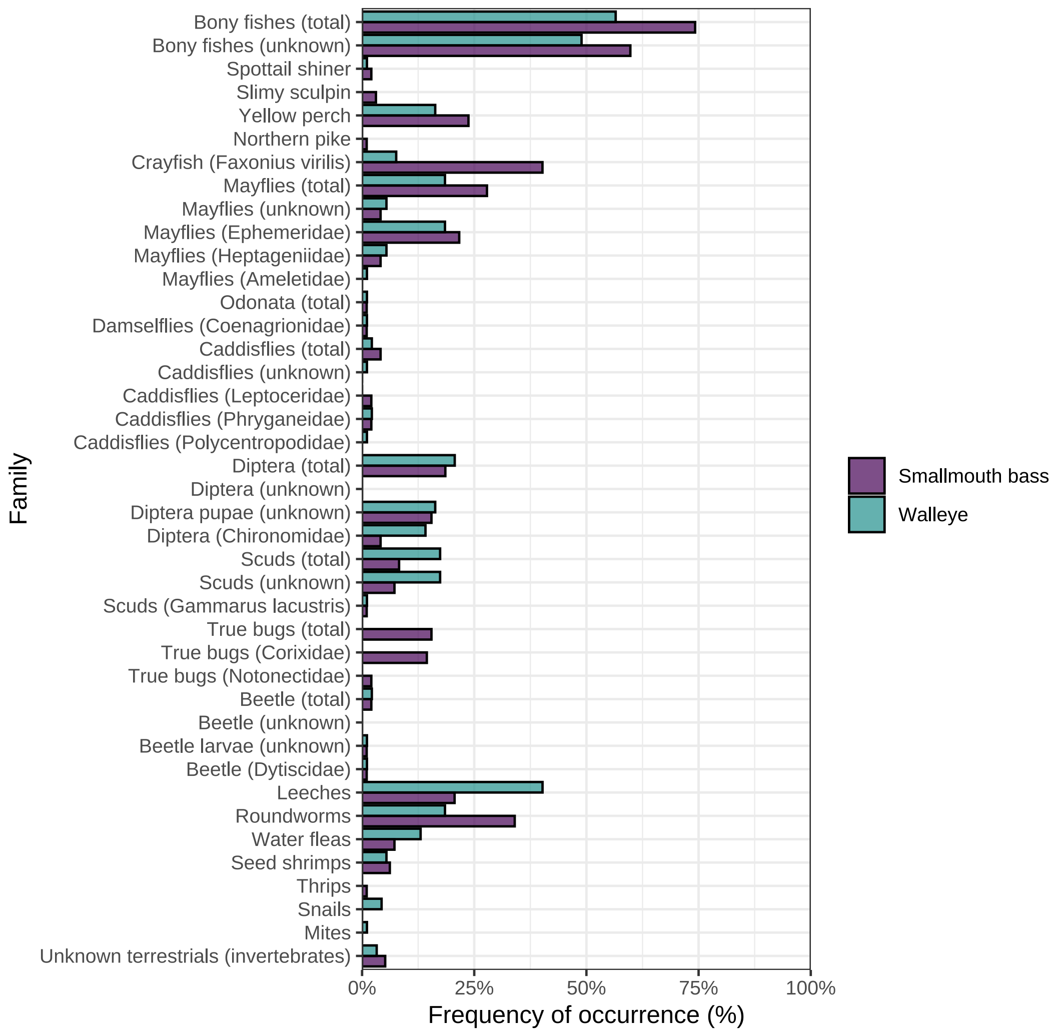

Figure 3.5. Visual diet analysis of stomach contents collected from smallmouth bass (*n* = 97) and walleye (*n* = 92) using frequency of occurrence. Scientific order names (Appendix B, Table B 3) were converted to common names. 'Total' represents the combined counts of identified and unidentified items in each category. 'Unknown' refers to unidentified diet items.

Crayfish and insects became important prey items for bass larger than 200 mm in length (Figure 3.6). Amphipods, leeches, and roundworms were less important. Walleye also relied heavily on bony fishes (ranging from 13% – 64% of their diets) (Figure 3.6). Leeches were a consistent part of their diet across all sizes, peaking at 47% in walleye over 300 mm. Crayfish, amphipods, and roundworms were less important in their diet. Additional details on size categories and mean total length (mm) for smallmouth bass and walleye are provided in Appendix B, Table B 4.

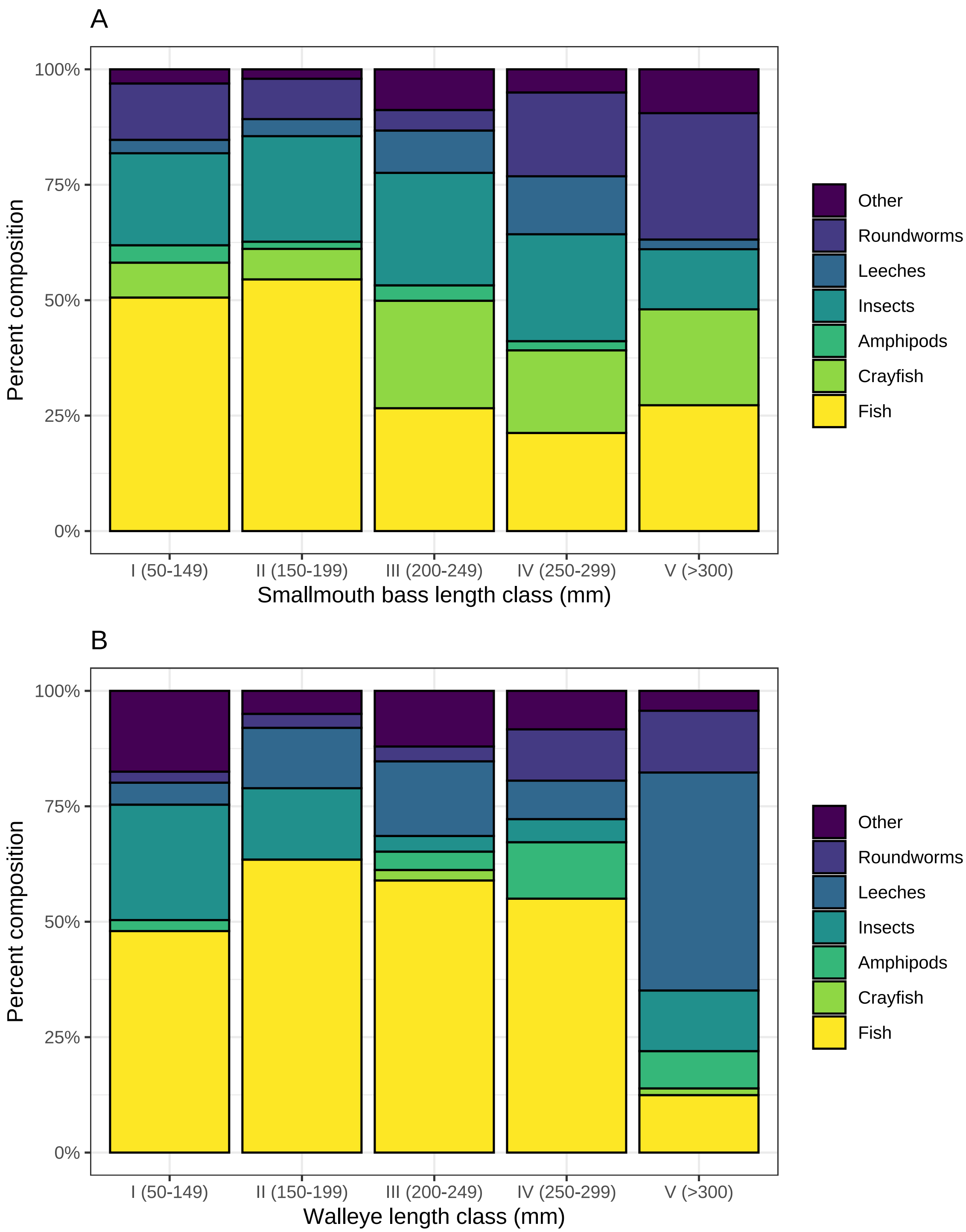

Figure 3.6. Comparison of diet composition by proportion and size class (I – V) for smallmouth bass (A) and walleye (B) collected in Clear Lake, Manitoba from June – August 2022. Mean percent composition is reported for the six most prevalent prey items (grouped by family) with other prey items grouped as ‘Other’.

