

**FOOD WEB INTERACTIONS AMONG WALLEYE, LAKE WHITEFISH, AND  
YELLOW PERCH IN GREEN BAY, LAKE MICHIGAN**

By

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## ABSTRACT

Green Bay supports important fisheries for walleye *Sander vitreus*, lake whitefish *Coregonus clupeaformis*, and yellow perch *Perca flavescens*. While walleye and lake whitefish populations have expanded in Green Bay, yellow perch numbers remain at historically low levels. As one of the primary piscivores in the Green Bay food web, walleyes could influence lake whitefish and yellow perch abundance, and yellow perch are important prey for walleye within many ecosystems. Specifically, walleye and yellow perch populations in southern Green Bay have exhibited contrasting trends in abundance since 1986. Walleye predation has been hypothesized to represent a potential recruitment bottleneck for yellow perch in Green Bay, which has been documented in other areas throughout the Great Lakes.

These three species likely interact in a variety of ways, including predation and diet overlap, but these interactions are poorly understood because contemporary information on diets is lacking. This information is needed to guide management decisions, because changes in population status of one species will likely affect fisheries for the other two species. The specific objectives of my research were to determine if: 1) lake whitefish and yellow perch represent important prey for walleyes in Green Bay; 2) diets of these three species vary spatially and temporally; 3) diet overlap among species is evident; and 4) the extent of walleye predation is sufficiently high to influence recruitment potential of lake whitefish and yellow perch in the portion of Green Bay south of Chambers Island (Zone 1).

Fish were collected each month from May through October in two zones of Green Bay during 2018 and 2019 using monofilament graded mesh gill nets. Additional fish were collected by natural resource agencies, commercial fishers, and recreational anglers. A total of 4,423 stomachs were dissected and diet items were removed and wet weighed to generate diet

compositions using diet information from 687 walleye, 533 lake whitefish, and 696 yellow perch with nonempty stomachs. For each species, diet composition was described using mean proportion by wet weight for each year, zone, and month combination. Analysis of similarities (ANOSIM) was used to test for spatial and temporal differences in diet composition, Pianka's (1974) index of niche overlap was used to calculate the extent of diet overlap, and a combination of bioenergetics and statistical catch-at-age (SCAA) modeling was used to estimate total walleye consumption of lake whitefish and yellow perch from May 1 through October 31 during 2018.

Diet compositions suggest that lake whitefish and yellow perch comprise between 5-6% of walleye diets overall, though temporal and spatial variation in diets was evident. Lake whitefish were seasonally important prey consumed only during May and June in Zone 1, comprising 36% of June walleye diets. Also, this study was the first to document the importance of lake whitefish to walleye diets within the Great Lakes. In both zones, yellow perch contributed to walleye diets at a broader temporal scale than lake whitefish, but perch never comprised more than 15% of walleye diets in any month throughout Green Bay.

Walleye diet compositions were significantly different between zones, potentially reflecting differences in prey fish availability. Additionally, significant temporal variation was identified in Zone 1, with distinct seasonal transitions in the consumption of prey species. Walleye diets were generally similar between 2018 and 2019, though fish collections during 2019 occurred at a reduced scale. Furthermore, variability in diet compositions was less evident for lake whitefish and yellow perch. However, a significant difference was detected between zones which was attributed to the greater contribution of round gobies *Neogobius melanostomus* in lake whitefish and yellow perch diets identified in Zone 2. Similarly, a significant temporal

change in yellow perch diets was detected, largely attributed to increased consumption of round gobies during the fall throughout Green Bay.

Diet overlap was strongest between lake whitefish and yellow perch, while weak to moderate overlap was observed between walleye and both lake whitefish and yellow perch. The highest degree of diet overlap between walleye and yellow perch occurred during October in Zone 1, corresponding with increased contribution of gizzard shad *Dorosoma cepedianum* to the diets of both species, and September in Zone 2, which was influenced most by predation on round goby and yellow perch. Moreover, diet overlap was highly influenced by the invertebrate prey group used in my diet analyses, as all invertebrate taxa were pooled. More specific identification of invertebrate taxa in diets would likely increase the resolution and reliability of my diet overlap indices, but this would be difficult because invertebrates were rarely intact in many diets, especially for lake whitefish.

In conjunction with observed growth and monthly diet data, a range of abundance estimates (i.e., 95% confidence limits) from SCAA models were used to predict the influence of walleye predation on lake whitefish and yellow perch recruitment potential. Based on the range of walleye consumption estimates and lake whitefish recruitment estimates, walleye consumption appeared unlikely to influence recruitment potential of lake whitefish in Zone 1 of Green Bay. However, given the high abundance of walleye and low abundance of yellow perch estimated in Zone 1, yellow perch recruitment potential is likely affected by walleye predation.

These results corroborate other studies that have identified walleye predation as a significant recruitment bottleneck for yellow perch populations throughout the Great Lakes. This study also suggests that previous concerns related to walleyes negatively impacting lake whitefish may be unrealistic. Additionally, alewife *Alosa pseudoharengus*, gizzard shad, and

invasive round gobies may serve as predation buffers for lake whitefish and yellow perch and predation by my three focal species may help in regulating round goby abundance in Green Bay. My results provide fisheries managers and stakeholders with important information regarding the complex interactions among walleyes, lake whitefish, and yellow perch in Green Bay, so that future management decisions can be made with a better understanding of the potential implications for all three fisheries and prey resources.

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## INTRODUCTION

Predation plays a significant role in structuring aquatic communities (Connell 1975; Carpenter et al. 1985; Hixon and Beets 1993) and predators may exert top-down effects on food webs by directly limiting (Gurevitch et al. 2000), regulating (Carpenter 1988), or extirpating (White et al. 2004) prey populations. Consequently, changes in predation can have cascading effects on lower trophic levels (Hairston et al. 1960; Carpenter et al. 1985). The effects of predation on the food web depend on many factors including predator and prey abundance, prey selectivity, and consumption rates (Abrams and Ginzburg 2000; Baum and Worm 2009; Grason and Miner 2012). Consequently, fully understanding the effects of predation in complex food webs can be difficult (Edwards et al. 1982; Bruno and O'Connor 2005; Baum and Worm 2009).

Interspecific competition for prey represents another important interaction that can influence food web dynamics (Polis and Winemiller 1995; Bruno and O'Connor 2005; Terborgh 2015). For competition to occur, predators must display overlap in their use of limited prey resources (Colwell and Futuyma 1971; Pianka 1974; Gotelli and Graves 1996) and the resource use, growth, or any other fitness-related factor of an individual must decline (Crowder 1990). Significant diet overlap can occur without competition if shared prey resources are abundant (Pianka 1974; Tolonen et al. 1999; Raborn et al. 2004). Identifying competition in wild populations can be challenging (Terborgh 2015; Leopold 2018) because of difficulties associated with determining whether shared prey resources are limiting, which depends on prey availability relative to predatory demands (Wiens 1977; Wiens 1993).

Changes in fish communities resulting from environmental change (Matthews 1998; Lapointe et al. 2014), introduction of invasive species (Ricciardi and MacIsaac 2011), fishery management actions (Eby et al. 2006), and environmental restoration efforts (Bullock et al.

2011) have all had significant effects on food webs in freshwater ecosystems around the world. Aquatic ecosystems are vulnerable to changing climate, which directly affect the thermal processes in lakes and may indirectly alter food webs (King et al. 1997; Robertson et al. 2016). These effects can lead to changes in system productivity, fish distributions, and interactions among species (Magnuson et al. 1997; Kling et al. 2003), increasing the chance for trophic cascades (Gorman et al. 2014). Invasive species have also affected aquatic food webs (Ricciardi and MacIsaac 2011) by altering nutrient cycles, habitats, and species interactions (Mack et al. 2000; Higgins and Vander Zanden 2009). Management actions, such as fish stocking, are widespread and have affected fish communities in freshwater systems around the world by increasing the abundance of predators or displacing native predators (Johnson and Martinez 2000; Eby et al. 2006). Furthermore, environmental restoration efforts can be successful in increasing diversity and abundance of select species (Benayas et al. 2009; Bullock et al. 2011); these changes may also affect food web dynamics.

The Laurentian Great Lakes represent the largest freshwater system in the world and support dynamic and complex aquatic food webs. All the Great Lakes have experienced substantial fish assemblage shifts during a history of frequent ecosystem changes (Madenjian et al. 2002). Some of the most significant changes have been caused by introductions of aquatic invasive species (Mills et al. 1993). For example, the round goby *Neogobius melanostomus*, a relatively recent invasive species that spread rapidly, are now established in many areas throughout the Great Lakes (Charlebois et al. 2001; Dillon and Stepien 2001). Round gobies may compete with native species such as mottled sculpin *Cottus bairdi*, slimy sculpin *Cottus cognatus*, spoonhead sculpin *Cottus ricei*, and logperch *Percina caprodes*, through resource competition (Bergstrom and Mensinger 2009), spawning interference (Janssen and Jude 2001),

and species displacement from preferred habitat (Dubs and Corkum 1996; Balshine et al. 2005). Conversely, round goby are an increasingly important prey species and have been found in the diets of numerous predator species including lake trout *Salvelinus namaycush* (Dietrich et al. 2006), smallmouth bass *Micropterus dolomieu* (Steinhart et al. 2004), burbot *Lota lota* (Johnson et al. 2005; Hares et al. 2015), walleye *Sander vitreus* (Johnson et al. 2005), lake whitefish *Coregonus clupeaformis* (Pothoven and Madenjian 2013), and yellow perch *Perca flavescens* (Truemper et al. 2006; Weber et al. 2010). Consumption of round goby by native species may provide for predatory regulation of round goby populations, as Madenjian et al. (2011) observed declines in goby abundance from 2004 to 2008 in Lake Erie, which coincided with increased prevalence of goby in burbot diets.

### ***Green Bay Ecosystem and Fishery***

Green Bay (which is part of Lake Michigan) is the world's largest freshwater estuary, efficiently functions as a nutrient trap, has exceptionally high biological productivity, and is thermally and chemically different than the main basin (Sager and Richman 1991; Smith et al. 1988). Historically, abundance of fish, waterfowl, and wild rice in Green Bay sustained native cultures (Qualls et al. 2013). The Fox River, which flows into southern Green Bay, and Green Bay itself have long supported the region's development and economy by providing a source of water, food, jobs, and recreation (WIDNR 2001). These economic activities had dramatic environmental impacts, with direct dumping of untreated sewage and industrial wastes severely contaminating sediments in many areas before the 1970s (WIDNR 1993). As development progressed, the lower portion of Green Bay, the Fox River below De Pere Dam, and the lower section of the Menominee River became substantially degraded by a combination of pollution

and habitat loss, which eventually led to their designation as Areas of Concern (AOC; International Joint Commission 1987; Wisconsin Department of Natural Resources 1993). Designated by the International Joint Commission between Canada and the United States, AOC are locations within boundary waters that have experienced substantial environmental degradation. Many beneficial use impairments have been identified in the AOC, including degradation of benthos, plankton, and fish populations; animal deformities and reproductive issues; eutrophication; drinking water risks or problems; and beach closings due to contamination by bacteria (International Joint Commission 1987). Ongoing clean-up efforts have improved conditions, but several issues such as polluted runoff, lost wetlands, and invasive species remain a threat (Qualls et al. 2013). Addressing these problems is critical for providing a healthy ecosystem and restoration opportunities.

Commercial fishers were among the first European settlers throughout the Green Bay watershed. Dating back to the 1800s, lake whitefish, lake sturgeon *Acipenser fulvescens*, and walleye were the top three species in commercial harvest (Goode 1884; Schneider and Leach 1979), though early commercial fishers primarily targeted lake whitefish, lake trout, and cisco *Coregonus artedii* (Kraft 1982). In 1885, fishery surveys were conducted throughout the Great Lakes and Green Bay was noted as one of the most important fisheries on Lake Michigan (Smith and Snell 1890). As settlement increased, the area's booming commercial fishing and lumber industries dramatically changed the Green Bay environment. A combination of overharvest, increased water pollution, lumber mill debris covering spawning substrates, and dam construction led to population declines for many species (Kraft 1982). Currently, Green Bay supports a limited commercial fishery for yellow perch in the southern bay and the lake whitefish

fishery remains the largest commercial fishery throughout Green Bay (Madenjian et al. 2002; Ebener et al. 2008).

Green Bay also supports one of the largest and most economically-important recreational fisheries in Wisconsin and Michigan. Recreational angling effort in the Wisconsin waters of Green Bay averaged over 850,000 angler hours per year over the past two decades, which comprises approximately 30% of Wisconsin angling effort for Lake Michigan (Peterson and Eggold 2005; Schmidt and Masterson 2018). In addition, recreational angling effort in the Michigan waters of Green Bay averaged over 550,000 angler hours per year during 1990 through 2010 (Zorn and Schneeberger 2011). Ultimately, the Green Bay fishery attracts anglers from across the continent and provides socioeconomic benefits for both Wisconsin and Michigan. The current recreational, commercial, and tribal subsistence fisheries primarily target walleye, lake whitefish, and yellow perch during most of the year (Zorn and Schneeberger 2011), making these three species vital to the Green Bay fishery.

### Walleye

By the mid-1900s, native walleye stocks in Green Bay had been depleted by a combination of habitat destruction, pollution, overexploitation, and interactions with invasive species (Schneider and Leach 1979; Schneider et al. 1991; Kapuscinski et al. 2010). Specifically, damming of tributaries, pollution, and destruction of wetlands impaired walleye reproduction and removed nursery habitats essential for juvenile survival (Schneider and Leach 1979; Kapuscinski et al. 2010). In addition, predation and competition with invasive alewife *Alosa pseudoharengus*, rainbow smelt *Osmerus mordax*, and sea lamprey *Petromyzon marinus* contributed to declines (Schneider et al. 1991). By the mid-1960s, walleye stocks in northern

Green Bay had reached historic lows and by 1973 only the Menominee River maintained a self-sustaining stock in southern Green Bay (Schneider et al. 1991).

With walleye stocks at historically low levels, commercial harvest was eliminated in Michigan in 1969 and in Wisconsin in 1978 (Kapuscinski et al. 2010). Water quality in Green Bay began to improve following passage of the Clean Water Act in 1972, and in the late 1960s and early 1970s both the Wisconsin (WIDNR) and Michigan Departments of Natural Resources (MIDNR) began to stock walleyes into Green Bay and associated tributaries (Zorn and Schneeberger 2011; Hogler and Surendonk 2018). Walleye stocks in southern Green Bay are currently self-sustaining and the WIDNR discontinued walleye stocking in 1984 after more than 86 million fry and 3.5 million fingerlings had been stocked (Schneider et al. 1991). However, limited stocking occurred in Sturgeon Bay through 2012 (Dembkowski et al. 2018). From 1969 through 2005, the MIDNR has stocked more than 40 million walleye fry and nearly 15 million fingerlings into portions of Little Bay de Noc (LBDN), Big Bay de Noc (BBDN), the Cedar River, and the Menominee River (Schneeberger 2000; Zorn and Schneeberger 2011) and these stocks are not considered to be self-sustaining (MIDNR 2012). Rehabilitation of self-sustaining walleye populations in Green Bay is an important management goal of the MIDNR and stocking will continue as part of ongoing efforts to supplement or restore local stocks (Schneider et al. 2007; Zorn and Schneeberger 2011; MIDNR 2012). Achieving self-sustaining walleye stocks is also listed as a goal in the fish community objectives of the Great Lakes Fishery Commission, Lake Committee for Lake Michigan (Eshenroder et al. 1995) and in their walleye rehabilitation guidelines for the Great Lakes (Colby et al. 1994).