Juvenile smallmouth bass (50 – 149 mm, size class I) mainly ate fish (51%) and insects (20%) (Figure 3.7). Among bass smaller than 100 mm (*n* = 9), 56% had fish in their stomachs, two had crayfish, and two had insects. Similarly, juvenile walleye (50 – 149 mm) consumed fish (48%) and insects (25%) (Figure 3.7). Across all sizes, smallmouth bass ate mainly bony fishes (39%) and insects (22%), while the walleye's diet was dominated by bony fishes (36%) and leeches (26%), with insects (14%) being less important (Figure 3.7).

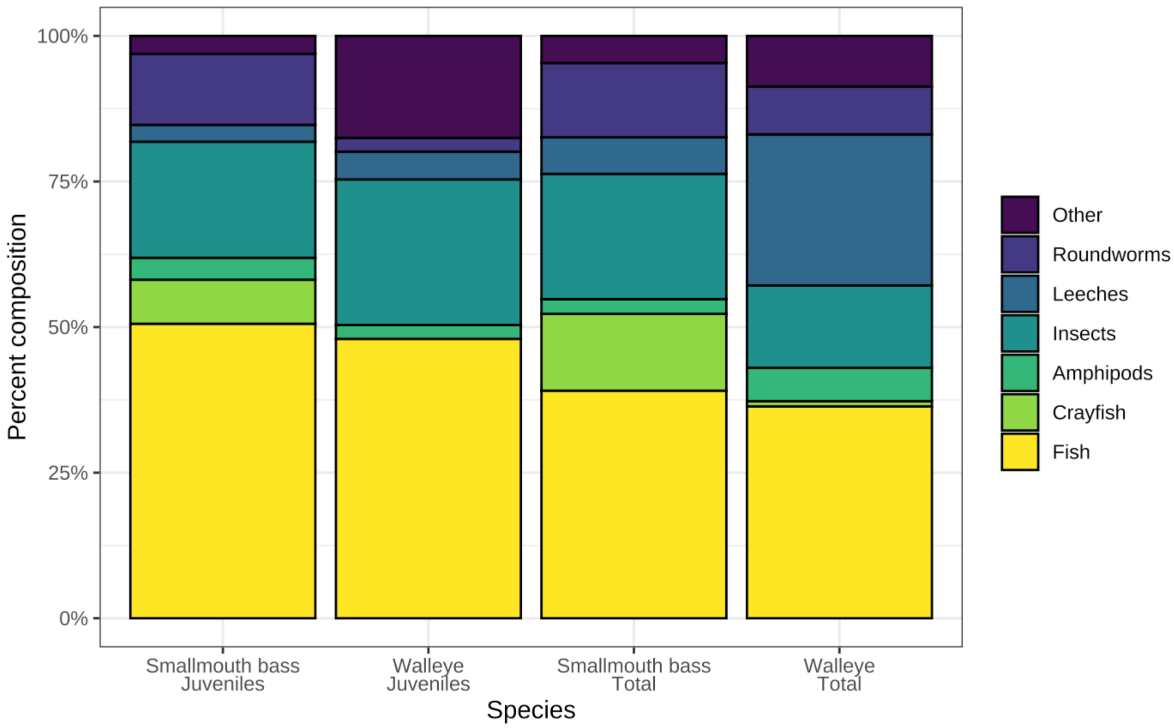

Figure 3.7. Comparison of diet composition by proportion and size class for smallmouth bass and walleye collected in Clear Lake, Manitoba from June – August 2022. Mean percent composition is reported for the six most prevalent prey items (grouped by family) recorded in both species' diets; all other prey items are grouped as 'Other'. Juveniles represent fish smaller than 149 mm total length (smallmouth bass *n* = 31, walleye *n* = 21). Totals represent all sizes for each species (smallmouth bass *n* = 97, walleye *n* = 92).

Diet Overlap

The diet overlap (α) between smallmouth bass and walleye was 0.477, indicating that there was not a significant overlap between these two species in Clear Lake. However, variations in dietary overlap were observed within each species when categorized by size class (Appendix B, Figure B 2). For smallmouth bass, the lowest overlap occurred between size class II and V (0.321), while the highest overlap was observed between size class I and II (0.734). For walleye, the lowest overlap occurred between size class I and V (0.191), while the highest overlap was between size class III and IV (0.602). Scores tended to be higher between adjacent size classes and decreased with greater size differences.

Smallmouth bass and walleye gut contents were different (PERMANOVA, $F_{(1)} = 6.21$, $p < 0.001$; Appendix B, Table B 5). The species explained a small (3%), but significant, amount of the variation in gut contents ($R^2 = 0.03$). Smallmouth bass and walleye diets also differed based on the capture method (PERMANOVA, $F_{(3)} = 2.45$, $p = 0.001$, $F_{(2)} = 5.53$, $p = 0.001$; Appendix B, Table B 6, respectively). Capture methods for walleye explained a greater proportion (11%) of the variation in gut contents compared to smallmouth bass (7%) ($R^2 = 0.11$ and $R^2 = 0.07$, respectively).

Specifically, diet contents of smallmouth bass collected by electrofishing were different from spearfishing and angling ($F_{(1)} = 5.12$, $p = 0.001$, $F_{(1)} = 2.18$, $p = 0.029$; Appendix B, Table B 6, respectively), indicating that fishing method explained 6% and 3% of the variation in diet contents ($R^2 = 0.06$ and $R^2 = 0.03$, respectively). For walleye, diet contents from electrofishing were different from gillnetting ($F_{(1)} = 9.97$, $p = 0.001$; Appendix B, Table B 6), indicating that the fishing method explained a greater proportion (10%) of the variation in gut contents ($R^2 = 0.10$).

NMDS provided visual insights into diet overlap trends, revealing notable distinctions in comparison to the PERMANOVA results. The analysis converged in 2 dimensions with a stress of 0.17, meeting the threshold for useable pattern analysis ($k = 2$, stress = 0.17; Figure 3.8). Visually, some similarity in diets were observed between smallmouth bass and walleye through NMDS, as shown by the proximity of points and clusters on the plot. Distinct patterns were observed between the species, specifically the separation of walleye greater than 300 mm (total length) on the first axis (Figure 3.8). A total of 40 walleye were within this size class, most of which were captured by gillnetting (93%).

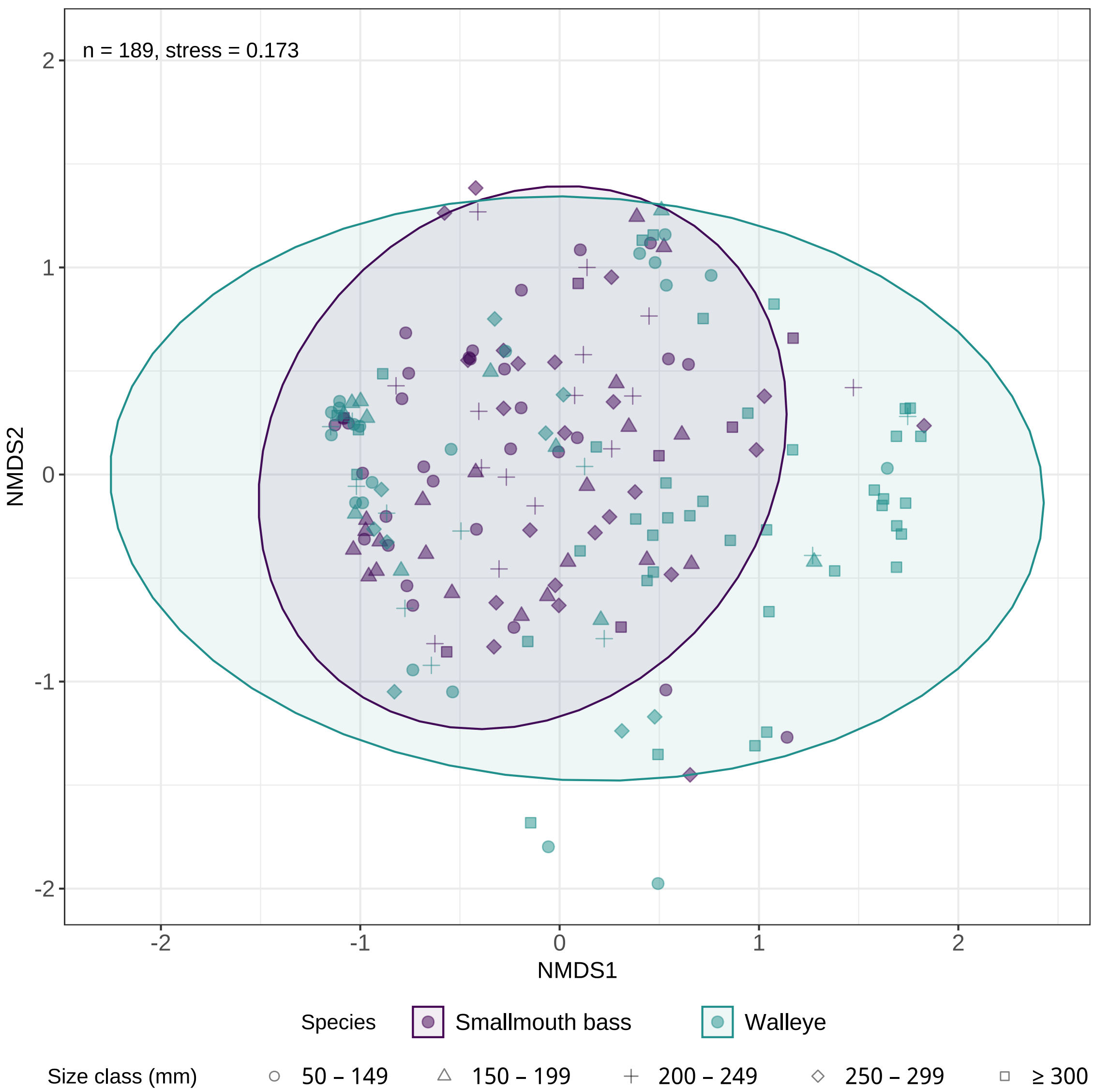

Figure 3.8. Nonmetric multidimensional scaling (NMDS) ordination based on Chao-Jaccard dissimilarities using prey items identified in stomachs of smallmouth bass (n = 97) and walleye (n = 92) in Clear Lake, Manitoba. Smallmouth bass (purple) and walleye (blue) ellipses represent 95% confidence intervals of species-specific centroids, while shapes represent the size classes. The analysis had a stress value of 0.17.

Spearman's correlation for prey abundances in fish guts with NMDS axis score displayed dietary trends (Figure 3.9). On the first axis, differences in diet were primarily driven by walleye with high abundances of leeches and lower consumption of fish, while smallmouth bass were associated with high abundances of insects and roundworms (NMDS axis 1: Spearman rank correlation coefficients, $\rho_{\text{Leeches (187)}} = 0.63$, $p < 0.001$; $\rho_{\text{Fish (187)}} = -0.61$, $p < 0.001$; $\rho_{\text{Insects (187)}} = 0.37$, $p < 0.001$; $\rho_{\text{Roundworms (187)}} = 0.31$, $p < 0.001$; Figure 3.9). On the second axis, differences in diet were primarily driven by smallmouth bass with high abundances of insects and lower consumption of fish, roundworms, and 'Other' by walleye (NMDS axis 2: Spearman rank correlation coefficients, $\rho_{Insects\ (187)} = 0.33$, $\rho_{Fish\ (187)} = -0.40$, $p < 0.001$; $p < 0.001$; $\rho_{Roundworms\ (187)} = -0.40$, $p < 0.001$; $\rho_{Other\ (187)} = -0.48$, $p < 0.001$; Figure 3.9).

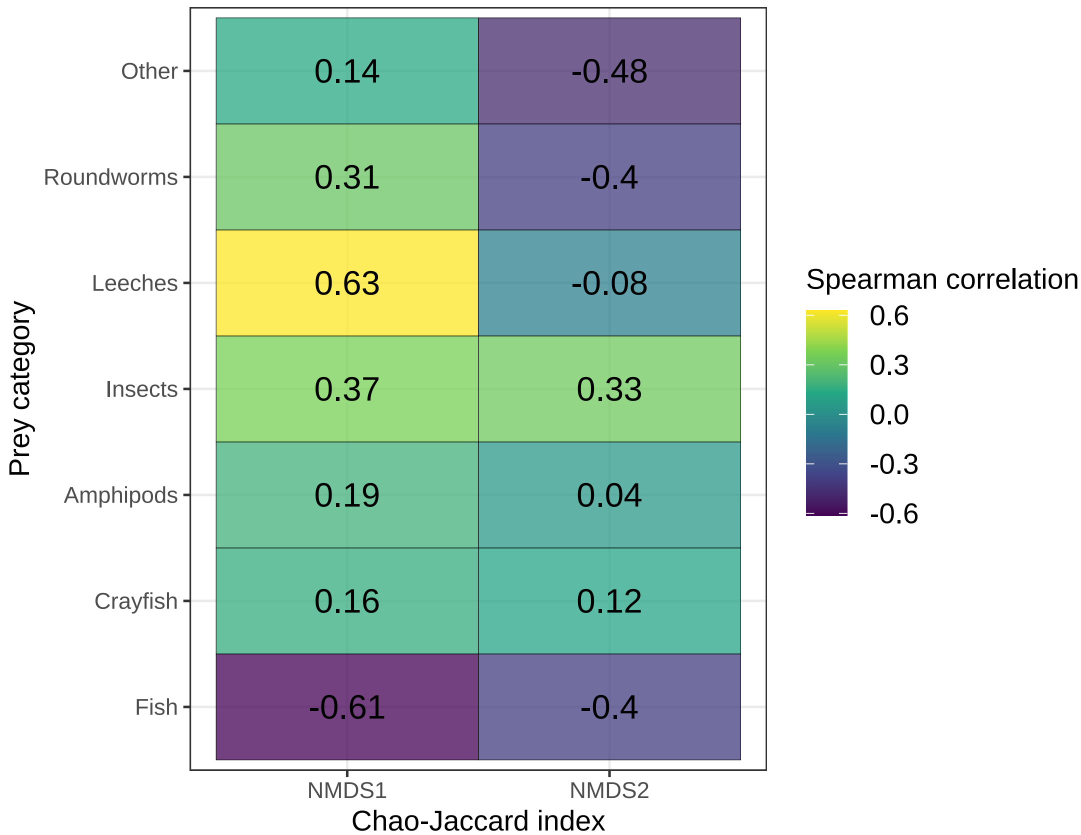

Figure 3.9. Spearman's correlation coefficients for prey abundances in species with nonmetric multidimensional scaling (NMDS) axis scores and Chao-Jaccard similarity index. The correlation coefficients indicate the strength of associations between fish species and diet items.

DISCUSSION

Both smallmouth bass and walleye had diverse diets that included bony fishes and invertebrates. Smallmouth bass also tended to eat larger prey like crayfish while smaller prey like invertebrates were more common for walleye. These findings align with previous studies that demonstrated smallmouth bass' preference for larger prey items (Pflugr and Pauley

1984, Weidel et al. 2000) and walleye's preference for small fish and invertebrates (Frey et al. 2003).

Diets varied among size classes for both smallmouth bass and walleye, with greater overlaps between adjacent classes. This suggests that as the species grow, their diets become more different, supporting the occurrence of ontogenetic shifts. While previous studies have documented that the diet of a smallmouth bass shifts from insectivory to piscivory when they reach a total length of about 150 mm (Weidel et al. 2000, Tabor et al. 2007), we found smallmouth bass smaller than 100 mm were consuming fish, crayfish, and insects. It is possible that smallmouth bass in Clear Lake may be undergoing dietary shifts earlier in their life cycle or they are growing more slowly compared to other populations. Margetts (2022) also found piscivory in smallmouth bass smaller than 115 mm but the cause of this shift and prevalence of this phenomenon remain unclear.

Factors influencing dietary shifts in smallmouth bass have been well documented, including prey availability, competition, environmental conditions, predation risk, and ontogenetic changes (Pflugr and Pauley 1984, Weidel et al. 2000, Sweka and Hartman 2003, Berra 2007, Beck 2013). Recognizing the dynamic nature of predator-prey interactions is essential for interpreting our results within the context of both inherent preferences and fluctuating prey availability. This dual influence underscores the complexity of predator-prey dynamics and emphasizes the need for a nuanced interpretation of the dietary shifts observed. Accounting for both preference ranking and prey availability is essential for a comprehensive understanding of the drivers behind dietary changes observed in the smallmouth bass and walleye population in Clear Lake. Future studies should assess how these factors impact dietary shifts in introduced smallmouth bass populations compared to their native range.

Among walleye, fish was the most common prey across all size classes, except for the largest category (exceeding 300 mm in total length), which frequently consumed leeches. Previous research indicates that walleye diet patterns exhibit spatiotemporal variation driven by factors such as habitat characteristics, prey diversity, and shifts in prey abundance (Staton et al. 2014, Happel et al. 2015, Koenig et al. 2022). In this study, observed differences in walleye diets likely stemmed from differences in habitat characteristics among capture sites. The majority of walleye in the > 300 mm size category were captured in areas of isolated habitat, which in turn may have influenced the availability and diversity of prey items.