Currently, the Green Bay walleye fishery supports annual recreational harvests that generally exceed 90,000 fish (Dembkowski et al. 2018; Schmidt and Masterson 2018). Walleye



also contribute to a tribal subsistence fishery that occurs in Michigan waters designated by the Great Lakes 2000 Consent Decree for the 1836 Treaty of Washington (Kappen et al. 2012). Furthermore, as a native predator, walleye play an important role in the Green Bay ecosystem and could influence other species such as lake whitefish and yellow perch that also support important fisheries within the region (Schneider et al. 1991). High walleye abundance has also prompted continued interest in allowing some commercial harvest of walleye in Wisconsin waters.

### Lake Whitefish

Lake whitefish are a native benthivore that have supported an important commercial fishery in Lake Michigan since the 1800s (Baldwin et al. 1979; Ebener 1997; VanDeHey et al. 2009). A combination of overharvest, habitat destruction, invasive species, and variable recruitment contributed to the collapse of lake whitefish stocks in Lake Michigan during the 1950s to 1970s (Wells and McLain 1973; Healy 1975; Ebener 1997). During the 1960s, sea lamprey control, introduction of salmonids, reduced competition, and reduced fishing pressure initiated the recovery of lake whitefish (Mohr and Nalepa 2005). The current lake whitefish fishery is the result of improved environmental conditions and rehabilitation initiatives which include increased regulation of commercial harvest, sea lamprey control, and improvements in water quality (Ebener 1997; Ebener et al. 2008).

Presently, lake whitefish support the largest and most economically-important commercial fishery on Lake Michigan (Ebener 1997), with the northern third of the lake (including Green Bay) supporting the majority of harvest (Madenjian et al. 2002; Ebener et al. 2008). Annual commercial landings of lake whitefish from Lake Michigan during 2010 to 2015

ranged from 1.4 to 2.4 million kg, representing a dockside value of US\$4.9 to US\$8.6 million (USGS 2019). Lake whitefish support state-licensed commercial fishers in both Wisconsin and Michigan and are also an important component in tribal subsistence fisheries in Michigan waters of Green Bay (Kappen et al. 2012; WIDNR 2017). Because of their ecological, cultural, and economic importance, lake whitefish in Lake Michigan are intensively managed in a cooperative effort between Wisconsin, Michigan, and the Chippewa-Ottawa Resource Authority (CORA; VanDeHey et al. 2009). Lake whitefish also support an increasingly important winter recreational fishery in southern Green Bay that attracts anglers from across North America, supporting harvests that generally exceed 110,000 fish (WIDNR 2017). Furthermore, fish community objectives for Lake Michigan call for maintaining self-sustaining stocks of lake whitefish and define expected yields for the lake whitefish fishery (Eshenroder et al. 1995).

Genetic analyses based on genotyping of microsatellite DNA loci have confirmed that the lake whitefish population in Lake Michigan is comprised of at least six genetically-distinct stocks (VanDeHey et al. 2009; Stott et al. 2010); however, some gene flow among stocks likely occurs (Stott et al. 2010). Adding to this complexity, lake whitefish now spawn in tributaries to southern Green Bay where spawning had not been observed for nearly a century. In the mid-1990s, annual WIDNR fall electrofishing surveys in the Menominee River began recording low levels of incidentally caught lake whitefish (Belonger 1995). By the mid-2000s the number of lake whitefish in the Menominee River was estimated to be in the 1000s (WIDNR 2017). Currently, the largest of these tributary spawning stocks occur in the Fox and Menominee Rivers, with smaller migrations in the Peshtigo and Oconto Rivers (WIDNR 2017).

## Yellow Perch

Yellow perch were once an economically-important species in Green Bay and Lake Michigan and have contributed to commercial and recreational fisheries since the late 1800s (Wells and McLain 1972; Baldwin et al. 1979; Kraft 1982). These fisheries continued throughout the last century, though the commercial fishery has been restricted to the waters of southern Green Bay since the late 1990s (Irwin et al. 2008). Yellow perch populations experienced substantial declines during the 1960s, presumably as a result of overfishing, deteriorating water quality, habitat loss, and negative interactions with invasive alewife (Wells 1977; Schneider and Leach 1979). For example, Madenjian et al. (2002) suggested that alewife abundances in the 1960s and early 1970s were sufficiently high to interfere with yellow perch reproduction. By 1982, alewife populations had declined, but the yellow perch fishery continued to experience high fishing pressure (Johnson et al. 1992).

Following alewife declines, the yellow perch population in southern Green Bay steadily increased during the late 1980s (WIDNR 2017). However, total biomass of yearling and older yellow perch in southern Green Bay was estimated at over 4 million kg in 1987 and declined below 300,000 kg by 2002 (WIDNR 2017). These fluctuations in abundance reflected patterns in recruitment, as several strong year classes were produced in the 1980s, with only two moderately strong year classes observed during WIDNR bottom trawling surveys in the 1990s (WIDNR 2017). However, excluding 2014, recent trawling surveys have shown improved yellow perch recruitment since 2002. Variation in yellow perch recruitment in the Great Lakes has been attributed to low water levels (Henderson 1985; Kallemeyn 1987), high abundance of potential predators and competitors such as walleyes and alewives (Forney 1971; Shroyer and McComish 2000), zooplankton availability (Dettmers et al. 2003), dramatic food web and ecosystem

changes induced by invasive zebra *Dreissena polymorpha* and quagga mussels *Dreissena bugensis* (i.e., Dreissenidae; Marsden and Robillard 2004; Janssen and Luebke 2004), and spawning population demographics (e.g., skewed sex ratios, low spawner abundance, size and condition; Heyer et al. 2001; Marsden and Robillard 2004; Lauer et al. 2005).

Northern Green Bay's yellow perch population followed similar trends. Due to variable recruitment and conservative management, yellow perch in northern Green Bay experienced an earlier rebound in the 1970s (Schneeberger 2000). Large fluctuations regularly occurred in these populations, and consequently stocking has often been suggested to enhance yellow perch populations and improve fishing. Records in the Great Lakes Fishery Commission stocking database indicate four minor yellow perch stocking efforts (Santucci et al. 2014). From 1989 to 1995, MIDNR stocked approximately 25,000 adults and 129,000 fingerlings, and in 2002 another 5,700 adults were stocked throughout LBDN (Santucci et al. 2014); the success of these stocking events remains undetermined. Apart from these stocking events in LBDN, yellow perch populations throughout Green Bay have been sustained entirely by natural reproduction (Zorn and Schneeberger 2011).

Currently, yellow perch support an important recreational fishery throughout Green Bay with the southern portion of the bay supporting the last remaining yellow perch commercial fishery on Lake Michigan, licensed through the state of Wisconsin. From 1986 to 1995, annual recreational harvest of yellow perch in Wisconsin waters of Green Bay ranged from 1.0 to 3.5 million fish, with harvest peaking in 1991 (WIDNR 2018). Since 1996, harvest has generally been below 500,000 fish (WIDNR 2017). Similarly, annual recreational harvest in northern Green Bay averaged over 200,000 fish from 1988 to 1993 and progressively declined through 2005 to averages less than 100,000 yellow perch (Zorn and Schneeberger 2011). Commercial

harvest, though reflecting the adoption of a quota system, is also below historic levels with annual commercial landings during 2010 to 2015 ranging from 21,274 to 38,368 kg and representing a dockside value of US\$116,946 to US\$211,076 (USGS 2019). Additionally, changes in harvest regulations for the recreational yellow perch fishery have been implemented to reduce harvest, including reductions in bag limits from 50 fish per day to 15 fish per day and a spring closure during the spawning season.

### ***Potential Interspecific Interactions***

As one of the dominant piscivores, walleye could have important influences on other species within Green Bay. Predatory demand by walleye may control prey populations directly, both through predation on adults and reducing recruitment potential by consuming young fish (Lyons and Magnuson 1987; Hartman and Margraf 1992). While walleye and lake whitefish populations have expanded in Green Bay, yellow perch numbers remain at historically low levels. Specifically, walleye and yellow perch populations in Wisconsin waters of Green Bay have exhibited contrasting trends in abundance since 1986 (correlation,  $r^2 > 0.75$ ), with walleye numbers increasing and yellow perch numbers sharply declining (I. Tsehay, Wisconsin Department of Natural Resources, unpublished data; Figure 1). Although interactions between walleye and yellow perch have not been previously assessed in Green Bay, walleye predation has been hypothesized to represent a potential recruitment bottleneck for yellow perch in Green Bay (I. Tsehay, personal communication).

Certainly, walleye predation has the potential to influence yellow perch and lake whitefish abundance, and yellow perch have been an important prey item in walleye diets within many ecosystems (Forney 1974; Lyons and Magnuson 1987; Lemm 2002). A pilot diet

assessment conducted by the WIDNR in collaboration with the Wisconsin Cooperative Fishery Research Unit (WICFRU) at the University of Wisconsin-Stevens Point (UWSP) during 2016 and 2017 suggested that yellow perch may represent only a minor component ( $\leq 5\%$  of diets) of adult walleye diets in southern Green Bay. However, low incidence of yellow perch in walleye diets could still translate into important population-level effects for yellow perch given the high relative abundance of walleyes in portions of Green Bay.

In addition, Stewart and Watkinson (2004) confirmed juvenile lake whitefish are common prey items for walleye in many large lakes throughout Manitoba, while adults are less preferred and only vulnerable to the largest size classes of walleye. Abundant lake whitefish populations throughout Canada have also been found to be a critical source for walleye growth and survival (Lemm 2002). In Green Bay, commercial fishers have expressed concern that walleyes may be influencing lake whitefish abundance through predation, a concern based on observations of lake whitefish being regurgitated from walleyes captured as by-catch in commercial trap nets. However, increased catch rates of juvenile lake whitefish during annual WIDNR bottom trawling surveys has indicated an expansion of lake whitefish throughout lower Green Bay (WIDNR 2017), and the return of tributary spawning stocks may provide new sources of recruitment. Possibly, the increasing abundance and availability of lake whitefish in southern Green Bay may explain the increase of lake whitefish observed in walleye diets by commercial fishers. Conversely, these observations have been limited temporally and mainly occurred following walleye spawning in May and June along the east shore of southern Green Bay. These observations suggest that lake whitefish may provide an important seasonal component to walleye diets during periods when preferred habitat of these species spatially overlap.

In northern Green Bay, changes in walleye and yellow perch diets were documented from 1988 through 2005 by Schneeberger (2000) and Zorn and Schneeberger (2011). Alewife occurrence in walleye diets had tripled and alewife were the most frequently observed walleye prey item by 2005. In contrast, walleye predation on rainbow smelt drastically declined over the same time period. Similarly, the once moderately important trout-perch *Percopsis omiscomaycus* component in walleye diets was not observed after round gobies became prevalent. Yellow perch consumed multiple different fish species before the 2000s including trout-perch, alewife, johnny darter *Etheostoma nigrum*, rainbow smelt, and spottail shiner *Notropis hudsonius*. Predation on these species has become negligible during the early 2000s. Beginning in 2002, round gobies were first observed in yellow perch diets, with occasional observations of young-of-year walleye and cannibalism. Furthermore, as round goby populations expanded during the early 2000s, they became an increasingly important component in the summer diets of both walleye and yellow perch.

Lake whitefish are usually not considered piscivorous; however, several studies suggest their diets may also include fish as ecosystems continue to change. For example, Pothoven (2005) noted that lake whitefish diets during spring, summer, and fall were dominated by fish in three areas of northern Lake Michigan. Similarly, Pothoven and Nalepa (2006) found lake whitefish diets during spring and summer were dominated by nine-spine stickleback *Pungitius pungitius* and round goby during at least one of the study seasons in Lake Huron. In Green Bay, Lehrer-Brey and Kornis (2014) found that round gobies were the most important diet item (46.6% by dry weight) near Little Sturgeon Bay during the winter in 2010 and 2011. Ultimately, if presence of round goby continues to increase in the diets of predator species throughout Green

Bay, they may result in significant diet overlap among predators while acting as an important prey buffer for other prey species.

Initial diet results from pilot work conducted during 2016 and 2017 by the WIDNR and WICFRU in southern Green Bay indicate round gobies were the dominant prey item in diets analyzed from 594 walleye (53% by wet weight) and 237 yellow perch (73% by wet weight); diets removed from 268 lake whitefish suggest invertebrates were the dominant prey item (80% by wet weight), but round gobies still contributed a large portion of their diet (18% by wet weight). Yellow perch and lake whitefish each comprised less than 2% of walleye diets. Furthermore, these preliminary diet results, and results documented by Zorn and Schneeberger (2011), suggest round gobies are an important prey item for walleyes, yellow perch, and lake whitefish during spring and fall in both southern and northern regions of Green Bay. Ultimately, round gobies may act as a buffer for other potential prey (including the three focal species) and significant predation may provide an important control mechanism for their invasive population.

However, fish and diet collections during this pilot study were constrained to short-term, seasonal WIDNR gill netting and electrofishing surveys, along with fishing tournament mortalities, ultimately limiting the spatial and temporal context of the work. Specifically, initial diet sampling was opportunistic in design and most fish (292 walleyes, 268 lake whitefish, and 222 yellow perch) were collected during 2016 and 2017 WIDNR juvenile gill netting assessments near Sturgeon Bay on the Green Bay side of the Door Peninsula in April. Additional walleyes ( $n = 174$ ) and yellow perch ( $n = 15$ ) were collected both years during WIDNR fall electrofishing runs conducted in southern Green Bay and 92 walleyes were collected at a tournament weigh-in held in Sturgeon Bay, June 2016.



One tool frequently utilized to evaluate predator-prey interactions is bioenergetic modeling. Bioenergetic models are employed to assess predatory demand which can reveal predator impacts, if any, on prey production and forage community structure (Hartman and Margraf 1992). Walleye predatory demand has been evaluated frequently using bioenergetics to assess impacts on forage fish populations. Hartman and Margraf (1992) explained the failure of the 1988 yellow perch year class in Lake Erie through a bioenergetics model of age-2 and younger walleye; they concluded that walleye predatory demand accounted for a 28-90% reduction in the abundance of age-0 yellow perch. In Green Bay, predatory demand by walleye has not been evaluated, and the use of bioenergetics would be beneficial in assessing the total predatory demand and consumption by walleye throughout Green Bay.