Schoener's similarity index was below the significance threshold of 0.6 (Schoener 1970), indicating that there was not a significant diet overlap between these two species in Clear Lake (overlap $\alpha = 0.477$). This finding aligns with prior research, which suggested that the two species might not be in direct competition for food resources (Frey et al. 2003). Differences in diet were primarily driven by walleye larger than 300 mm eating more leeches and fewer fish. In Falcon Lake, Manitoba, Fedonrk (1966) found that the presence of crayfish reduces the diet overlap between smallmouth bass and walleye. If smallmouth bass deplete the crayfish population in Clear Lake, this may increase diet overlap to the point of ecological significance, increasing competition with native species for food resources. It could also drive cascading impacts on the ecosystem. Because crayfish are important consumers of algae and macrophytes, their decline could result in undesirable increases in the abundance of algae and aquatic plants.

The absence of significant diet overlap between smallmouth bass and walleye in Clear Lake does not necessarily imply minimal competition for food resources. Lack of overlap can result from competitive exclusion, where one predator is effectively excluded from preying on a particular resource, creating the appearance of no overlap. If smallmouth bass deplete the crayfish population, they may compensate by increasing their consumption of alternative prey, such as yellow perch. A higher predation pressure on yellow perch by smallmouth bass could lead to increased competition with walleye. Wuellner et al. (2011) found that dominant smallmouth bass exhibited aggressive behaviours, exploiting prey before competitors had a chance to feed, while also engaging in interference competition. Recognizing that smallmouth bass' aggressive nature may allow them to outcompete walleye under prey-limiting conditions, although resource partitioning may occur over time (Wuellner et al. 2011). Further research is needed to identify factors influencing resource use to clarify whether exploitative competition, driven by factors such as crayfish depletion, may be occurring between these two species.

Elucidating the factors that influence diet and feeding behaviour at different life stages requires collecting individuals of a wide range of sizes. Because smallmouth bass were recently introduced, older and therefore larger size classes were difficult to collect. There were no smallmouth bass caught between 300 – 435 mm, representing an absence of fish aged 4 – 7 years. When assessing dietary overlap, samples are ideally collected from areas occupied by both species. We employed multiple capture methods to achieve size class representation, but found that diet results were influenced by the capture method, especially in walleye. While electrofishing was effective for capturing small walleye in areas where habitat was shared with smallmouth bass, a supplemental method was needed to capture larger walleye. Gillnetting was effective for capturing large walleye, but had an unacceptable rate of bycatch in areas of shared habitat. This led us to shift to gillnetting in areas less suitable for smallmouth bass. Future studies should aim to obtain a range of size classes but ensure that collection is done in habitat suitable for both species while limiting bycatch to the extent possible.

Smallmouth bass and walleye gut contents varied seasonally in Clear Lake. The data in this study were collected in the summer (from June 16 – August 12, 2022), which may have influenced the level of piscivory we observed in both species. Though not the focus of this study, diets of smallmouth bass and walleye can be influenced by seasonal variation in prey availability (Fisheries and Oceans Canada 2010, Beck 2013). To obtain a comprehensive understanding of fish diets and species interactions in Clear Lake, sampling of prey availability, could be beneficial to identify feeding preferences. If competition is present, prompt management interventions may be required.

Management Recommendations

The introduction of invasive smallmouth bass in Clear Lake raised concerns about its potential impacts on native fish populations, particularly walleye. Our main objective was to quantify their diets and assess the degree of diet overlap. The outcomes from this study provide specific management recommendations for smallmouth bass in Clear Lake.

1. *Determine broader food web impacts of the smallmouth bass invasion*.

Walleye is the primary species harvested by Keeseekoowenin Ojibway First Nation (KOFN) and is highly sought-after by local recreational fishers. This study was focused on assessing competitive interactions between bass and walleye, but the introduction of smallmouth bass has broader food web implications for Clear Lake. To characterize the potential impacts of bass on the ecosystem and better understand the population-level effects of trophic interactions, further assessment of native species in Clear Lake is needed. For example, smallmouth bass frequently consumed yellow perch, an important resource for other native populations such as northern pike.

If electrofishing is being used for control, then information could be collected on bycatch species. To reduce impacts on native species, non-destructive diet analysis techniques such as DNA barcoding of fish feces could be considered. DNA barcoding of stomach contents has been shown to identify a greater number of prey species compared to morphological identification (Riccioni et al. 2018), but the technique still requires euthanasia or invasive extraction of gut contents (*i.e.*, manual regurgitation) (Symondson 2002, Guillerault et al. 2017, Nelson et al. 2017). A promising alternative is a non-invasive technique that performs DNA barcoding of fish feces, which can be gently expelled from a fish, allowing the fish to be released unharmed (Corse et al. 2010, Vachon unpublished data). Although feces-based diet analysis has been used for birds and mammals (Ando et al. 2020, Spence et al. 2022), its application in aquatic species has been limited. This technique has the potential to be widely applicable, particularly in the characterization of diets for species that hold cultural or conservation significance, including species at risk.

2. *Study population dynamics of crayfish*.

Studying the population dynamics of crayfish in Clear Lake, including the potential effects of smallmouth bass predation, would provide insight into the trophic interactions occurring within the ecosystem. This could be achieved by conducting ongoing monitoring of the virile crayfish (*Faxonius virilis*) population. Monitoring surveys conducted in the summers of 2021 and 2022 showed a decline in crayfish abundance during this period (Parks Canada unpublished data). However, further investigation is needed to determine whether this decline was due to smallmouth bass predation, other ecological factors, or simply natural variability over time. Previous studies have shown that smallmouth bass introductions may reduce crayfish abundance (Mather and Stein 1993), which could indirectly alter habitat complexity and cause changes in the benthic invertebrate community (Kerr and Grant 2000). Given that crayfish consume periphyton and macrophytes (Nyström et al. 1996, Bondar et al. 2005), a decrease in crayfish abundance may boost populations of periphyton and macrophytes, and disrupt the pathways involved in decomposing detritus. Therefore, monitoring of benthic algae and macrophytes may be beneficial.

Conclusion

In conclusion, this study examined the dietary overlap between invasive smallmouth bass and walleye in Clear Lake. The findings revealed that (1) bony fishes were the most frequently consumed prey for both species, (2) there was not a significant dietary overlap between the two species, and (3) differences in diet were driven primarily by walleye feeding habits. The invasion of smallmouth bass in Clear Lake has broader food web implications, including impacts on native fish populations and the availability of important prey species like yellow perch. Identifying food web impacts, studying population dynamics of crayfish, and exploring the use of non-destructive diet analysis techniques would be beneficial for guiding management decisions and supporting the long-term health of the Clear Lake ecosystem.

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CHAPTER 4 CONCLUSION AND MANAGEMENT RECOMMENDATIONS

Results from this research project revealed some key findings and practical management recommendations concerning the smallmouth bass invasion in Clear Lake, Manitoba. This chapter covers key findings from both studies, the significance of this research, general management recommendations, and recommendations for Clear Lake.

KEY FINDINGS

Suppression

Catch rates for spearfishing in Clear Lake (43.9 ± 17.5 fish h^{-1}, ±SE) were more than triple those for angling in Cultus Lake (13.0 ± 1.7 fish h^{-1}, ±SE). Spearfishing was also able to capture both smaller and larger adult males compared to angling in Cultus Lake and electrofishing in Clear Lake (Kolmogorov-Smirnov, $Z_{(102)} = 0.36$, $p = 0.037$; $Z_{(21)} = 0.73$, $p = 0.003$, respectively). Our results suggest that spearfishing is able to improve catch rates and biomass yields, thereby highlighting its potential as an effective method for invasive smallmouth bass control.

Angling achieved the lowest catch per unit effort (CPUE) of the methods compared in this study, proving to be the least effective method for capturing smallmouth bass. In Clear Lake, electrofishing was effective at capturing juvenile smallmouth bass but not adults. Because strategies that only target adults can lead to overcompensation (Loppnow et al. 2013), a multi-pronged approach may be needed to capture both juveniles and adults. Strategies that target eggs and fry (via adult removal) combined with young-of-the-year (YOY) removal are most effective (Loppnow 2017). In Clear Lake, we found that spearfishing was effective for capturing adult smallmouth bass and electrofishing was effective for capturing juveniles, so combining these methods may be beneficial for controlling invasive bass and preventing overcompensation.

In this study, spearfishers rapidly developed skills to effectively capture mature males, and there was no bycatch. As the study progressed, the number of missed shots decreased (Spearman rank correlation coefficients, $\rho_{missed\ (75)} = -0.47$, $p = 0.01$), indicating that accuracy improved. The total number of shots taken to capture a fish also decreased (Spearman rank correlation coefficients, $\rho_{total\ (75)} = -0.29$, $p < 0.01$), indicating that skills improved with time and experience.

Diet Overlap

Both smallmouth bass and walleye had diverse diets that included bony fishes and invertebrates. Smallmouth bass also tended to eat larger prey like crayfish while smaller prey like invertebrates were common for walleye. While previous studies have documented that the diet of a smallmouth bass shifts from insectivory to piscivory when they reach a total length of about 150 mm (Weidel et al. 2000, Tabor et al. 2007), we found smallmouth bass smaller than 100 mm were consuming fish, crayfish, and insects. It is possible that smallmouth bass in Clear Lake may be undergoing dietary shifts earlier in their life cycle or they are growing more slowly compared to other populations.

Among walleye, fish was the most common prey across all size classes, except for the largest category (exceeding 300 mm in total length), which frequently consumed leeches. Observed differences in walleye diets likely stemmed from differences in habitat characteristics among capture sites. The majority of walleye in the > 300 mm size category were captured in areas of isolated habitat, which in turn may have influenced the availability and diversity of prey items.

Schoener's similarity index was below the significance threshold of 0.6 (Schoener 1970), indicating that there was not a significant overlap between these two species in Clear Lake (overlap $\alpha = 0.477$). PERMANOVA results were consistent, smallmouth bass and walleye gut contents were different (PERMANOVA, $F_{(1)} = 6.21$, $p < 0.001$). Smallmouth bass and walleye diets also differed based on the capture method (PERMANOVA, $F_{(3)} = 2.45$, $p = 0.001$, $F_{(2)} = 5.53$, $p = 0.001$, respectively).

NMDS provided visual insights into diet overlap trends, revealing notable distinctions in comparison to the PERMANOVA results. Distinct patterns were observed between the species, specifically the separation of walleye greater than 300 mm (total length) on the first axis ($k = 2$, stress = 0.17). A total of 40 walleye were within this size class, most of which were captured by gillnetting (93%).

Spearman's correlation results suggested similar dietary trends as the NMDS plot. On the first axis, differences in diet were primarily driven by walleye with high abundances of leeches and lower consumption of fish, while smallmouth bass were associated with high abundances of insects and roundworms (NMDS axis 1: Spearman rank correlation coefficients, $\rho_{\text{Leeches (187)}} = 0.63$, $p < 0.001$; $\rho_{\text{Fish (187)}} = -0.61$, $p < 0.001$; $\rho_{\text{Insects (187)}} = 0.37$, p <

0.001; $\rho_{Roundworms\ (187)} = 0.31$, $p < 0.001$). On the second axis, differences in diet were primarily driven by smallmouth bass with high abundances of insects and lower consumption of fish, roundworms, and 'Other' by walleye (NMDS axis 2: Spearman rank correlation coefficients, $\rho_{Insects\ (187)} = 0.33$, $\rho_{Fish\ (187)} = -0.40$, $p < 0.001$; $p < 0.001$; $\rho_{Roundworms\ (187)} = -0.40$, $p < 0.001$; $\rho_{Other\ (187)} = -0.48$, $p < 0.001$).

SIGNIFICANCE OF RESEARCH

This was the first study to assess the practical use of spearfishing as a control method for invasive smallmouth bass. Findings could be used to inform the co-development of a strategy to collaboratively manage invasive bass in Clear Lake. Broadly, it will also improve the ability of regulators and managers to make decisions about invasive bass control, including for established infestations and rapid response to new occurrences.

The diet analysis study sheds light on prey frequency and feeding habits of smallmouth bass and walleye in Clear Lake, including their tendencies towards larger or smaller prey items. This study also highlights the need for monitoring of prey availability and diversity, as well as the potential impacts on the broader food web dynamics within Clear Lake. Management recommendations are discussed in more detail below.

MANAGEMENT RECOMMENDATIONS

General Recommendations for Smallmouth Bass Invasions

Different systems may require different techniques to enhance removal methods, improve catchability, and achieve control. The outcomes from Chapter 2 provide informative general management recommendations for smallmouth bass control.

1. *Use spearfishing for adult removal where appropriate*.

Where feasible, fisheries managers should consider the method as part of a multi-pronged approach to managing invasive smallmouth bass. To determine whether spearfishing is appropriate for their program, managers would want to consider the following: bycatch, costs, local regulations, safety, water quality, training, and system-specific information about the gear types that are most effective for adult removal. As regulations on spearfishing vary by jurisdiction, it is important to be aware of local regulations and apply for permits if required. Fisheries managers should also consider specialized training, evacuation plans, boat traffic, and logistics. Spearfishing requires a specific set of skills. Training in first aid, oxygen administration, and completing routine dive rescue drills can help ensure the safety of crews. Professional training is not essential but may be beneficial. Using a certified trainer could teach proper techniques, expedite skill development, and ensure safe practices are followed. By combining safety measures and strategic planning, spearfishing can be an effective supplementary control strategy for managing invasive smallmouth bass.

2. *Determine size and structure of the invasive smallmouth bass population*.

Mark-recapture studies provide insights into population dynamics, reproductive success, and survival rates of invasive smallmouth bass (Restif et al. 2012, van Poorten and Beck 2021). Based on population estimates, a simulation model could be developed to project the potential population dynamics of invasive smallmouth bass over time and under different control treatments (*i.e.*, spearfishing and electrofishing). For instance, Loppnow and Venturelli (2014) developed an individual-based model to simulate options for smallmouth bass control via induced nest failure. Their research suggested there are many feasible combinations of YOY removal and supplemental removal that could achieve control in less than 10 years. Estimating the optimal duration and frequency of treatments can contribute to evidence-based decision-making for implementing effective control strategies.

3. *Study movement and spatial distribution of the smallmouth bass*.

Acoustic telemetry can be used to track the bass' movements and spatial distribution, which may provide insights into habitat use and movement patterns (Gutowsky et al. 2020). This information could be used to enhance removal methods and improve catchability (Loppnow et al. 2013). This information may also help locate aggregations of smallmouth bass during spawning or winter shoaling and inform targeted control (Bajer et al. 2011). Since increased fishing pressure has been shown to help control invasive fish (Moore et al. 2005), sharing location data would help citizen scientists in locating bass, enabling effective targeting for removal. This approach provides an additional method of control while engaging the community in removal efforts.

Smallmouth Bass Management in Riding Mountain National Park

The introduction of invasive smallmouth bass in Clear Lake raised concerns about its potential impacts on native fish populations, particularly walleye. Our main objective was to quantify their diets and assess the degree of diet overlap. The outcomes from Chapter 3 provide specific management recommendations for smallmouth bass in Clear Lake.

1. *Determine broader food web impacts of the smallmouth bass invasion*.

Walleye is the primary species harvested by Keeseekoowenin Ojibway First Nation (KOFN) and is highly sought-after by local recreational fishers. This study was focused on assessing competitive interactions with walleye, but the introduction of smallmouth bass has broader food web implications for Clear Lake. To characterize the potential impacts of bass on the ecosystem and better understand the population-level effects of trophic interactions, further assessment of native species in Clear Lake is needed. For example, smallmouth bass frequently consumed yellow perch, an important resource for other native populations such as northern pike.

If electrofishing is being used for control, then information could be collected on bycatch species. To reduce impacts on native species, non-destructive diet analysis techniques such as DNA barcoding of fish feces could be considered. DNA barcoding of stomach contents has been shown to identify a greater number of prey species compared to morphological identification (Riccioni et al. 2018), but the technique still requires euthanasia or invasive extraction of gut contents (*i.e.*, manual regurgitation) (Symondson 2002, Guillerault et al. 2017, Nelson et al. 2017). A promising alternative is a non-invasive technique that performs DNA barcoding of fish feces, which can be gently expelled from a fish, allowing the fish to be released unharmed (Corse et al. 2010, Vachon unpublished data). Although feces-based diet analysis has been used for birds and mammals (Ando et al. 2020, Spence et al. 2022), its application in aquatic species has been limited. This technique has the potential to be widely applicable, particularly in the characterization of diets for species that hold cultural or conservation significance, including species at risk.

2. *Study population dynamics of crayfish*.