Walleye, lake whitefish, and yellow perch likely interact in a variety of ways, including predation and diet overlap, but these interactions are poorly understood because contemporary information on diets is lacking, especially for the Wisconsin waters of Green Bay. Schneeberger (2000) and Zorn and Schneeberger (2011) provided information on walleye and yellow perch diets, but only for northern Green Bay. Similarly, Pothoven (2005) described lake whitefish diets in the main basin of Lake Michigan and Lehrer-Brey and Kornis (2014) described lake whitefish diets in Green Bay, but only during the winter. Diet information and trends observed on the main basin of Lake Michigan are likely not transferable to Green Bay given the substantial differences in these ecosystems in terms of limnology and fish communities. Furthermore, previous diet research is outdated, and findings may not hold true anymore given the substantial changes observed in the Green Bay ecosystem. Previous diet work also suggests that these three species may share prey resources, including various invasive species such as spiny water flea *Bythotrephes spp.*, round goby, rainbow smelt, and alewife. Information on diet overlap among

the three species, and the extent to which they utilize various prey species, is lacking at relevant spatial and temporal scales. Understanding these effects requires more intensive diet sampling at broader spatial and temporal scales coupled with estimates of abundance from statistical catch-at-age (SCAA) models and bioenergetics simulations.

### ***Research Needs and Objectives***

A better understanding of interactions among walleye, lake whitefish, and yellow perch is needed to guide management decisions, because changes in population status of one species will likely affect fisheries for all three species. These potential effects translate into important socio-economic trade-offs that must be considered in the decision-making process. Greater resolution in diet sampling is needed to determine the extent of walleye predation on lake whitefish and yellow perch stocks and the diet overlap among these species. The overall goal of my project was to provide fisheries managers and stakeholders with information regarding potential interactions among walleyes, lake whitefish, and yellow perch in Green Bay, so that management decisions can be made with a better understanding of the potential implications for all three fisheries and prey resources. The specific objectives of my research were to determine if: 1) lake whitefish and yellow perch represent important prey for walleyes in Green Bay ( $\geq 20\%$  of diets by weight); 2) diets of these three species vary spatially and temporally; 3) diet overlap among species is evident; and 4) the extent of walleye predation is sufficiently high to influence recruitment potential of lake whitefish and yellow perch in the portion of Green Bay south of Chambers Island (Zone1).

## METHODS

### *Study Area*

Green Bay is Lake Michigan's largest bay (study area  $\approx 4,440 \text{ km}^2$ ) and is situated within the borders of Wisconsin and Michigan. Green Bay comprises 7.4% of the total surface area of Lake Michigan (Mortimer 1978) and its watershed drains approximately  $40,469 \text{ km}^2$ , representing one-third of the Lake Michigan drainage basin (Bertrand et al. 1976; Harris and Wegner 2010). Mean and maximum depths are 20-m and 53-m, respectively. Green Bay has a distinct south-to-north depth and productivity gradient; the southern portion of the bay is shallow and eutrophic while the northern bay is deeper and relatively oligotrophic (USEPA 1978; Smith et al. 1988; Qualls et al. 2013). Eight tributaries of major importance drain into Green Bay, with the largest and most significant being the Fox River (Bertrand et al. 1976), located at the far southern end near the city of Green Bay, Wisconsin. The other major tributaries in Wisconsin are the Peshtigo, Oconto, and Menominee Rivers; the Menominee River forms the boundary between the states of Wisconsin and Michigan. Major Michigan tributaries include the Cedar, Ford, Escanaba, and Whitefish Rivers. These major tributaries are located along the western shore of Green Bay. Furthermore, Green Bay features a diversity of substrates, macrophytes, temperatures, currents, and bathymetry (Smith et al. 1988).

This study was conducted throughout the open waters of Green Bay (i.e., not tributaries) and the bay was geographically divided into a southern (Zone 1) and northern zone (Zone 2; Figure 2). Located primarily within Wisconsin waters, Zone 1 encompasses waters from the southernmost point of Green Bay extending north along the west shore to Beattie Creek just north of Beattie Point in Michigan, and along the east shore to Sunset Beach Park just south of Fish Creek Harbor in Wisconsin. Zone 1 includes Sturgeon Bay extending through the Green

Bay-Lake Michigan shipping canal to the U.S. Coast Guard Station just before the Sturgeon Bay Piers. The boundary line from Beattie Creek extends straight across Green Bay to Sunset Beach Park and separates Zone 1 and Zone 2. The western boundary of Zone 2 is entirely within Michigan and encompasses both LBDN and BBDN. The east shore of Zone 2 begins in Wisconsin and extends north to Isle View Park near Northport and extends across to the southernmost tip of the Garden Peninsula in Michigan. Zone 2 includes Plum, Detroit, Washington, Rock, St. Martin, Poverty, Summer, and Little Summer Islands.

The zone boundaries were chosen to account for differences in bathymetry and productivity, with Chambers Island creating a large natural boundary between zones (Figure 2). Zone 1 has an approximate surface area of 1,666 km<sup>2</sup>, is relatively shallow (mean depth  $\approx$  14-m; maximum depth  $\approx$  34-m) with minimally complex bathymetry, eutrophic in southern portions to mesotrophic near Sturgeon Bay due to water transfer between Green Bay and Lake Michigan (USEPA 1978; Smith et al. 1988), receives water from four of the major tributaries (Fox, Peshtigo, Oconto, and Menominee Rivers), and includes the AOC. Zone 2 has an approximate surface area of 2,774 km<sup>2</sup>, is relatively deep (mean depth  $\approx$  22-m; maximum depth  $\approx$  53-m) with highly complex bathymetry, mainly oligotrophic (LBDN is mesotrophic to eutrophic and BBDN is oligotrophic to mesotrophic; USEPA 1978; Smith et al. 1988), and receives water from four of the major tributaries (Cedar, Ford, Escanaba, and Whitefish Rivers).

### ***Fish Collection***

Collection of fish and diets occurred during May through October in 2018 and 2019. I collected fish from each zone using six monofilament experimental gill nets. Four gill nets were 1.8-m deep and 91.4-m long, with six individual 15.2-m panels of stretch mesh measuring 51-,

64-, 76-, 89-, 102-, and 127-mm. Two modified gill nets were 1.8-m deep and 121.9-m long, with four individual 30.48-m panels. One of these modified gill nets was built specifically for targeting walleye, with panels of stretch mesh measuring 89-, 102-, 114-, and 127-mm. The other modified gill net was built specifically for targeting yellow perch, with panels of stretch mesh measuring 51-, 64-, 76-, and 89-mm. Gill nets were set on the bottom in various depths and locations and fished for short durations ranging from 1-2 hours, depending on water temperature and catch rates.

Fish for diet analysis were also obtained during other WIDNR, MIDNR, and U.S. Fish and Wildlife Service (USFWS) sampling (e.g., gill netting, bottom trawling, electrofishing, and fyke netting). Commercial fishing operations contributed nearly all lake whitefish collected during this study. These fish were either purchased with project funds, or biological data and associated stomachs were collected at commercial fish cleaning houses and preserved in 95% ethanol for later dissection in the laboratory. Commercial samples largely consisted of fish captured in trap nets; however, fish captured by gill nets and purse seines were also obtained, as a larger percentage of fish from these gears contained diets. In addition, I engaged with recreational anglers at various fish cleaning facilities and worked closely with MIDNR creel clerks to supplement diet collections.

My sampling targets in 2018 were to obtain 100 walleyes, lake whitefish, and yellow perch from each zone during each month, totaling 3,600 fish collected for diet processing. Most fish were sacrificed, immediately stored on ice, frozen, and brought back to the laboratory. Biological data and stomach contents were collected in the field from some fish (e.g., during electrofishing assessments). A gastric lavage was used to regurgitate diet items which were stored in 95% ethanol and these fish were released alive. Furthermore, additional diet sampling

at a reduced scale was conducted in 2019 to evaluate temporal variation in diet compositions. Sampling targets for 2019 were to obtain 100 walleyes, lake whitefish, and yellow perch from one zone during each month, totaling 1,800 fish collected for diet processing. Fish in 2019 were collected from 2018 sampling locations and, whenever possible, on the same dates to reduce bias associated with temporal and spatial variation in diet compositions within zones. Design of this additional sampling was determined based on spatial and temporal variation in diet composition observed from 2018 sampling. Specifically, zone-month strata were selected to minimize the proportion of fish containing empty stomachs based on my 2018 diet collections. Consequently, in 2019, Zone 1 sampling occurred in May and October, and Zone 2 sampling occurred in June, July, August, and September, except August collections of lake whitefish were obtained from Zone 1.

### ***Diet Processing***

In the laboratory, fish were thawed, measured to the nearest mm (total length; TL), and weighed to the nearest gram. Sex and maturity were determined by visual inspection of gonads and otoliths were removed for age estimation from fish containing diet items. Stomachs were removed and dissected, and the mouth and throat of each fish was examined for regurgitated diet items. Diet items were identified to the lowest possible taxonomic level (e.g., species, genus), enumerated, and wet weighed to the nearest 0.001 g by taxonomic group. When possible, fish found in diets were measured (nearest mm) for either total, fork, standard, or backbone length. When visual identification to species or genus was difficult, fish remnants that could be discerned as individual fish were identified using otoliths (i.e., round goby), gizzards (i.e., gizzard shad *Dorosoma cepedianum*), and cleithra. Using the cleithra identification guide for

Michigan fishes compiled by Traynor et al. (2010), cleithra were carefully examined to identify distinguishing characteristics that are unique to the species level. Other fish remnants discerned as individual fish, but missing characteristic otolith, gizzard, or cleithra structures, were individually weighed, stored in 95% ethanol, and when possible, a probable species designation was noted. Fish remnants that could not be discerned as individual fish were group weighed and classified as unidentified fish remnants.

Similar to Kelling et al. (2016), I used genetic techniques to reduce the number of unidentified fish in diets; genetic techniques (i.e., DNA barcoding) were conducted by the Molecular Conservation Genetics Laboratory (MCGL) at UWSP. Whole genomic DNA from fish remnants visually unidentifiable to species or genus were extracted, quantified, and normalized (Kelling et al. 2016). Next, a targeted portion of the cytochrome oxidase subunit I (COI) was sequenced, and specimens were identified to species using the Mega BLAST algorithm (Altschul et al. 1997) in the National Center for Biotechnology Information (NCBI) database. If visual identification of probable species agreed with DNA barcoding for > 90% of unidentified fish samples, visual identifications were assigned to unidentified fish when DNA barcoding failed or resulted in predatory host contamination.

Invertebrates found in diets were bulk weighed and stored in 95% ethanol for later identification. Pilot work completed by WICFRU and work completed by Zorn and Schneeberger (2011) suggested that diets of many yellow perch and most lake whitefish will include partially digested invertebrates that may be difficult to identify and enumerate. When possible, individual identification and enumeration was conducted for walleye and yellow perch invertebrate diet samples; identification and enumeration was conducted by the Aquatic Biomonitoring Laboratory (ABL) at UWSP for invertebrates found in lake whitefish diets. A

subsample ( $n = 100$ ) of these bulk-weighed samples were examined by the ABL so that invertebrate taxa being utilized as prey by lake whitefish could be generally described for each zone-month combination. When individual identification and enumeration of invertebrate prey was not feasible, invertebrate components were classified as unidentified invertebrates.

### *Age Estimation*

Walleye, lake whitefish, and yellow perch otoliths were extracted ventrally, wiped clean, stored in plastic vials, and allowed to dry for  $\geq 2$  weeks before additional preparation. Similar to Dembkowski et al. (2017), walleye and yellow perch otoliths collected during 2018 were broken in half along a transverse plane through the focus. The surface of the otolith exposed by the break was lightly polished using 1000-2000 grit sandpaper and placed in a dish of plumber's putty so that the polished surface was facing up. The otolith half was viewed under a stereomicroscope (Nikon® SMZ1500; Nikon Corporation, Tokyo, Japan) at 20-50x magnification. A drop of immersion oil (Type A; Cargillie Laboratories, Cedar Grove, NJ) was applied to the polished surface to improve clarity and annuli were illuminated by moving a fiber optic light around the edge of the otolith.

Similar to Muir et al. (2008) and Dembkowski et al. (2017), otoliths from lake whitefish collected during 2018, and from walleye and yellow perch in 2019, were embedded in a two-part epoxy mixture (EpoxiCure™ 2; Buehler, Lake Bluff, IL) for 24 hours before sectioning; ages were not estimated for lake whitefish collected during 2019. A 1-mm transverse section was cut through the focus of each otolith using a low speed saw (IsoMet® 1000; Buehler). Otolith sections were mounted to glass microscope slides with super glue (Loctite Gel Control®; Henkel Corporation, Rocky Hill, CT) and lightly polished using 1000-2000 grit sandpaper. Sections



were viewed with transmitted light under the same stereomicroscope and magnification as described previously. A drop of immersion oil was applied to the otolith surface to improve clarity. An attached digital camera (Nikon® DS-Fi3; Nikon Corporation) captured images of each otolith section which were acquired using Nikon® NIS Elements Advanced Research Software (Nikon Corporation). For both age estimation techniques, visible annuli were enumerated, and the otolith edge was counted as an annulus for fish collected before July 15th.

***Objective 1: Importance of Lake Whitefish and Yellow Perch as Walleye Prey***

Used to address objectives 1, 2, 3, and 4, the diet compositions of walleye, yellow perch, and lake whitefish were described using mean proportion by wet weight  $p_{ij}$  (Chipps and Garvey 2007; Hartman and Hayward 2007):

Equation 1.1 
$$p_{ij} = \frac{1}{N} \sum_j^N \left( \frac{W_{ij}}{\sum_i^n W_{ij}} \right) ,$$

where

- $p$  = mean proportion by wet weight
- $W$  = the wet weight (g)
- $i$  = prey type
- $j$  = predator species
- $N$  = the total number of predators observed with prey in their stomachs
- $n$  = the total number of prey types observed in the predator stomachs.

Including all diet items identified visually and by genetic methods, diet composition was calculated for each species in each year, zone, and month combination. Pooled across months, calculation of diet composition was further subdivided into walleye age groups within each zone, as transitions in diet composition between walleye age groups were apparent in 2018. Walleye were subdivided into ages 0-3, 4-6, and 7-20 (i.e., each walleye age group collectively referred to as juveniles, young adults, and old adults, respectively). These groupings were chosen based on walleye diet proportion inputs that were pooled by age-group and used in the bioenergetics

simulations for objective 4 (described below). Prey taxa with mean values of  $p_{ij} \geq 20\%$  were considered important diet items for the three focal species. Invertebrate taxa consumed were described using percent frequency of occurrence  $f_{ij}$  (Chipps and Garvey 2007):

Equation 1.2 
$$f_{ij} = \left( \frac{J_{ij}}{N_j} \right) * 100 ,$$

where

$f$  = percent frequency of occurrence

$J$  = the number of predator diets containing prey item  $i$

$i$  = prey type

$j$  = predator species

$N$  = the total number of predators observed with prey in their stomachs.

Invertebrate taxa frequently utilized as prey by walleye, lake whitefish, and yellow perch were generally described for each zone-month combination.