Studying the population dynamics of crayfish in Clear Lake, including the potential effects of smallmouth bass predation, would provide insight into the trophic interactions occurring in Clear Lake. This could be achieved by conducting ongoing monitoring of the virile crayfish (*Faxonius virilis*) population. Monitoring surveys conducted in the summers of 2021 and 2022 showed a decline in crayfish abundance during this period (Parks Canada unpublished data). However, further investigation is needed to determine whether this decline was due to smallmouth bass predation, other ecological factors, or simply natural variability over time. Previous studies have shown that smallmouth bass introductions may reduce crayfish abundance (Mather and Stein 1993), which could indirectly alter habitat complexity and cause changes in the benthic invertebrate community (Kerr and Grant 2000). Given that crayfish consume periphyton and macrophytes (Nyström et al. 1996, Bondar et al. 2005), a decrease in crayfish abundance may boost populations of periphyton and macrophytes, and disrupt the pathways involved in decomposing detritus. Therefore, monitoring of benthic algae and macrophytes may be beneficial.

CONCLUSION

Spearfishing showed potential as a technique for suppressing invasive smallmouth bass in Clear Lake. Spearfishing may also be appropriate for controlling other invasive fish species that have similar behaviours and vulnerable life stages. There are 41 bony fish families that display nest-guarding behaviour (Blumer 1982). While this study focused on invasive smallmouth bass, spearfishing may be applicable for controlling other large-bodied, nest-guarding, invasive, freshwater fish in Canada and beyond.

The invasion of smallmouth bass in Clear Lake has broader food web implications, including impacts on native fish populations and the availability of important prey species like yellow perch. Identifying food web impacts, studying population dynamics of crayfish, and exploring the use of non-destructive diet analysis techniques would be beneficial for guiding management decisions and supporting the long-term health of the Clear Lake ecosystem.

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APPENDIX A

Table A 1. Scientific angling protocol used in Clear Lake, developed based on methods described by Philipp et al. (2015). Different anglers could be selected between phases (after the 10-minute break) and anglers could choose to start with either phase. Phases could be repeated once. Nests were visited by anglers in a boat anchored ~ 10 m away or directly from docks when possible. Each cast landed the lure directly on the nest, and an underwater camera recorded fish behaviour (counts of hits and follows).

Phase	Action	Description
Phase 1	3-lure/15 cast	Five casts using three lures in a set order. Casts continued until the fish was captured, or it received all 15 casts.
Phase 2	3-lure/3 min jig	One minute jig using three lures in a set order. Jigs continued until the fish was captured, or it received all three jigs.
Break	10-min break	If the fish was not captured, it was left undisturbed for 10 minutes.

Table A 2. Electrofishing specifications for weighted transects versus targeted spot control conducted in Clear Lake, Manitoba.

Transects	Water temperature (°C)	Depth (m)	Power (Watts)	Voltage (Volts)	Current (Amps)	Effort (h)	Total
Weighted	19.7	0.5	1140	118	10	1.1	14
Targeted Control	19.4	0.5	981	109	10	5.3	20
Total	–	–	–	–	–	6.5	34

Table A 3. Summary of the best-fit generalized linear mixed model (Gamma family with a log link). The coefficient estimates, confidence intervals (*CI*), and p-values (p), are given for the predictors.

Predictors	Estimates	*CI*	p
Spearfishing (Intercept)	37.86	19.69 – 72.79	**<0.001**
Angling	0.34	0.15 – 0.75	**0.008**
Observations	106		
Marginal R^2 / Conditional R^2	0.09 / 0.15		

Table A 4. Model selection table for generalized linear mixed model (Gamma family with a log link) to identify main effects on catch per unit effort (CPUE). The formula describes a model in which the response variable 'CPUE' is modeled as a function of 'Method' and 'Experience,' while accounting for individual variability in intercepts among different levels of the grouping variable 'FisherID.' The final model selected is indicated in bold.

Formula	K	df	logLik	AICc	Delta	Weight
CPUE ~ Method + Fisher	**3**	**4**	**-401.2**	**810.8**	**0.00**	**0.358**
CPUE ~ Method + Experience	2	4	-401.3	811.0	0.22	0.321
CPUE ~ Intercept + Fisher	2	3	-403.2	812.6	1.75	0.149
CPUE ~ Method + Experience + Fisher	4	5	-401.2	813.0	2.16	0.122
CPUE ~ Experience + Fisher	3	4	-403.2	814.7	3.91	0.051

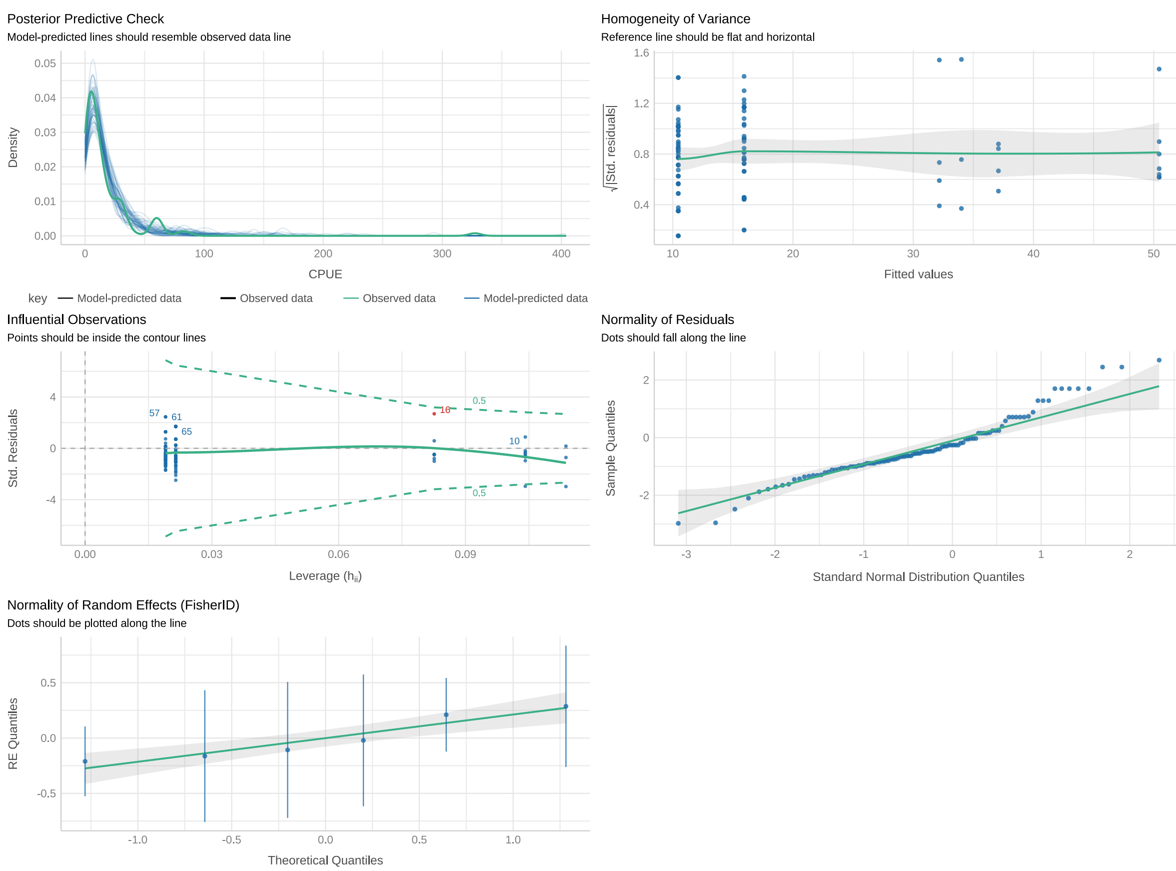

Figure A 1. Model diagnostics for best-fit generalized linear mixed model (Gamma family with a log link) used to identify main effects on catch per unit effort (CPUE).

Table A 5. Mean catch per unit effort (CPUE) of smallmouth bass captured in Clear Lake, Manitoba (spearfishing, scientific angling, electrofishing), and Cultus Lake, British Columbia (angling). Catches were categorized by life stage and fishing technique used. Dashes (–) indicate the life stage was not captured/targeted. Attempts represent individual efforts for spearfishing and angling. Electrofishing attempts represent weighted transects (14) and targeted spot control (20). See Figure 2.5 for counts of captures by life stage.