### ***Objective 2: Variation in Diet Compositions***

Unidentified prey fish were excluded from all analyses for objective 2 (Elliot et al. 1996; Luo et al. 2019). Analysis of similarities (ANOSIM) was used to test for differences in the diet compositions between sampling zones each month during 2018, between successive months within each zone during 2018, and between 2018 and 2019 within each zone-month for walleye, lake whitefish, and yellow perch (Pothoven et al. 2017; Luo et al. 2019). In addition, diet compositions were further tested for differences between walleye age groups (described previously; pooled across months) within each zone during 2018, as transitions in diet composition between walleye age groups were apparent. The ANOSIM approach is a multivariate analog of analysis of variance, with a nonparametric permutation applied to a Bray–Curtis rank dissimilarity matrix of samples (Clarke and Green 1988; Clarke and Warwick 2001).

Bray and Curtis (1957) dissimilarity matrices quantify the compositional dissimilarity index between diet compositions of individual fish ( $BC_{ij}$ ), and expressed as:

Equation 2.1 
$$BC_{ij} = \frac{1-2C_{ij}}{S_i+S_j} ,$$

where

$BC$  = the compositional dissimilarity index between diet compositions of individual fish  
 $C$  = the sum of the lesser counts for each of the diet species found in both individual fish  
 $S$  = the total number of specimens counted within the respective predator stomach  
 $i$  = predator individual  $i$   
 $j$  = predator individual  $j$ .

Diet composition data were square-root-transformed to reduce the importance of dominant prey species (Clarke and Warwick 2001) and used to create the Bray–Curtis dissimilarity matrix.

To indicate significant differences, ANOSIM generates  $p$ -values and  $R$ -values. Resulting  $p$ -values indicated the significance level for ANOSIM and were considered significant at  $p = 0.001$ . Resulting  $R$ -values measured the degree of separation in diet compositions between zone, month, and year comparisons for walleye, lake whitefish, and yellow perch;  $R$ -values equal to 0 indicated groups that were indistinguishable,  $R$ -values equal to 1 indicated complete separation between groups, and  $R$ -values  $< 0$  indicated variation within groups exceeded the separation between groups (Clarke and Gorley 2001).

Prey species contributing most to observed differences between diet compositions among groupings of walleye, lake whitefish, and yellow perch in each zone, month, and year were identified by applying a similarity percentages routine (SIMPER). A SIMPER analysis uses the Bray–Curtis dissimilarity index to compare observed differences among the proportional mass of each prey species consumed by each grouping of walleye, lake whitefish, and yellow perch. ANOSIM and SIMPER were performed using the vegan package (Oksanen et al. 2019) in Program R version 3.6.1 (R Core Team 2019).

### ***Objective 3: Diet Overlap***

Diet overlap between predator species was described in 2018 for each zone-month combination using a pairwise calculation of Pianka's index of niche overlap  $O_{jk}$  (Pianka 1974; Matthews et al. 1982; Christensen et al. 2005):

Equation 3.1

$$O_{jk} = \frac{\sum_i^n p_{ij} * p_{ik}}{\sqrt{\sum_i^n (p_{ij})^2 * \sum_i^n (p_{ik})^2}},$$

where

$O$  = Pianka's index of niche overlap

$p$  = the average proportion of prey type  $i$  in the diets of respective predator species

$i$  = prey type

$j$  = predator species  $j$

$k$  = predator species  $k$

$n$  = the total number of prey types observed in the diets of both predator species.

In addition, diet overlap indices were further calculated for walleye age groups (described previously; pooled across months) within each zone. Pianka's index values range from 0 to 1, with 0 indicating no diet overlap and 1 indicating complete diet overlap (Christensen et al. 2005). Values  $\geq 0.75$  indicated strong diet overlap and values  $\leq 0.40$  indicated weak diet overlap (Pianka 1976; Matthews et al. 1982).

### ***Objective 4: Effects of Walleye Predation on Lake Whitefish and Yellow Perch Recruitment***

#### **Individual Level: Age-Specific Walleye Consumption of Lake Whitefish and Yellow Perch**

The Wisconsin bioenergetics model, originally developed by Kitchell et al. (1977) and refined by Hewett and Johnson (1992), was used to estimate age-specific total walleye consumption (i.e., individual and population level) of lake whitefish and yellow perch in Zone 1 of Green Bay from May 1 through October 31 during 2018. Bioenergetics model simulations were performed using Fish Bioenergetics 4.0 (Deslauriers et al. 2017). The model was fit using

observed walleye growth combined with temperature, predator physiological parameters, and predator and prey energy densities to estimate food consumption. Bioenergetics models are based on an energy mass-balance equation:

Equation 4.1 
$$C = G + R + F + U,$$

where

$C$  = consumption (g)

$G$  = growth, indexed as the change in mass of the predator during the simulation period

$R$  = respiration

$F$  = egestion

$U$  = excretion.

Units of  $G$  are calculated through population measurements (i.e., age-specific differences in mean walleye weight between May and October),  $R$  is a function of fish weight, temperature, and activity; and  $F$  and  $U$  are functions of temperature and diet (Kitchell et al. 1977; Hanson et al. 1997; Hartman and Hayward 2007). Consumption modeling requires a set of predator-specific physiological parameters, water temperature, predator and prey energy densities, and predator diet information and growth. Species-specific physiological parameters are included in the bioenergetics modeling application (Fish Bioenergetics 4.0; Hanson et al. 1997; Deslauriers et al. 2017). The model calculated daily consumption by walleye during the modeling period and each model estimated the proportion of maximum consumption ( $P_{Cmax}$ ) based on the observed growth.

Using a YSI© 556 MPS sonde (YSI Incorporated, Yellow Springs, OH), temperature profiles were obtained by recording water temperature (nearest 0.01 °C) at every 1-2 m following the retrieval of each gill net. Supplemental temperature readings were obtained from other WIDNR, MIDNR, and USFWS sampling events. Thermal conditions experienced by walleyes were summarized as month-specific mean water temperatures based on these temperature profiles and supplemental water temperature data.

I attempted to use spatially relevant (i.e., specific to Lake Michigan or the Great Lakes region) predator and prey energy density values when available. Adult walleye (ages 4-20) energy density (J/g wet weight) was estimated as the mean energy density of 20 adult walleye collected from the Fox River below De Pere dam (C. P. Madenjian, U.S. Geological Survey, personal communication). I could not identify published energy density values for juvenile walleyes (ages 1-3) from within Lake Michigan or the Great Lakes region; energy density values for these fish were obtained from a laboratory study conducted by Madenjian and Wang (2013). Energy density values of identifiable prey items were gathered from the literature for macroinvertebrates and fish (Table 1). For pooled diet items (e.g., other fish and invertebrates), energy densities were estimated as the mean energy density of taxonomically similar diet items for each month. The energy density for unidentified fish was the mean value of all prey fish encountered during each respective month. Some energy densities were estimated using values reported by multiple sources of literature; these were averaged using monthly values from each source. Energy densities for walleye, lake whitefish, unidentified fish, and invertebrates were held constant for the duration of each simulation (Table 1).

Walleye were stratified by age groups (i.e., juveniles, young adults, and old adults; described previously) to maximize the sample size for age-specific diet proportion inputs used in each bioenergetic simulation; age-0 walleyes were excluded from bioenergetics modeling. Prey items were grouped into the following nine categories: round goby, rainbow smelt, alewife, gizzard shad, yellow perch, lake whitefish, other fish, unidentified fish, and invertebrates. Other fish included freshwater drum *Aplodinotus grunniens*, white perch *Morone americana*, brown trout *Salmo trutta*, emerald shiner *Notropis atherinoides*, and spottail shiner, which represented a relatively small proportion of overall diets. Invertebrates also represented a minor proportion of

overall diets that consisted of three families and included Chironomidae (larvae and pupae), Hirudinidae (i.e., leaches), and Dreissenidae. Using equation 1.1, diet composition was estimated for each walleye age-group and sampling month. To estimate consumption trajectories more adequately and reduce the consequences of linear interpolation during sampling intervals, diet compositions were estimated for each distinct sampling event during a single month to minimize interval durations when data were available (Whitledge and Hayward 2000; Hartman and Hayward 2007); sampling events were defined as consecutive sampling days where walleye were collected from respective age groups.

Each walleye cohort (i.e., age-class) for ages 1-9 was modeled individually using age-specific growth and age-group specific diet composition inputs (i.e., age classes within each age-group had the same diets but were modeled with different growth); walleye ages 10-20 were pooled for modeling growth to maximize available data while providing a reasonable estimate of growth, as few walleye were collected in these older age classes. Mean weight (g) was calculated for each walleye cohort using all individuals collected during May through July (initial weight) and August through October (final weight). Growth of walleye was expressed as the difference between the final and initial mean weights for each cohort from May 1 through October 31 in 2018.

Individual walleye consumption of lake whitefish and yellow perch was estimated for each walleye cohort as the sum of daily consumption estimates (g) for each respective prey item throughout the modeling period. Templates that included the inputs for each bioenergetic simulation modeling individual walleye consumption for each walleye cohort (individual consumption simulations = 10) were saved and used later to model walleye consumption at the population level.

### Population Level: Age-Specific Walleye Consumption of Lake Whitefish and Yellow Perch

Age-specific abundances of walleye, lake whitefish, and yellow perch in southern Green Bay were estimated using SCAA models formulated and run by WIDNR personnel. These models largely incorporated data that were already available from WIDNR electrofishing, bottom trawling, gill netting, commercial harvest monitoring, and creel surveys. In addition to the nominal abundance estimates (i.e., maximum posterior density estimates, equivalent to best guess or maximum likelihood estimate), 95% confidence limits (CL) were estimated for walleye based on Markov chain Monte Carlo simulations (I. Tsehay, personal communication). To estimate population-level walleye consumption of lake whitefish and yellow perch and provide an estimate of variability, nominal abundance estimates, as well as upper and lower 95% CL, from SCAA models for each walleye cohort were separately modeled in the mortality sub-model that is built within each respective individual walleye consumption bioenergetics model template (described previously; population level consumption simulations = 30). These sub-models were simulated as discrete populations for each cohort, extrapolating the estimated consumption from one individual walleye to consumption by the population (Hanson et al. 1997).

To account for the effects of mortality on walleye abundance over the bioenergetics simulation period, an interval total mortality rate ( $A$ ; adjusted to represent the simulation period) was used to estimate the net consumption by each walleye cohort. Instantaneous total mortality rate ( $Z$ ) was first estimated from three catch curves regressing  $\log_e$  abundance against age (Ricker 1975) using SCAA model estimates of abundance for walleye ages 1-3 (juveniles), 4-6 (young adults), and 7-20 (old adults). Subsequently, estimates of  $Z$  were multiplied by 0.5 years to represent an interval mortality rate for the simulation period, converted to  $A$  using the equation



$A = 1 - e^{-Z}$ , and used as inputs within the respective age-specific bioenergetics mortality sub-models as outlined previously for abundance.

Age-specific walleye consumption of lake whitefish and yellow perch was estimated for each walleye cohort as the sum of daily consumption estimates (g) for each respective prey item throughout the modeling period. Total consumption of each prey item was estimated as the sum of daily consumption estimates across all walleye cohorts.

#### Apportioning Walleye Consumption to Specific Lake Whitefish and Yellow Perch Age Classes

The original wet weights of partially digested lake whitefish and yellow perch were reconstructed by converting all partial prey fish lengths (i.e., backbone, fork, and standard) to TL when necessary, and subsequently converting TL to wet weight using available data and published weight-length regression equations (Table 2). Lake whitefish and yellow perch found in walleye diets were generally assigned ages using age-length keys developed from data obtained during WIDNR bottom trawling surveys that targeted young fish representative of the prey sizes found in walleye diets.

For each walleye cohort, the estimated population level walleye consumption (i.e., biomass) of lake whitefish and yellow perch was multiplied by the overall proportion (by wet weight) of each respective prey age-class observed in the diets of walleye to apportion consumption estimates to specific lake whitefish and yellow perch age classes. Age-specific walleye consumption of each prey age-class was then divided by the mean weight of respective lake whitefish and yellow perch age classes consumed to express consumption in numbers of fish ( $C_N$ ) rather than biomass ( $C_B$ ). To minimize error, conversions from  $C_B$  to  $C_N$  were computed independently during each month for each age-class of prey (Beauchamp et al. 2007). For

example, large estimation errors can arise during these conversions when juvenile prey fish are growing rapidly, causing monthly mean prey weights to greatly differ (e.g., Cyterski et al. 2003). Total population level consumption of specific lake whitefish and yellow perch age classes was estimated as the sum of age-specific consumption estimates across all walleye cohorts.

#### Effects of Walleye Consumption on Lake Whitefish and Yellow Perch Recruitment Potential

Age-specific mean abundance (nominal estimate), as well as upper and lower 95% CL, of lake whitefish and yellow perch was calculated from SCAA estimates using models developed during the past five years (i.e., 2014 through 2018). The resulting abundance estimates were only available for age-3 lake whitefish, age-1 yellow perch, and age-2 yellow perch. Because walleye frequently consumed prey younger than ages available in the SCAA models (e.g., lake whitefish ages 0-2 and age-0 yellow perch), recruitment potential of lake whitefish and yellow perch was estimated using expected population fecundity. Expected population fecundity was calculated based on SCAA abundance estimates, using species-specific sex ratios, maturity schedules, age-specific mean weights (g), and size-specific fecundity estimates (Table 3; S. P. Hansen and T. J. Paoli, Wisconsin Department of Natural Resources, personal communication); to estimate yellow perch fecundity, I used the formula provided by Brazo et al. (1975):  $\text{fecundity} = 138.215 + 187.054 * \text{weight(g)}$ . Based on mortality rates from SCAA models and rates gathered from relevant literature (Dahlberg 1978; Freeberg et al. 1990; Kaemingk et al. 2014), annual survival rate ( $S$ ) from egg to age-1 was set at 1%; survival from age-1 to age-3 was set at 60%. The resulting abundance estimates for these age classes were considered as indices of lake whitefish and yellow perch recruitment potential. Upper and lower 95% CL of age-specific lake whitefish

and yellow perch abundance estimates were used to describe variation in lake whitefish and yellow perch recruitment potential.

For each age-class of lake whitefish and yellow perch consumed by walleye, the percentage of recruitment potential lost to walleye predation was calculated (i.e.,  $C_N$  divided by recruitment potential), under the premise that walleye predation would need to reduce recruitment potential by  $\geq 20\%$  to be considered important in regulating recruitment of lake whitefish and yellow perch. I chose the 20% benchmark because a reduction of  $< 20\%$  would likely be less detectable given uncertainty in sampling design and SCAA model estimates. Various combinations of the upper and lower 95% CL estimates for walleye consumption and prey recruitment potential were compared to describe the variability in the percentage recruitment potential of lake whitefish and yellow perch lost to walleye predation.

## RESULTS

### *Fish Collection*

Numbers of walleyes, lake whitefish, and yellow perch collected, percent with empty stomachs, and mean total lengths varied by year, zone, and month (Tables 4, 5, and 6). Throughout the study period, stomachs from 1,368 walleye were examined (985 in 2018 and 383 in 2019), with 50% containing empty stomachs ( $n = 487$  in 2018 and 194 in 2019; Table 4). Walleyes were collected by gill net ( $n = 1,134$ ), trap net ( $n = 84$ ), electrofishing ( $n = 63$ ), bottom trawl ( $n = 41$ ), hook and line ( $n = 41$ ), and fyke net ( $n = 5$ ; Table 7). The overall mean  $\pm$  standard error (SE) TL of walleye was  $463 \pm 4$  mm (TL range: 134-772 mm; Table 4). Stomachs from 1,763 lake whitefish were examined (1,468 in 2018 and 295 in 2019), with 70% containing empty stomachs ( $n = 1,065$  in 2018 and 165 in 2019; Table 5). Lake whitefish were collected by

trap net ( $n = 1,255$ ), gill net ( $n = 391$ ), purse seine ( $n = 52$ ), electrofishing ( $n = 35$ ), and bottom trawl ( $n = 30$ ; Table 7). The overall mean  $\pm$  SE TL of lake whitefish was  $465 \pm 1$  mm (TL range: 243-646 mm; Table 5). Stomachs from 1,292 yellow perch were examined (1,063 in 2018 and 229 in 2019), with 46% containing empty stomachs ( $n = 511$  in 2018 and 85 in 2019; Table 6). Yellow perch were collected by gill net ( $n = 1,003$ ), fyke net ( $n = 115$ ), electrofishing ( $n = 79$ ), bottom trawl ( $n = 55$ ), and hook and line ( $n = 40$ ; Table 7). The overall mean  $\pm$  SE TL of yellow perch was  $208 \pm 1$  mm (range, 105-375 mm; Table 6).

### ***Objective 1: Importance of Lake Whitefish and Yellow Perch as Walleye Prey***

The use of DNA barcoding reduced the amount of unidentified fish (pooled across months) in walleye diets from 39% to 11% during 2018 and from 35% to 6% during 2019 (Figure 3). Lake whitefish and yellow perch represented  $< 10\%$  of walleye diets in both zones when diets were pooled across months in 2018 (Appendix A). During 2018, contribution of lake whitefish to walleye diets in Zone 1 increased from May ( $p_{ij} = 7\%$ ) through June, becoming important prey during June ( $p_{ij} = 36\%$ ; Figure 4). Lake whitefish were seasonal forage and were not observed in walleye diets after June. In both zones, yellow perch contributed to walleye diets at a broader temporal scale than lake whitefish, but yellow perch never comprised more than 15% of walleye diets in any month in either zone during 2018 (Figure 4).

In 2019, walleyes were only collected during May and October in Zone 1 and during June through September in Zone 2. Lake whitefish and yellow perch were not considered important contributors to walleye diets in either zone during these sampling periods ( $p_{ij} < 20\%$ ; Figure 4). As in 2018, lake whitefish were consumed by walleye during May 2019 in Zone 1 ( $p_{ij} = 8\%$ ). However, yellow perch were absent in Zone 1 walleye diets during 2019 and were only

consumed during June ( $p_{ij} = 0.3\%$ ), July ( $p_{ij} = 0.5\%$ ), and September ( $p_{ij} = 9\%$ ) in Zone 2 (Figure 4).

Lake whitefish and yellow perch represented  $< 10\%$  of juvenile walleye diets ( $p_{ij} = 3$  and  $6\%$ , respectively) in Zone 1 (Figure 5) when 2018 diet data were pooled across months. Juvenile walleye consumed post-larval (i.e., age-0) lake whitefish ( $n = 12$ ) during mid-late June. Lake whitefish were absent in the diets of young-adult walleye, while yellow perch comprised only a small proportion of diets ( $p_{ij} = 0.9\%$ ). Lake whitefish were considered important prey for old-adult walleye in Zone 1, representing  $32\%$  of their diets (Figure 5). Old-adult walleye consumed age-1 ( $n = 14$ ), age-2 ( $n = 26$ ), and age-3 ( $n = 16$ ) lake whitefish from mid-May through mid-June. Yellow perch represented only  $3\%$  of old-adult walleye diets in Zone 1. In Zone 2, lake whitefish were not observed in walleye diets and yellow perch always represented less than  $11\%$  of walleye diets among all age groups (Figure 5). Juvenile walleye consumed both age-0 ( $n = 14$ ) and age-1 ( $n = 4$ ) yellow perch from early May through mid-late June. Conversely, walleye beyond the juvenile age-group consumed yellow perch from mid-August through late October. Only one yellow perch (age-0) was eaten by a young-adult walleye during late October, while old-adult walleye consumed age-0 ( $n = 2$ ), age-1 ( $n = 2$ ), and age-2 ( $n = 1$ ) yellow perch from mid-August through late October.

## ***Objective 2: Variation in Diet Compositions***

### **Walleye**

The diet compositions of all walleye did not differ between Zone 1 and Zone 2 during May, July, and September, but were significantly different between zones during June, August, and October (Table 8). The lowest degree of diet separation between zones occurred during June,

with the highest separation occurring in October. The observed difference in walleye diets between zones during June was largely attributed to a greater prevalence of lake whitefish and rainbow smelt in Zone 1, while alewife contributed more to diets in Zone 2 (Table 8; Figure 4). During August, the observed difference between zones was attributed to a greater prevalence of gizzard shad in Zone 1, while alewife and round goby contributed more in Zone 2 (Table 8; Figure 4). During October, the observed difference between zones was attributed to a greater prevalence of gizzard shad in Zone 1, while round goby contributed more in Zone 2 (Table 8; Figure 4).

In Zone 1, walleye diet compositions were significantly different between successive months with the exception of August and September (Table 8). The lowest degree of diet separation between months occurred from May to June, with the highest separation occurring between September and October. The observed difference in walleye diets between May and June in Zone 1 was largely attributed to a greater prevalence of round goby and rainbow smelt in May, while lake whitefish and alewife contributed more to walleye diets during June (Table 8; Figure 4). The observed difference between June and July diets was attributed to a greater prevalence of lake whitefish in June, while alewife and round goby contributed more to diets during July (Table 8; Figure 4). The observed difference in walleye diets between July and August and diets between September and October was attributed to a greater prevalence of alewife in July and September, while gizzard shad contributed more during August and October (Table 8; Figure 4). In Zone 2, walleye diet compositions were only significantly different between the months of May and June (Table 8). The observed difference was largely attributed to a greater prevalence of round goby and rainbow smelt in May, while alewife contributed more to walleye diets during June (Table 8; Figure 4).

In Zone 1, walleye diet compositions did not differ between 2018 and 2019 during May and October (Table 8). In Zone 2, diets were significantly different between years during June which was largely attributed to a greater prevalence of alewife in 2018, while round goby contributed more to walleye diets during 2019 (Table 8; Figure 4). Alternatively, walleye diet compositions in Zone 2 did not significantly differ between years during July, August, and September (Table 8). Additionally, Zone 1 walleye diet compositions pooled across months did not differ between juveniles and young adults, but diet compositions for these two younger age groups were significantly different than observed for old-adult walleye (Table 9). The lowest degree of diet separation occurred between juvenile and old-adult walleye, with the highest separation occurring between young adults and old adults. The observed difference between juvenile and old-adult walleye was largely attributed to a greater prevalence of gizzard shad, round goby, and rainbow smelt in juvenile diets, while lake whitefish contributed more to the diets of old adults (Table 9; Figure 5). The observed difference between young- and old-adult walleye was attributed to a greater prevalence of gizzard shad and alewife in the diets of young adults, while lake whitefish and rainbow smelt contributed more to the diets of old adults (Table 9; Figure 5). In Zone 2, walleye diet compositions did not differ between juvenile and young-adult walleye, and between juveniles and old adults (Table 9). Conversely, young- and old-adult walleye diets were significantly different which was largely attributed to a greater prevalence of gizzard shad in the diets of young adults, while alewife and round goby contributed more to the diets of old adults (Table 9; Figure 5).

## Lake Whitefish

The use of DNA barcoding reduced the amount of unidentified fish in lake whitefish diets from 2% to < 1% when 2018 diet data were pooled across months and no unidentified fish were encountered during 2019 (Figure 3). The diet compositions of all lake whitefish were not different between Zone 1 and Zone 2 during June, July, September, and October, but were significantly different between zones during May and August (Table 10). The lowest degree of diet separation between zones occurred during May, with greater separation occurring in August. The observed difference between diet compositions during May and August was largely attributed to a greater prevalence of invertebrates in Zone 1 diets, while round goby contributed more to lake whitefish diets in Zone 2 (Table 10; Figure 6).

In both Zone 1 and Zone 2, lake whitefish diet compositions did not significantly differ between successive months from May through October (Table 10). Similarly, diet compositions in both zones did not significantly differ between years during all months evaluated (Table 10).

## Yellow Perch

The use of DNA barcoding reduced the amount of unidentified fish in yellow perch diets from 11% to 5% when 2018 diet data were pooled across months and from 7% to 1% during 2019 (Figure 3). Diet compositions of all yellow perch did not differ between Zone 1 and Zone 2 during May, June, and September, but were significantly different between zones during July, August, and October (Table 11). The lowest degree of diet separation between zones occurred during July, with the highest separation occurring in October. The observed difference between diet compositions during July, August, and October was largely attributed to a greater prevalence



of invertebrates in Zone 1 diets, while round goby contributed more to yellow perch diets in Zone 2 (Table 11; Figure 7).

In Zone 1, yellow perch diet compositions between successive months were only different between August and September (Table 11). The observed difference between August and September was largely attributed to a greater prevalence of invertebrates in diets during August, while round goby contributed more to yellow perch diets in September (Table 11; Figure 7). In Zone 2, yellow perch diet compositions were only significantly different between September and October. Similarly, the observed difference between September and October was attributed to a greater prevalence of invertebrates in diets during September, while round goby contributed more to yellow perch diets in October (Table 11; Figure 7).

In Zone 1, yellow perch diets did not significantly differ between 2018 and 2019 during May (Table 11). However, diet compositions in Zone 2 were significantly different between years during September (Table 11). The observed difference during September was largely attributed to a greater prevalence of round goby during 2018, while invertebrates contributed more to yellow perch diets during 2019 (Table 11; Figure 7). Alternatively, diet compositions in Zone 2 did not significantly differ between years during July and August (Table 11).

### ***Objective 3: Diet Overlap***

Weak diet overlap between walleye and lake whitefish was observed ( $O_{jk} = 0.203$ ) when diet information was pooled for both zones across all months (Table 12). Within each zone, diet overlap between walleye and lake whitefish was weak when all months were pooled (Zone 1  $O_{jk} = 0.042$ ; Zone 2  $O_{jk} = 0.391$ ). Monthly index values (May through October) indicated no overlap to weak overlap in Zone 1 (range of  $O_{jk} = 0.000$ -0.105) and weak to moderate overlap in Zone 2

(range of  $O_{jk} = 0.088-0.653$ ; Table 12). Moderate overlap between walleye and yellow perch was apparent ( $O_{jk} = 0.451$ ; Table 12) when diet information was pooled across zones and months. However, diet overlap between walleye and yellow perch was much weaker in Zone 1 ( $O_{jk} = 0.195$ ) than in Zone 2 ( $O_{jk} = 0.723$ ) when all months were combined. Conversely, monthly diet overlap ranged from weak to moderate in both Zone 1 (range of  $O_{jk} = 0.008-0.503$ ) and Zone 2 (range of  $O_{jk} = 0.276-0.744$ ; Table 12).

Strong diet overlap was apparent between lake whitefish and yellow perch ( $O_{jk} = 0.905$ ) when diet information was pooled across zones and months (Table 12). Diet overlap between lake whitefish and yellow perch was considered strong in Zone 1 ( $O_{jk} = 0.963$ ), while only moderate overlap was identified in Zone 2 ( $O_{jk} = 0.668$ ) when diet information was pooled across months. In Zone 1, monthly values of  $O_{jk}$  between lake whitefish and yellow perch ranged from 0.905 to 0.999 (i.e., strong diet overlap) during May through August. However, lake whitefish and yellow perch appeared to share few prey resources during September and diet overlap was considered weak ( $O_{jk} = 0.067$ ) until October when moderate overlap became apparent ( $O_{jk} = 0.736$ ; Table 12). Monthly diet overlap between lake whitefish and yellow perch in Zone 2 was comparable to the results from Zone 1, with strong overlap increasing during May ( $O_{jk} = 0.770$ ) through August ( $O_{jk} = 0.927$ ), decreasing to moderate overlap during September ( $O_{jk} = 0.471$ ) and weak overlap during October ( $O_{jk} = 0.255$ ; Table 12).

Juvenile walleye exhibited strong diet overlap with young adults ( $O_{jk} = 0.835$ ) in Zone 1, but only moderate overlap with old adults in 2018 when diet information was pooled across months ( $O_{jk} = 0.675$ ; Table 13). Similarly, diet overlap between young-adult and old-adult walleye was also moderate ( $O_{jk} = 0.540$ ) in Zone 1 (Table 13), reflecting the significantly different diet compositions already described (Table 9). In Zone 2, diet overlap between all

walleye age groups was strong (range of  $O_{jk} = 0.830-0.870$ ; Table 13). In contrast with Zone 1, values of  $O_{jk}$  for Zone 2 (Table 13) did not reflect the significantly different diets of old-adult walleye that were identified in my analyses associated with Objective 2 (Table 9).

#### ***Objective 4: Effects of Walleye Predation on Lake Whitefish and Yellow Perch Recruitment***

Temperatures varied by month, location, and depth; mean thermal conditions experienced by walleye increased from 10.0 °C during May to a peak of 21.1 °C in July and dropped to 8.1 °C by the end of October (Figure 8). Diet proportion input files were modified to constrict bioenergetic simulations from interpolating lake whitefish consumption past the last day in June to prevent lake whitefish from inappropriately remaining in walleye consumption models beyond the interval observed from my diet results (Table 14). Similarly, diet inputs for each walleye age-group were modified to restrict bioenergetic simulations from interpolating the consumption of yellow perch into July because no perch were observed in diets during this month (Table 14).

Growth was observed for most walleye cohorts, increasing in mean weight from May through October (Table 15). Observed growth for age-6 walleye and pooled age classes 10-20 were negative over the sampling period. Subsequently, zero growth was assumed for these ages and the initial and final weights were input as the mean weight of all individuals collected from each respective cohort (Table 15). Growth was positive for the remaining cohorts (i.e., ages 1-5 and 7-8) and ranged between an increase of 147-369 g in mean weight. The nominal walleye population estimate from SCAA models was 1.8 million fish (lower 95% CL = 259,266; upper 95% CL = 5,026,213) in Wisconsin waters of Green Bay south of Chambers Island (Zone 1; Table 15). Estimated mortality rates decreased the abundance of juvenile walleye cohorts by

approximately 24%, young-adult walleye by 28%, and old-adult walleye by 16% over the 184 simulation days (Table 15).

Proportion of maximum consumption ( $P_{Cmax}$ ) ranged from 0.250 to 0.611 among walleye cohorts (Figure 9). Estimates of  $P_{Cmax}$  were similar among juvenile cohorts (range of  $P_{Cmax}$  = 0.605-0.611). Estimates of  $P_{Cmax}$  for adult walleye ages (range of  $P_{Cmax}$  = 0.250 to 0.379) were comparatively lower than the values calculated for juveniles (Figure 9).