	CPUE (fish h^{-1}) ± SE				CPUE (kg h^{-1}) ± SE			
Life stage	Spearfishing[1]	Angling[1]	Electrofishing[1]	Angling[2]	Spearfishing[1]	Angling[1]	Electrofishing[1]	Angling[2]
Mature Males	43.9 ± 17.5	2.7 ± 1.8	1.03 ± 0.5	13.0 ± 1.7	29.7 ± 11.5	1.2 ± 0.8	0.3 ± 0.2	3.9 ± 0.6
nesting	46.5 ± 19.7	2.7 ± 1.8	–	–	32.6 ± 12.8	1.2 ± 0.8	–	–
non-nesting	23.1 ± 3.1	–	–	–	6.7 ± 0.9	–	–	–
Mature Females	210.1 ± 165.7	–	1.9 ± 0.7	16.9 ± 2.8	275.1 ± 234.9	–	0.5 ± 0.2	1.8 ± 0.4
Juveniles	7.1 ± 2.3	–	78.3 ± 17.2	18.7 ± 3.4	0.5 ± 0.2	–	6.1 ± 1.4	1.4 ± 0.4
male	37.0 ± 13.0	–	5.4 ± 1.7	–	2.7 ± 0.9	–	0.5 ± 0.2	–
female	27.3 ± 3.9	–	10.3 ± 3.0	–	2.6 ± 0.6	–	1.0 ± 0.3	–
undetermined	2.7 ± 1.9	–	62.5 ± 16.1	18.7 ± 3.4	0.1 ± 0.1	–	4.5 ± 1.3	1.4 ± 0.4
Total	34.1 ± 16.1	2.7 ± 1.8	81.2 ± 17.3	15.3 ± 1.0	32.3 ± 22.0	1.2 ± 0.8	6.9 ± 1.5	2.8 ± 0.3
Attempts	77	4	34	172	77	4	34	172
Captures	n = 33	n = 2	n = 693	n = 172	n = 33	n = 2	n = 693	n = 172

[1] Clear Lake data, failed efforts included in CPUE calculation.
[2] Cultus Lake data, failed efforts excluded in CPUE calculation.

Table A 6. Summary table of capture site and nesting characteristics for smallmouth bass captured by spearfishing in Clear Lake, MB. Water temperature (C°) and measurements (m) are represented as means while the nest developmental stage are represented as counts. Nesting refers to adult smallmouth bass associated with a nest. Non-nesting refers to smallmouth bass not associated with a nest (*i.e.*, juveniles, females, and non-spawning males).

	Surface	Bottom	Depth	Developmental Stage				Width
	(C°)	(C°)	(m)	0[a]	1[b]	2[c]	3[d]	(m)
Nesting	19.26	19.19	1.55	13	1	0	1	0.66
Non-Nesting	17.28	17.27	1.15	–	–	–	–	–
Total	19.29	19.25	1.41	13	1	0	1	0.66

Nest developmental stage was based on methods used in Ridgway and Friesen (1992) and Tufts et al. (2019).
[a] stage 0 – nest built with male present but no eggs.
[b] stage 1 – eggs present on the nest.
[c] stage 2 – eggs hatched into embryos that remain on the bottom (*i.e.*, bottom fry).
[d] stage 3 – fry elevated off the bottom and still associated with the nest (*i.e.*, swim-up fry).

Table A 7. Summary table of boat electrofishing catch. Note: walleye and smallmouth bass were not considered as bycatch because they are both considered the target species.

Species	Electrofishing	
	Kept	Returned
Smallmouth bass (*Micropterus dolomieu*)	693	0
Yellow perch (*Perca flavescens*)	0	494
Walleye (*Sander vitreus*)	49	93
White sucker (*Catostomus commersonii*)	0	15
Northern pike (*Esox lucius*)	0	13
Lake whitefish (*Coregonus clupeaformis*)	0	0
Spottail shiner (*Notropis hudsonius*)	0	19
Trout-perch (*Percopsis omiscomaycus*)	0	17
Blacknose dace (*Rhinichthys atratulus*)	0	5
Slimy sculpin (*Cottus cognatus*)	0	1
Bycatch	$n = 657$	
Total	$n = 1399$	

Table A 8. Summary of time spent on reconnaissance. General reconnaissance occurred on days before suppression. Reconnaissance was also conducted throughout the spawning period. Hybrid days represent sessions where both spearfishing and angling occured. Person hours were calculated by multiplying the total effort (hours) by the number of crew on that day and summed per reconnaissance type.

Reconnaissance	Days	Effort (h)	Person Hours
General	4	15.27	67.33
Spearfishing	8	51.12	335.68
Angling	2	15.35	47.37
Hybrid	4	16.93	123.30
Total	18	98.67	573.68

APPENDIX B

Table B 1. Summary table of boat electrofishing catch. Walleye and smallmouth bass were not considered as bycatch because they were both considered the target species.

Species	Electrofishing	
	Kept	Returned
Smallmouth bass (*Micropterus dolomieu*)	693	0
Yellow perch (*Perca flavescens*)	0	494
Walleye (*Sander vitreus*)	49	93
White sucker (*Catostomus commersonii*)	0	15
Northern pike (*Esox lucius*)	0	13
Lake whitefish (*Coregonus clupeaformis*)	0	0
Spottail shiner (*Notropis hudsonius*)	0	19
Trout-perch (*Percopsis omiscomaycus*)	0	17
Blacknose dace (*Rhinichthys atratulus*)	0	5
Slimy sculpin (*Cottus cognatus*)	0	1
Total	742	657

Table B 2. Summary table of gillnetting catch. Walleye and smallmouth bass were not considered as bycatch because they were both considered target species.

Species	Gillnetting				
	Net 1	Net 2	Net 3	Net 4	Net 5
Smallmouth bass (*Micropterus dolomieu*)	1	0	0	0	0
Yellow perch (*Perca flavescens*)	0	0	97	0	0
Walleye (*Sander vitreus*)	27	7	13	8	4
White sucker (*Catostomus commersonii*)	0	0	2	1	0
Northern pike (*Esox lucius*)	1	1	9	2	2
Lake whitefish (*Coregonus clupeaformis*)	0	0	6	0	0
Bycatch	1	1	114	3	2
Total	29	8	127	11	6

Table B 3. Frequency of prey occurrence in guts analyzed. Scientific names for orders and families are used. Identified and unidentified items are combined in 'total'. The 'unknown' category represents diet items that were not identified to family based on condition in the gut.

Order-Family	Smallmouth bass	Walleye
Bony fishes total	74.23% (59.79% unknown)	56.52% (48.91% unknown)
Cypriniformes - *Notropis hudsonius*	2.06%	1.09%
Scorpaeniformes - *Cottus cognatus*	3.09%	0.00%
Perciformes - *Perca flavescens*	23.71%	16.30%
Esociformes - *Esox lucius*	1.03%	0.00%
Decapoda - *Faxonius virilis*	40.21%	7.61%
Ephemeroptera total	27.84% (4.12% unknown)	18.48% (5.43% unknown)
Ephemeroptera - Ephemeridae	21.65%	18.48%
Ephemeroptera - Heptageniidae	4.12%	5.43%
Ephemeroptera - Ameletidae	0.00%	1.09%
Zygoptera - Coenagrionidae	1.03%	1.09%
Trichoptera total	4.12% (0.00% unknown)	2.17% (1.09% unknown)
Trichoptera - Leptoceridae	2.06%	0.00%
Trichoptera - Phryganeidae	2.06%	2.17%
Trichoptera - Polycentropodidae	0.00%	1.03%
Diptera total	18.56% (15.46% unknown)	20.65% (16.30% unknown)
Diptera - Chironomidae	4.12%	14.13%
Amphipoda total	8.25% (7.22% unknown)	17.39% (17.39% unknown)
Amphipoda - *Gammarus lacustris*	1.03%	1.09%
Hemiptera - Corixidae	14.43%	0.00%
Hemiptera - Notonectidae	2.06%	0.00%
Coleoptera total	2.06% (1.03% unknown)	2.17% (1.09% unknown)
Coleoptera - Dytiscidae	1.03%	1.09%
Hirudinea	20.62%	40.22%
Nematoda	34.02%	18.48%
Cladocera	7.22%	13.04%
Ostracoda	6.19%	5.43%
Thysanoptera	1.03%	0.00%
Gastropoda	0.00%	4.35%
Arachnida	0.00%	1.09%
Unknown terrestrials (invertebrates)	5.15%	3.26%