Identical diet proportions were assumed for specific walleye ages within each age-group, but total consumption varied due to differences in age-specific growth. The consumed biomass ( $C_B$ ) of major prey was divided by the mean weight (g) of each respective prey fish consumed to express consumption in numbers ( $C_N$ ) rather than biomass (Table 16; Appendices E and F). Modeled at nominal abundance, the walleye population consumed 4,130,231 kg (lower 95% CL = 665,996 kg; upper 95% CL = 11,010,459 kg) of prey biomass. Contributing to this prey biomass were an estimated 46,608,204 age-0 (post-larval) lake whitefish, 1,013,287 age-1 lake whitefish, 123,487 age-2 lake whitefish, 34,653 age-3 lake whitefish, 83,035,134 age-0 yellow perch, 4,397,736 age-1 yellow perch, and 397,179 age-2 yellow perch (Table 16). Modeled at the lower and upper 95% CL of abundance, consumption by the walleye population ranged from 5,222,409 to 135,591,918 lake whitefish and from 6,185,874 to 291,221,843 yellow perch, most of which were age-0 fish consumed by juvenile walleye cohorts (Table 16). Consumption by the walleye population also varied by month (Figure 10), reflecting temporal changes in diet proportions and thermal habitats experienced by walleye (Figures 4 and 8).

Age-specific estimates of lake whitefish and yellow perch recruitment potential calculated from population fecundity-mortality scenarios are reported in Table 17. At the nominal consumption and recruitment estimates, the projected walleye population in Zone 1

consumed 3% (range, 0.3-13%) of available age-0 lake whitefish, 7% (range, 2-24%) of age-1 lake whitefish, 1% (range, 0.3-5%) of age-2 lake whitefish, and 0.7% (range, 0.1-3%) of age-3 lake whitefish (Figure 11). High variability was observed in the estimated yellow perch recruitment potential lost to walleye predation, with predicted percentage of yellow perch age classes consumed by walleye ranging from 2% to >100% (nominal, 37%) for age-0 yellow perch, from 24% to >100% (nominal, >100%) for age-1 yellow perch, and 7% to 95% (nominal, 29%) for age-2 yellow perch (Figure 11).

The recruitment potential of lake whitefish lost to walleye predation was only considered important (24% lost) for age-1 lake whitefish when modeled at the upper 95% CL of walleye abundance and lower 95% CL of lake whitefish recruitment potential (Figure 11). In contrast, the recruitment potential lost to walleye predation for all yellow perch ages was considered important (> 20% loss) in nearly all modeling scenarios. For example, a reduction in yellow perch recruitment potential < 20% only occurred when modeled at the lower 95% CL of walleye abundance and at the nominal and upper 95% CL of yellow perch recruitment potential, with the exception of age-1 yellow perch where walleye consumption exceeded 20% of projected perch recruitment for all combinations modeled (Figure 11). Furthermore, walleye consumption exceeded the estimated yellow perch recruitment potential (>100%) for all yellow perch age classes when modeled at the upper 95% CL of walleye abundance and the nominal level of yellow perch recruitment potential (Figure 11).

## DISCUSSION

### *Objective 1: Importance of Lake Whitefish and Yellow Perch as Walleye Prey*

My results indicate that lake whitefish may represent seasonally important prey for walleye in southern Green Bay. The importance of lake whitefish in walleye diets during June 2018 in southern Green Bay was a unique finding for walleye populations in the Great Lakes. Throughout Canada, lake whitefish are prey for walleye in many large lakes (Lemm 2002; Stewart and Watkinson 2004) and numerous diet studies have also identified the importance of other coregonine species in walleye diets (Devine et al. 2005; Ivan et al. 2011; Pothoven et al. 2017). My results provide evidence of new predator-prey interactions between these two important species within Green Bay. Before the mid-1990s, lake whitefish had not been observed spawning in tributaries to southern Green Bay for nearly a century. Furthermore, increased catch rates of juvenile lake whitefish during annual WIDNR bottom trawling surveys has indicated an expansion of lake whitefish throughout lower Green Bay (WIDNR 2017), and the return of tributary spawning stocks may provide new sources of recruitment. The increasing abundance and availability of lake whitefish in southern Green Bay may explain why whitefish are now seasonally important prey for walleye in lower Green Bay.

Based on our criteria and their contribution to walleye diets, yellow perch were not important prey for walleyes in Green Bay ( $\leq 20\%$  of diet by wet weight). However, given the high abundance of walleyes and low abundance of yellow perch in southern Green Bay (Figure 1), even minimal consumption at the individual level equates to high consumption at the population level. Low contribution of yellow perch in Green Bay walleye diets was comparable to walleye diets observed in the main basin of Lake Huron (Pothoven et al. 2017) and in Chequamegon Bay, Lake Superior (Devine et al. 2005). This contrasts with other systems where

yellow perch were important prey for walleye. Specifically, Pothoven et al. (2017) identified the proportion of yellow perch during April-mid-June exceeded 20% of overall walleye diets in Saginaw Bay, Lake Huron. Similarly, yellow perch comprised 95% of age-1 walleye diets during June in western Lake Erie in the late 1980s (Hartman and Margraf 1992). Furthermore, Lyons and Magnuson (1987) identified yellow perch as the most prevalent prey found in walleye diets during years when young-of-the-year perch are abundant in Sparkling Lake, Wisconsin. However, walleye in Green Bay consumed a diversity of prey resources, with alewife, round goby, and gizzard shad dominating their diets and these results are consistent with the findings of other studies in the Great Lakes (Dobiesz 2003; Zorn and Schneeberger 2011; Pothoven et al. 2017).

## ***Objective 2: Variation in Diet Compositions***

### **Walleye**

The spatial differences I observed among walleye diets were due in part to walleye consuming a greater diversity of prey types in Zone 1. Additionally, gizzard shad and alewife contributed the most to walleye diets in Zone 1, whereas round goby and alewife contributed the most to walleye diets in Zone 2. These differences were likely attributed to differences in fish assemblages and densities of walleye prey observed between southern and northern Green Bay. Southern Green Bay is shallower, warmer, more turbid and productive than northern Green Bay (USEPA 1978; Smith et al. 1988; Qualls et al. 2013) and provides better habitat for gizzard shad and likely provides for higher densities of most walleye prey as a result of these differences (Becker 1983). In addition, differences in forage fish communities likely explained the lack of temporal diet variation in Zone 2, where walleye consumed similar prey among months. Water

clarity could also influence walleye prey selection (Little et al. 1998; Sheppard 2015). Sheppard (2015) identified a greater diet diversity for walleye in the southern basin of Lake Winnipeg, Manitoba relative to the northern basin and suggested the difference may be associated with higher turbidity in southern Lake Winnipeg. Higher turbidity likely decreases visual acuity and has been linked to increased prey diversity in the diets of walleye from the Slave River (Little et al. 1998). Pothoven et al. (2017) concluded that walleye diets did not differ among walleye from the northern and southern regions of Lake Huron. Similar to the differences between southern and northern Green Bay, the northern and southern regions of Lake Huron have differing prey supplies, walleye densities, water clarity, and differ thermally (Peat et al. 2015; Pothoven et al. 2017). However, walleyes migrate out of southern Lake Huron (Saginaw Bay) occurring in mid-June (Peat et al. 2015), which could explain why Pothoven et al. (2017) did not observe the spatial differences in walleye diets that my results identified between zones in Green Bay.

Walleye diets were generally similar between years within each zone and across months in Zone 2. However, walleye diets in Zone 1 continually changed during 2018 and I observed significant transitions from lake whitefish, round goby, and rainbow smelt dominated diets to a diet dominated by alewife and gizzard shad. Similarly, Jovanovic (2013) and Liao et al. (2004) reported that walleye diet compositions varied seasonally in Saginaw Bay, Michigan (a part of Lake Huron) and Spirit Lake, Iowa. Additionally, Pothoven et al. (2017) found distinct seasonal differences in the diet assemblages among walleye collected during two open water time periods from 2009-2011 in Lake Huron. The observed variation in walleye diets among seasons were likely associated with fluctuations in prey availability, especially the increase in age-0 prey during late summer and fall in Green Bay (Knight et al. 1984).



Similar to my results, Jovanovic (2013) reported that walleye diets differed among walleye age classes during May through September 2009. Diets of old-adult walleye in Green Bay were significantly different than the diets of younger walleye age groups. In Zone 2, diets of old-adult walleye included less invertebrate prey and greater percentages of fish, which was consistent with previous research (Knight et al. 1984; Liao et al. 2002). This is likely a result of increased size-selective preferences and piscivory at these older ages. Furthermore, juvenile walleye consumed young lake whitefish and yellow perch, whereas adult walleye consumed older individuals. The observed differences in walleye diets among age groups may also be associated with gape limitations during the juvenile stages (Knight et al. 1984; Lyons and Magnuson 1987; Jovanovic 2013).

### Lake Whitefish

Lake whitefish diets in Green Bay exhibited little temporal or spatial variation, although diet compositions differed between zones during May and August 2018. However, my analyses did not account for potential transitions among different invertebrate prey taxa. Numerous studies throughout the Great Lakes have identified seasonal and geographic changes in lake whitefish diets when invertebrate prey taxa were identified to more specific categories (Pothoven 2005; Pothoven and Nalepa 2006; Pothoven and Madenjian 2013), but this was beyond the scope of my study. Pothoven and Nalepa (2006) found that lake whitefish in Lake Huron primarily consumed Chironomidae during the spring and large-bodied zooplankton throughout the summer, reflecting seasonal availability of prey (Barbiero et al. 2001). In contrast, my results indicated the occurrence of Chironomidae in lake whitefish diets peaked during August. After the decline of their dominant food source (i.e., *Diporeia spp.*) and the proliferation of invasive

mussels (i.e., Dreissenidae), lake whitefish consumption of shelled prey substantially increased in southern Lake Michigan, Lake Ontario, and South Bay, Lake Huron (Pothoven et al. 2001; Owens and Dittman 2003; Rennie et al. 2009). Reflective of this trend, mollusks (e.g., Dreissenidae and Pisidiidae) were important forage consumed by a large percentage of lake whitefish throughout my study.

During the late 1990s and early 2000s, regional differences in lake whitefish diets throughout Lake Michigan reflected regional densities of their prey (Pothoven 2005). This may explain why round goby contributed less to lake whitefish diets in Zone 1 than in Zone 2, a trend also observed for walleye and yellow perch. My results also support previous work demonstrating that piscivory may be important for lake whitefish (Pothoven 2005; Pothoven and Nalepa 2006; Pothoven and Madenjian 2013; Lehrer-Brey and Kornis 2014). Specifically, lake whitefish consumed round goby throughout Green Bay, but were important prey in northern Green Bay. My results indicated round gobies were less important prey for lake whitefish in southern Green Bay, whereas Lehrer-Brey and Kornis (2014) identified round goby as the most important winter diet item for lake whitefish at similar sampling locations in southern Green Bay. Walsh et al. (2007) found that round goby populations have expanded into deeper waters as their abundance continues to increase. This expansion could increase the rate at which round gobies are encountered and consumed by lake whitefish in offshore areas of Green Bay, which has been observed for many Great Lakes fishes that utilize round gobies as prey (Kornis et al. 2012).

Finally, the consumption of round goby by lake whitefish should be considered when evaluating predator-prey dynamics in Green Bay, and possibly other regions of the Great Lakes. Even if only a small fraction of the lake whitefish population is consuming round goby, the

magnitude of the expanding lake whitefish population in lower Green Bay (age-3+ abundance approximately 42 million; I. Tsehay, unpublished data) relative to that of walleye and yellow perch suggests that the influence of lake whitefish predation on round goby may be substantial. Lake whitefish should not only be considered a benthivore when evaluating the flow of energy in the Green Bay food web but also as a piscivore that could have significant effects on certain prey, such as round goby.

### Yellow Perch

Numerous studies throughout the Great Lakes have identified spatial and temporal diet variation within yellow perch populations (Parrish and Margraf 1994; Staton et al. 2014; Happel et al. 2015). Similarly, yellow perch diets in Green Bay were characterized by spatial variation between zones. A unique component of my findings is that round goby comprised the highest proportion of yellow perch diets in northern Green Bay, while invertebrates were most prevalent in the south. Adult yellow perch are largely piscivorous but are known to consume a wide variety of prey when fish are less available (Morrison et al. 1997). Furthermore, diet shifts from invertebrates in spring to prey fish during summer and fall are well documented for yellow perch in Lake Erie (Knight et al. 1984; Schaeffer and Margraf 1986; Parrish 1988). This shift occurred later in Green Bay, as the contribution of invertebrates to yellow perch diets was greater through the summer. In northern Alberta's Sucker Lake, Roloson et al. (2016) found annual changes in yellow perch diets were largely driven by changes in the consumption of invertebrates. Similarly, in Green Bay, the difference between the diets of yellow perch during September 2018 and 2019 was driven by a shift in consumption from round goby to invertebrates. Similar to lake whitefish,

my analyses of yellow perch diets did not include identification of specific invertebrate taxa, which may have revealed additional variation in diets.

Diet composition of yellow perch in northern Green Bay during my study differed from historical observations where alewife, johnny darter, and trout-perch were more prevalent, and the occurrence of cannibalism was much higher (Zorn and Schneeberger 2011). However, my results were consistent with other studies demonstrating that the prevalence of round goby in yellow perch diets has increased throughout the Great Lakes (Truemper and Lauer 2005; Staton et al. 2014). My diet results were also consistent with previous studies that documented Chironomidae, *Bythotrephes spp.*, and various Ephemeroptera families (i.e., mayflies) as common prey consumed by yellow perch (Duncan et al. 2011; Zorn and Schneeberger 2011; Staton et al. 2014). High consumption of Chironomidae by yellow perch has been thought to occur in relation to emergence patterns (Duncan et al. 2011). The prevalence of mayflies in Green Bay yellow perch diets I observed during 2018 was consistent with Ephemeroptera prevalence in perch diets documented by Zorn and Schneeberger (2011) in northern Green Bay from 1989 through 2005. Similarly, *Bythotrephes spp.* were by far the most frequent invertebrate taxa consumed by yellow perch in northern Green Bay from 1989 through 2005 (Zorn and Schneeberger 2011).

### ***Objective 3: Diet Overlap***

Walleye were opportunistic in utilizing a greater diversity of prey resources than lake whitefish and yellow perch resulting in relatively weak diet overlap. Weak diet overlap was observed and expected between walleye and lake whitefish given that lake whitefish primarily consumed invertebrate prey and a low diversity of fish prey (round goby and alewife). I also

observed weak diet overlap between walleye and yellow perch in most months for similar reasons, although yellow perch did eat a wider range of fish prey than lake whitefish. The highest degree of diet overlap between walleye and yellow perch was observed during October, which corresponded with increased consumption of gizzard shad by both walleye and yellow perch. Keast (1977) suggested that higher diet overlap may result from predators favoring certain prey when prey populations are abundant, and my October diet results appeared to reflect this pattern relative to availability of gizzard shad.

Diet overlap was more evident between lake whitefish and yellow perch, which was largely attributed to high contributions of invertebrates in the diets of both species. Specifically, high occurrence of Chironomidae, *Bythotrephes spp.*, and Dreissenidae influenced the overall proportion of invertebrates consumed by lake whitefish and yellow perch, increasing the similarities between their diets. Unlike walleye, lake whitefish and yellow perch are known to selectively forage on various invertebrate taxa, which are commonly preferred when readily available (Pothoven and Nalepa 2006; Roloson et al. 2016). Furthermore, piscivory by lake whitefish has increased since the invasion of round goby throughout the Great Lakes (Pothoven and Madenjian 2013). Although yellow perch were more piscivorous than lake whitefish, this did not appear to influence their diet overlap, as the influence of invertebrate prey types far outweighed prey fish in resulting overlap index values.

Similar to results reported by Knight et al. (1984), diet overlap was high among walleye age groups in Green Bay, with the lowest overlap occurring in Zone 1 between younger age groups (i.e., juveniles and young adults) and old-adult walleye. This was likely due to greater proportions of larger prey fish species in the diets of old-adult walleye. Specifically, reduced

overlap was attributed largely to consumption of lake whitefish and freshwater drum by older adult walleye.

***Objective 4: Effects of Walleye Predation on Lake Whitefish and Yellow Perch Recruitment***

My simulations suggest walleye predation may not play a significant role in regulating lake whitefish recruitment in Zone 1 given the high abundance of lake whitefish in southern Green Bay. However, if walleye abundance remains high and lake whitefish abundance declined, the effects of walleye predation on lake whitefish recruitment could be higher if prevalence of lake whitefish in walleye diets remained similar. Additionally, I only examined the effects of predation using walleye diet information during May 1 through October 31 in 2018. To some degree, walleye consumption of lake whitefish likely occurs outside of this window, potentially increasing the effects of walleye predation on lake whitefish recruitment. The distributional overlap between these two species is likely greatest during winter when lake whitefish move into shallower nearshore habitats in Green Bay (Lehrer-Brey and Kornis 2014). Shifts in distributional overlap between walleye and lake whitefish were apparent in my study. Walleye and juvenile lake whitefish were both captured in WIDNR gill netting assessments in early May, along with commercial trap nets during May and June when post-spawn walleyes moved into deeper waters. These observations coincided with increased walleye consumption of lake whitefish during these months. Conversely, walleye and lake whitefish were not captured in the same gears and locations during the summer and early fall. Additionally, juvenile walleye consumed post-larval lake whitefish during June, which coincided with projected young-of-the-year lake whitefish offshore movements (Wehse et al. 2016) and outmigration from the major tributaries (Houghton et al. 2016).

My modeling indicates that walleye predation is probably an important factor regulating yellow perch recruitment in southern Green Bay. Green Bay's yellow perch abundance in Zone 1 has declined since the early 1990s, which has coincided with increased walleye abundance (I. Tsehaye, unpublished data). Previous studies have observed decreases in age-0 yellow perch abundance and recruitment resulting from increases in walleye abundance (Hartman and Margraf 1993; Pierce et al. 2006). For example, Pierce et al. (2006) noted a significant decrease in small yellow perch abundance once walleye stocking was resumed in Lake Thirteen, Minnesota. Additionally, Forney (1974) observed a 99% decrease in trawl catch rates of age-0 yellow perch from August 1968 through May 1969 that was attributed to heavy predation by walleye in Oneida Lake, New York. Hartman and Margraf (1993) estimated age-0 yellow perch production in both typical and best-case scenarios which produced a range of potential walleye predatory impact on the age-0 yellow perch cohort in western Lake Erie. Comparable to my range of mean walleye consumption estimates, the proportion of the age-0 yellow perch population consumed by walleye in Green Bay (range, 29-49%) fell within the range (28-90%) observed by Hartman and Margraf (1993) when they concluded yellow perch recruitment was controlled by walleye predation in Lake Erie during 1988.

In my simulations, consumption by juvenile walleye accounted for 68% of the total prey biomass consumed by the walleye population, indicating juvenile walleye have the greatest potential to influence yellow perch recruitment. Predation by juvenile walleye is also important because these fish are more prevalent than older age groups and they exhibit faster growth rates (Hartman and Margraf 1992; Ward et al. 2008). Age-1 walleye were estimated to be the most abundant age-class in Zone 1 and were responsible for 21% of total prey biomass consumed. Although age-2 walleye were the second most abundant age-class, they were estimated to

consume more prey biomass (25%) than age-1 walleye in Zone 1. Hartman and Margraf (1993) indicated age-2 walleye as the major predator of age-0 yellow perch in Lake Erie, suggesting an expected 2-year lag between the production of a strong walleye year-class and a poor year-class of yellow perch resulting from walleye predation. In Green Bay, age-1 walleye were the greatest consumers of age-0 yellow perch, whereas age-2 walleye were the largest consumers of age-1 yellow perch. If this general trend were to persist and predation is sufficiently high in Green Bay, the production of a strong walleye year-class and a predation-induced poor year-class of yellow perch would be expected to occur without a time lag (Figure 1). Conversely, in the western basin of Lake Erie, Zhang et al. (2018) found that annual variation in age-1 walleye density and predation did not appear to be the major cause of variability in yellow perch recruitment dynamics, and instead, appeared to be mainly caused by variation in low-frequency ecological factors (e.g., invasive species and eutrophication). Therefore, walleye predation is likely not the sole factor influencing yellow perch recruitment in Green Bay. To increase the reliability of assessing food web interactions and consumption models, these low-frequency ecological factors affecting yellow perch recruitment should be identified and incorporated into future modeling.

Walleye and yellow perch abundance estimates were not available for northern Green Bay; therefore, it is difficult to assess whether walleye predation might influence yellow perch recruitment potential. Although I could not include walleye population consumption estimates for Zone 2, the results from individual walleye consumption modeling suggested that the walleye population would likely have the greatest influence on age-0 yellow perch (Appendices E and H). Estimates of individual walleye consumption of yellow perch was greater in Zone 2 than in Zone 1, but walleye abundance in Zone 2 is likely much lower, as supplemental stocking by the MIDNR still occurs in efforts to rehabilitate walleye stocks (Schneider et al. 2007; Zorn and



Schneeberger 2011; MIDNR 2012). Zorn and Schneeberger (2011) demonstrated that population dynamics of yellow perch show both similarities and differences with populations elsewhere in Lake Michigan. Thus, my ability to fully understand predator-prey interactions between walleye and yellow perch populations in northern Green Bay relies heavily on data specific to northern Green Bay that were not currently available.

### ***Major Sources of Variation and Error***

While differences in sampling gears and locations within a sampling zone could result in unexplained variation in my diet samples (Elliott et al. 1996), the spatial and temporal coverage of my sampling required utilization of fish collected from various gears by multiple resource agencies and user groups to meet sampling targets. Digestion that occurred while fish were held in nets (e.g., commercial trap nets) and the rate at which fish regurgitated diet items captured by different gears likely resulted in a loss of diet observations and potential error if these rates vary among prey items (Elliot et al. 1996).

Visual identification of partially digested prey items is often difficult and the importance of reducing unidentified prey items has been highlighted in other studies by using DNA barcoding techniques to improve accuracy of diet indices (Smith et al. 2005; Barnett et al. 2010; Kelling et al. 2016). For example, Kelling et al. (2016) found that without the use of DNA barcoding, the extent of diet overlap was lower than when using DNA barcoding and, in some cases, altered conclusions made from diet overlap indices. The use of DNA barcoding in my evaluation also reduced the amount of unidentified fish in diet samples, which greatly improved the resolution for estimates of diet composition and overlap.

Monthly fish collections occasionally exhibited a high percentage of fish containing empty stomachs, resulting in small sample sizes for certain zone-month combinations which may have skewed diet proportions. In Zone 2 during May, it is unlikely juvenile walleye cohorts consumed only one prey type while adult walleye ages consumed a variety of species, as did juvenile walleye during subsequent months. In Zone 1, a small sample size of age-2 walleye would have led to the conclusion that their diets excluded age-0 lake whitefish and yellow perch. This would have been unrealistic considering age-1 and age-3 walleye both consumed age-0 lake whitefish and yellow perch during 2018. Diet proportions used in bioenergetics models for juvenile walleye cohorts were subsequently pooled to increase sample size. Modeling consumption separately would have skewed diet compositions and consumption estimates, potentially influencing my general conclusions.

Growth for age-6 walleye and pool of ages 10-20 was assumed to be zero during the bioenergetics modeling period, as negative growth was observed during 2018 in Zone 1. Estimates of walleye consumption would have increased if growth had occurred, ultimately increasing the influence of walleye predation on lake whitefish and yellow perch recruitment. However, this would have only strengthened my conclusions regarding the effects of walleye predation on yellow perch recruitment as more perch would have been consumed. The assumption of zero growth for specific walleye ages would not have affected my conclusions regarding the effects of walleye predation on lake whitefish recruitment because whitefish were not observed in the diets of age-6 walleye. Furthermore, walleye ages 10-20 would have needed to consume nearly 30 times more whitefish to have influenced lake whitefish recruitment; the amount of growth required to achieve that level of consumption in the bioenergetics model would be biologically unrealistic.

My results represent only a general interpretation of the influence of walleye predation on yellow perch recruitment because abundance estimates varied substantially (i.e., 95% CI) due to errors associated with the complexity of SCAA model development. The precision or accuracy of my bioenergetics results must be weighed against other possible sources of error. For example, errors in model estimates of walleye consumption may be much smaller than errors associated with the estimated walleye abundance or mortality by which the model uses for population predictions (Brandt and Hartman 1993). In attempt to minimize these errors, walleye consumption estimates were represented as a range of values by integrating 95% CL's into bioenergetic models. In addition, walleye consumption estimates can be greatly influenced by even small errors associated with model inputs of water temperature, walleye growth, diet compositions, and energy density values.

### ***Management Implications***

The results of this study provide a better understanding of the interactions among walleye, lake whitefish, and yellow perch throughout Green Bay. These results will help guide management decisions by determining how changes in the population status of one species will likely influence fisheries for all three species. These potential effects translate into important socio-economic trade-offs that must be considered during the management process. For example, management actions promoting high walleye abundance may provide significant economic benefit by attracting recreational anglers. However, if walleye predation is influencing yellow perch recruitment, management actions that support high walleye abundance could limit or reduce fishing opportunities for yellow perch. Furthermore, WIDNR and MIDNR biologists can use these results to identify management strategies (e.g., changes in harvest regulations) that

might decrease predation pressure on yellow perch, while maintaining the quality of the walleye fisheries. Conversely, my results suggested walleye predation was likely not a major factor regulating abundance of lake whitefish and changes to walleye management may not affect lake whitefish populations via reductions in predation or diet overlap. The results from my study provide the most current and relevant information describing the interactions among these three species within Green Bay and can be used by stakeholder groups to better explain the importance, implications, or need for future management actions.

This study improved the available information on food web dynamics which also has important implications for current restoration efforts in Green Bay. Restoration targets for the designated AOC in lower Green Bay included specified predator-prey ratios, which require a better understanding of predator-prey dynamics in the Green Bay ecosystem to adequately assess and reach those targets. Additionally, walleye, lake whitefish, and yellow perch are listed as focal species in these recovery plans. Prior to my study, minimal information on predator-prey dynamics was available to evaluate and achieve AOC recovery targets, and predator-prey ratios are specified in recovery targets for the Lower Fox River-Green Bay Area of Concern. Hence, my results will be useful in addressing this information gap.

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**TABLE 1.** Energy density (ED; wet weight basis) values for walleye and major prey groups collected in Zone 1 of Green Bay, Lake Michigan from May through October during 2018.

Species or group	Month(s)	ED (J/g)	Sources
Round goby	May	3,707	Bunnell et al. (2005); Kim (2007); Pothoven et al. (2017)
	June	3,636	
	July	3,674	
	Aug	3,636	
	Sept	3,696	
	Oct	3,815	
Rainbow smelt	May	5,309	Rand et al. (1994); Dobiesz (2003); Madenjian et al. (2018)
	June	5,235	
	July	5,209	
	Aug	5,022	
	Sept	5,294	
	Oct	5,598	
Alewife	May	4,312	Madenjian et al. (2006)
	June	5,035	
	July	4,184	
	Aug	4,514	
	Sept	5,741	
	Oct	6,172	
Gizzard shad	May-July	5,812	Miranda and Muncy (1989); Eggleton and Schramm (2002); Pothoven et al. (2017)
	Aug-Oct	5,057	
Yellow perch	May	4,431	Kershner (1996); Henderson et al. (2000); Pothoven et al. (2014)
	June	4,381	
	July	4,681	
	Aug	4,688	
	Sept	4,704	
	Oct	4,678	
Lake whitefish	May-Oct	5,851	Pothoven et al. (2006)
Other fish	May	4,889	Elliott (1976); Pierce et al. (1980); Hartman (1989); Hartman and Margraf (1992); Bryan et al. (1996); Kershner (1996); Eggleton and Schramm (2002); Pizzul et al. (2009); Pothoven and Höök (2015)
	June	4,873	
	July	4,867	
	Aug	4,952	
	Sept	5,056	
	Oct	5,084	
Invertebrates	May-Oct	3,682	Cummins and Wuycheck (1971); Schneider (1992)
Unidentified fish	May-Oct	4,965	Mean ED of all prey fish sources (months pooled)
Juvenile walleye	May-Oct	5,879	Madenjian and Wang (2013)
Adult walleye	May-Oct	7,214	C. P. Madenjian, personal communication

**Note:** Numeric values represent the mean of all energy density values by prey group and month(s) reported by the sources shown. Other fish included the mean of freshwater drum, white perch, brown trout, emerald shiner, and spottail shiner energy densities. Invertebrates included the mean of Chironomidae, Hirudinidae, and Dreissenidae energy densities. Juvenile walleyes were age-1 through age-3 and adult walleyes were age-4 through age-20.

**TABLE 2.** Length (mm) and weight (g) conversions for selected prey fish consumed by walleye in Zone 1 of Green Bay, Lake Michigan from May through October during 2018.