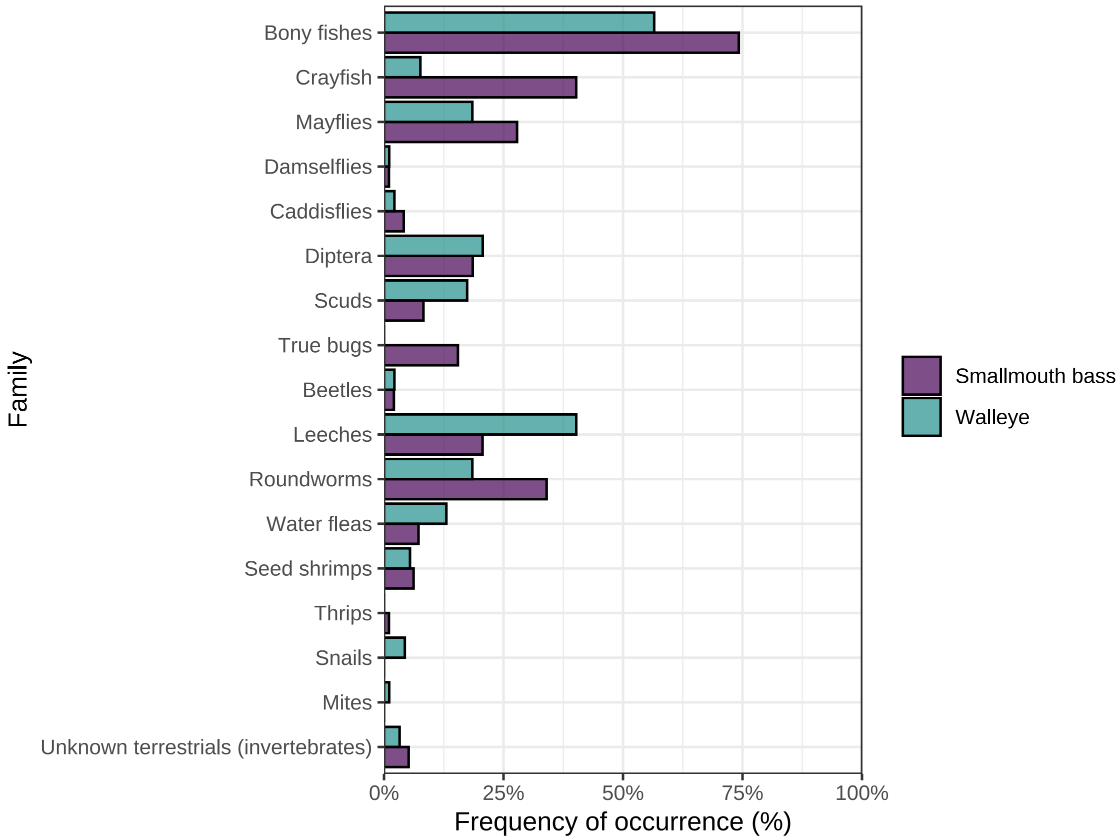

Figure B 1. Visual diet analysis of stomach contents collected from smallmouth bass (n = 97) and walleye (n = 92) using frequency of occurrence. Scientific order names were converted to common names for ease of understanding. See Table B 3 for scientific order and family names. Bony fishes include spottail shiner, slimy sculpin, yellow perch, and northern pike.

Table B 4. Total length (mm) classes for smallmouth bass (n = 97) and walleye (n = 92) dietary shift analysis.

		Smallmouth bass		Walleye	
Total Length range (mm)	Size Class	Total Length (mm) ± SD	Sampled n	Total Length (mm) ± SD	Sampled n
50 – 149	I	108.7 ± 14.4	31	85.9 ± 9.0	21
150 – 199	II	180.6 ± 11.2	21	165.6 ± 12.2	11
200 – 249	III	223.1 ± 18.4	15	217.2 ± 13.7	11
250 – 299	IV	278.2 ± 13.0	23	273.9 ± 14.9	9
≥ 300	V	474.7 ± 26.5	7	475.0 ± 84.7	40
Total	I-V	208.6 ± 99.4	97	298.7 ± 173.3	92

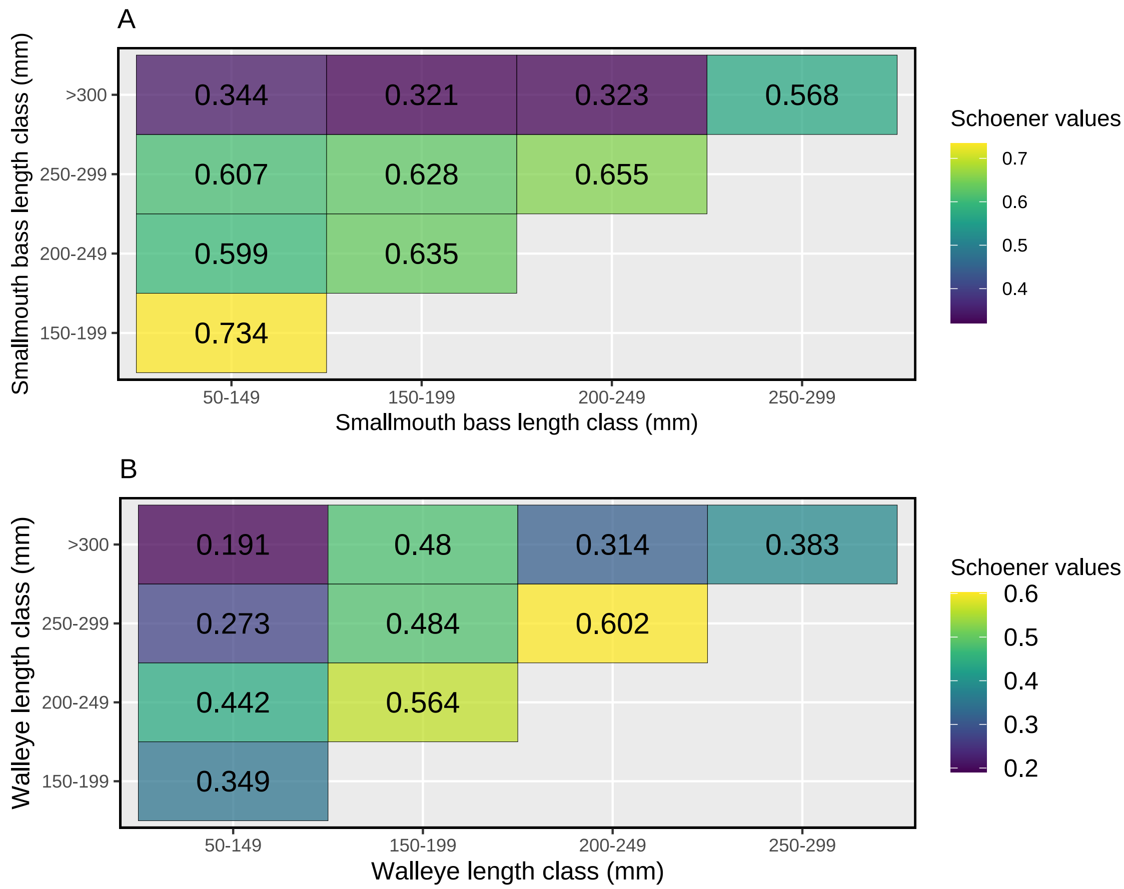

Figure B 2. Schoener's similarity matrix between size classes (I – V) for smallmouth bass (A) and walleye (B) in Clear Lake, Manitoba. Scores represent comparisons of mean proportions of gut contents for each diet item. Scores > 0.6 and < 0.4 are considered ecologically important and represent high and low levels of diet overlap.

Table B 5. Results of PERMANOVA analysis testing for differences in diet contents between smallmouth bass and walleye. The table displays the degrees of freedom (df), sums of squares, R-squared values (R^2), F-statistic (F), and associated significance (p-value).

	df	Sum of Squares	R^2	F	p-value
Species	1	2.284	0.0322	6.2128	0.001
Residual	187	68.751	0.9678	–	–
Total	188	71.035	1.0000	–	–

Table B 6. Summary table comparing species diet contents by the fishing method used. Table includes methods compared, degrees of freedom (df), sums of squares, R-squared values (R^2), F-statistics (F), and associated significance (p-value).

Species/methods	df	Sum of Squares	R^2	F	p-value
Smallmouth bass					
Spearfishing vs. E-fishing	1	1.6618	0.0567	5.1065	0.0010
Spearfishing vs. Angling	1	0.4109	0.0275	1.1039	0.3350
Spearfishing vs. Gillnetting	1	0.3820	0.0319	1.0227	0.5440
E-fishing vs. Angling	1	0.6694	0.0340	2.1821	0.0290
E-fishing vs. Gillnetting	1	0.2557	0.0157	0.8585	0.5410
Angling vs. Gillnetting	1	0.3277	0.1004	0.8927	0.6100
Walleye					
E-fishing vs. Gillnetting	1	3.5600	0.1007	9.9702	0.0010
E-fishing vs. Angling	1	0.4517	0.0359	1.4128	0.3540
Gillnetting vs. Angling	1	0.4075	0.0203	1.0587	0.4030

APPENDIX C

Data Availability Statement

The data and code used in this study are available for access and further analysis to ensure transparency and reproducibility. The datasets and R code can be obtained from the following sources:

Data and code to replicate Chapter 2:
https://github.com/alexprudhomme1/spearfishing_smb.git

Data and code to replicate Chapter 3:
https://github.com/alexprudhomme1/diet_smb.git