Prey species	Conversion	Equation	Source
Lake whitefish	BL → TL	$TL = 1.48 * BL$	Knight et al. (1984)
	SL → TL	$TL = 1.182 * SL$	Van Oosten (1939)
	TL → Wt	$Wt = 0.000006 * TL^{3.0674}$	Data from Wehse et al. (2017)
Yellow perch	BL → TL	$TL = 1.48 * BL + 0.96$	Knight et al. (1984)
	FL → TL	$TL = FL * 1.044$	Schneider (1984)
	SL → TL	$TL = 1.18 * SL + 4.6$	Elliott et al. (1996)
	TL → Wt	$Wt = 0.000003116 * TL^{3.232}$	Elliott et al. (1996)
Round goby	BL → TL	$TL = (BL + 1.836) / 0.567$	Tarraborelli et al. (2010)
	SL → TL	$TL = 1.1386 * SL + 3.73983$	Current Diet Study (2018)
	TL → Wt	$Wt = 0.000009 * TL^{3.09}$	Tarraborelli et al. (2010)
Rainbow smelt	BL → TL	$TL = 1.38 * BL - 0.72$	Knight et al. (1984)
	SL → TL	$TL = 1.23 * SL - 5.3$	Elliott et al. (1996)
	TL → Wt	$Wt = 0.000002451 * TL^{3.153}$	Elliott et al. (1996)
Alewife	BL → TL	$TL = 1.37 * BL + 8.10$	Knight et al. (1984)
	FL → TL	$TL = FL / 0.869$	Strus and Hurley (1992)
	SL → TL	$TL = 1.23 * SL - 2.4$	Luo et al. (2019)
	TL → Wt	$Wt = 0.00000402 * TL^{3.108}$	Elliott et al. (1996)
Gizzard shad	BL → TL	$TL = 1.45 * BL + 3.08$	Knight et al. (1984)
	FL → TL	$TL = FL / 0.898$	Kosmenko (2015)
	SL → TL	$TL = 1.26 * SL - 0.22$	Knight et al. (1984)
	TL → Wt	$Wt = 10^{3.09 * \log_{10}(TL) - 5.191}$	Hartman and Margraf (1992)

**Note:** BL = backbone length; FL = fork length; SL = standard length; TL = total length; Wt = weight.

**TABLE 3.** Zone 1 lake whitefish (LWF) and yellow perch (YEP) age-specific abundance, sex ratios (% female), maturation schedules (% mature), mean weight (Wt), and mean fecundity (eggs per fish) used to calculate the expected population fecundity during 2018 in Green Bay, Lake Michigan. Abundance estimates were obtained from statistical catch-at-age (SCAA) models from the WIDNR and the lower (lower 95% confidence limit), mean, and upper (upper 95% confidence limit) estimates are provided.

Prey	Age	SCAA abundance estimates			Percentage (%)		Mean/average	
		Lower	Mean	Upper	Female	Mature	Wt (g)	Fecundity
LWF	4	5,706,024	6,937,648	8,169,272	49	8	269	5,363
	5	4,437,705	6,144,726	7,851,747	49	66	425	8,473
	6	3,622,491	5,017,708	6,412,925	49	72	543	10,826
	7	2,833,650	3,989,548	5,145,446	49	91	661	13,178
	8	2,144,776	3,154,596	4,164,416	49	98	761	15,172
	9	1,360,415	2,335,238	3,310,061	49	100	854	17,026
	10	856,898	1,332,352	1,807,805	49	100	945	18,840
	11	613,576	870,180	1,126,785	49	100	987	19,678
	12	469,871	555,064	640,257	49	100	1,047	20,874
	13	295,828	359,288	422,747	49	100	1,069	21,313
	14	191,281	250,548	309,815	49	100	1,104	22,010
	15	132,723	178,568	224,412	49	100	1,153	22,987
	16	88,082	111,453	134,824	49	100	1,232	24,562
	17	69,110	75,942	82,774	49	100	1,338	26,676
	18	52,005	57,088	62,170	49	100	1,274	25,400
	19	32,351	39,563	46,774	49	100	1,332	26,556
	20+	33,212	55,176	77,139	49	100	1,242	24,762
YEP	2	441,224	558,633	676,041	66	60	145	27,261
	3	165,842	225,899	285,956	66	100	225	42,225
	4	64,575	94,031	123,486	66	100	354	66,355
	5	33,949	45,481	57,013	66	100	469	87,867
	6	19,790	25,656	31,522	66	100	500	93,665
	7	10,172	13,485	16,798	66	100	500	93,665
	8+	12,092	14,881	17,670	66	100	624	116,860

**Note:** Mean fecundity (eggs per fish) was calculated using weight-specific fecundity for lake whitefish (19.937 eggs/g; S. P. Hansen, Wisconsin Department of Natural Resources, personal communication) and for yellow perch using the formula provided by Brazo et al. (1975): fecundity =  $138.215 + 187.054 * \text{weight(g)}$ .



**TABLE 4.** Number of walleyes collected (*N*), percent with empty stomachs (% Empty), mean  $\pm$  SE total length (TL; mm), and TL range for each year (2018 and 2019), zone, and sampling month (May through October) from Green Bay, Lake Michigan.

Year	Zone	Month(s)	N	% Empty	Mean TL $\pm$ SE	TL Range
2018	1	May	149	55	420 $\pm$ 10	226-739
		June	107	41	542 $\pm$ 13	186-750
		July	72	44	439 $\pm$ 11	212-630
		Aug	83	66	429 $\pm$ 13	157-666
		Sept	44	75	469 $\pm$ 11	285-604
		Oct	88	18	479 $\pm$ 11	134-696
	2	May	55	58	543 $\pm$ 15	316-745
		June	68	43	459 $\pm$ 18	197-709
		July	107	49	437 $\pm$ 16	190-730
		Aug	90	61	440 $\pm$ 16	146-696
		Sept	80	59	401 $\pm$ 15	172-695
		Oct	42	24	482 $\pm$ 15	269-640
2019	1	May	59	36	449 $\pm$ 11	279-680
		Oct	29	38	500 $\pm$ 19	312-724
	2	June	53	32	616 $\pm$ 9	496-772
		July	79	58	426 $\pm$ 13	200-677
		Aug	64	67	519 $\pm$ 15	247-709
		Sept	99	57	429 $\pm$ 12	183-720
		TOTALS				
2018	1	May-Oct	543	48	461 $\pm$ 5	134-750
	2	May-Oct	442	51	452 $\pm$ 7	146-745
	Total		985	49	457 $\pm$ 4	134-750
2019	1	May; Oct	88	36	466 $\pm$ 10	279-724
	2	June-Sept	295	55	481 $\pm$ 8	183-772
	Total		383	51	478 $\pm$ 6	183-772
Total	1	May-Oct	631	47	462 $\pm$ 5	134-750
	2	May-Oct	737	53	464 $\pm$ 5	146-772
	Total		1,368	50	463 $\pm$ 4	134-772

**Note:** Specified in the month column, (-) indicates numeric table values were calculated from a range of months and (;) indicates numeric table values were calculated from only the months shown.

**TABLE 5.** Number of lake whitefish collected (*N*), percent with empty stomachs (% Empty), mean  $\pm$  SE total length (TL; mm), and TL range for each year (2018 and 2019), zone, and sampling month (May through October) from Green Bay, Lake Michigan.

Year	Zone	Month(s)	<i>N</i>	% Empty	Mean TL ± SE	TL Range
2018	1	May	154	46	429 ± 4	243-566
		June	66	79	447 ± 4	402-532
		July	100	86	471 ± 3	418-640
		Aug	164	55	477 ± 2	431-557
		Sept	186	90	450 ± 2	320-542
		Oct	146	83	460 ± 3	315-563
	2	May	106	59	482 ± 3	403-622
		June	203	70	474 ± 2	416-592
		July	183	84	466 ± 2	423-574
		Aug	85	69	494 ± 4	413-587
		Sept	20	80	446 ± 6	412-507
		Oct	55	80	547 ± 6	445-646
2019	1	May	62	40	363 ± 5	293-450
		Aug	75	33	490 ± 3	438-601
		Oct	22	9	465 ± 8	399-533
	2	June	80	88	476 ± 2	435-543
		July	33	61	471 ± 6	370-554
		Sept	23	100	513 ± 7	438-564
TOTALS						
2018	1	May-Oct	816	72	456 ± 1	243-640
	2	May-Oct	652	73	481 ± 2	403-646
	Total		1,468	73	467 ± 1	243-646
2019	1	May; Aug; Oct	159	33	437 ± 5	293-601
	2	June-July; Sept	136	83	481 ± 3	370-564
	Total		295	56	457 ± 3	293-601
Total	1	May-Oct	975	66	453 ± 1	243-640
	2	May-Oct	788	75	481 ± 1	370-646
	Total		1,763	70	465 ± 1	243-646

**Note:** Specified in the month column, (-) indicates numeric table values were calculated from a range of months and (;) indicates numeric table values were calculated from only the months shown.

**TABLE 6.** Number of yellow perch collected (*N*), percent with empty stomachs (% Empty), mean  $\pm$  SE total length (TL; mm), and TL range for each year (2018 and 2019), zone, and sampling month (May through October) from Green Bay, Lake Michigan.

Year	Zone	Month(s)	<i>N</i>	% Empty	Mean TL $\pm$ SE	TL Range
2018	1	May	154	80	232 $\pm$ 4	145-375
		June	95	29	207 $\pm$ 5	136-321
		July	92	16	208 $\pm$ 4	142-323
		Aug	67	6	159 $\pm$ 4	112-242
		Sept	35	46	217 $\pm$ 5	160-286
		Oct	138	39	202 $\pm$ 3	135-308
	2	May	109	83	213 $\pm$ 5	108-343
		June	13	54	177 $\pm$ 8	149-262
		July	88	60	167 $\pm$ 2	140-223
		Aug	116	62	195 $\pm$ 3	147-315
		Sept	52	40	217 $\pm$ 4	165-283
		Oct	104	27	231 $\pm$ 4	137-341
2019	1	May	66	48	278 $\pm$ 6	122-369
		Oct	1	100	183	183
	2	July	65	46	177 $\pm$ 4	137-282
		Aug	23	9	257 $\pm$ 7	188-299
		Sept	74	27	190 $\pm$ 6	105-322
TOTALS						
2018	1	May-Oct	581	41	208 $\pm$ 2	112-375
	2	May-Oct	482	56	203 $\pm$ 2	108-343
	Total		1,063	48	206 $\pm$ 1	108-375
2019	1	May; Oct	67	49	277 $\pm$ 6	122-269
	2	July-Sept	162	32	194 $\pm$ 4	105-322
	Total		229	37	218 $\pm$ 4	105-369
Total	1	May-Oct	648	42	215 $\pm$ 2	112-375
	2	May-Oct	644	50	201 $\pm$ 2	105-343
	Total		1,292	46	208 $\pm$ 1	105-375

**Note:** Specified in the month column, (-) indicates numeric table values were calculated from a range of months and (;) indicates numeric table values were calculated from only the months shown.

**TABLE 7.** Number of walleyes, lake whitefish, and yellow perch collected (*N*) by each sampling method and collaborative personnel groups in Green Bay, Lake Michigan from May-October during 2018 and 2019. Percent with empty stomachs (% Empty) are depicted in the last column as the percentage of the total number of each species collected by each sampling method.

Species	Methods and collectors	<i>N</i>	% Empty
Walleye			
Method	Gill net	1,134	52
	Trap net	84	38
	Electrofishing	63	10
	Bottom trawl	41	59
	Hook and line	41	73
	Fyke net	5	100.0
Collector	WI Cooperative Fishery Research Unit	713	
	WI Department of Natural Resources	269	
	MI Department of Natural Resources	176	
	US Fish and Wildlife Service	85	
	Commercial fishers	84	
	Recreational anglers	41	
Lake whitefish			
Method	Trap net	1,255	80
	Gill net	391	35
	Purse seine	52	85
	Electrofishing	35	97
	Bottom trawl	30	43
	Commercial fishers	1,466	
Collector	WI Department of Natural Resources	200	
	US Fish and Wildlife Service	91	
	WI Cooperative Fishery Research Unit	6	
Yellow perch			
Method	Gill net	1,003	46
	Fyke net	115	65
	Electrofishing	79	47
	Bottom trawl	55	6
	Hook and line	40	63
	Commercial fishers	52	
Collector	WI Cooperative Fishery Research Unit	589	
	WI Department of Natural Resources	346	
	MI Department of Natural Resources	197	
	US Fish and Wildlife Service	68	
	Recreational anglers	40	

**TABLE 8.** Output from ANOSIM and SIMPER analyses of variation in Green Bay walleye diet compositions between zones during 2018, months within zones during 2018, and years within zones. Significance values ( $p$ -value; significant values in bold) and Rho statistics ( $R$ -value) are tabulated. Listed are prey that cumulatively (%) explain at least 70% of the observed dissimilarity between groups and their contribution (%) to the dissimilarity.

Comparison data source	Source of variation	ANOSIM		SIMPER (%)		
		$p$ -value	$R$ -value	Prey species	Contribution	Cumulative
2018 zones	May-May	0.959	-0.068			
	June-June	<b>0.001</b>	0.191	Alewife	33	33
				Lake whitefish	26	59
				Rainbow smelt	15	74
	July-July	0.340	0.004			
	Aug-Aug	<b>0.001</b>	0.259	Gizzard shad	33	33
				Alewife	23	56
				Round goby	21	77
	Sept-Sept	0.516	-0.009			
	Oct-Oct	<b>0.001</b>	0.301	Gizzard shad	43	43
				Round goby	35	78
				Lake whitefish	24	24
2018 Zone 1	May-June	<b>0.001</b>	0.207	Round goby	23	47
				Rainbow smelt	21	68
				Alewife	12	80
	June-July	<b>0.001</b>	0.217	Alewife	39	39
				Lake whitefish	26	65
				Round goby	12	77
	July-Aug	<b>0.001</b>	0.364	Alewife	42	42
				Gizzard shad	37	79
	Aug-Sept	0.026	0.148			
	Sept-Oct	<b>0.001</b>	0.536	Gizzard shad	43	43
				Alewife	28	71
				Round goby	34	34
2018 Zone 2	May-June	<b>0.001</b>	0.343	Alewife	31	65
				Rainbow smelt	18	83
	June-July	0.058	0.033			
	July-Aug	0.274	0.007			
	Aug-Sept	0.070	0.031			
	Sept-Oct	0.152	0.017			
	May-May	0.040	0.040			
	Oct-Oct	0.256	0.006			
Years Zone 1	June-June	<b>0.001</b>	0.166	Alewife	46	46
Years Zone 2				Round goby	44	90
	July-July	0.162	0.015			
	Aug-Aug	0.724	-0.023			
	Sept-Sept	0.198	0.012			

**TABLE 9.** Output from ANOSIM and SIMPER analyses of variation in Green Bay walleye diet compositions (months pooled) between juvenile (ages 0-3), young-adult (ages 4-6), and old-adult (ages 7-20) walleye age groups for each zone collected in 2018 (months pooled) from Green Bay, Lake Michigan from May-October. Significance values (*p*-value; significant values in bold) and Rho statistics (*R*-value) are tabulated. Listed are prey that cumulatively (%) explain at least 70% of the observed dissimilarity between groups and their contribution (%) to the dissimilarity.

Zone	Tested age groups	ANOSIM		SIMPER (%)		
		<i>p</i> -value	<i>R</i> -value	Prey species	Contribution	Cumulative
1	0-3 and 4-6	0.231	0.006			
	0-3 and 7-20	<b>0.001</b>	0.052	Gizzard shad	22	22
				Lake whitefish	21	43
				Round goby	15	58
				Rainbow smelt	14	72
	4-6 and 7-20	<b>0.001</b>	0.131	Gizzard shad	25	25
				Alewife	22	47
				Lake whitefish	20	67
				Rainbow smelt	12	79
2	0-3 and 4-6	0.020	0.043			
	0-3 and 7-20	0.152	0.014			
	4-6 and 7-20	<b>0.001</b>	0.100	Alewife	33	33
				Round goby	26	59
				Gizzard shad	15	74

**TABLE 10.** Output from ANOSIM and SIMPER analyses variation in Green Bay lake whitefish diet compositions between zones during 2018, months within zones during 2018, and years within zones. Significance values (*p*-value; significant values in bold) and Rho statistics (*R*-value) are tabulated. Listed are taxa that cumulatively (%) explain at least 70% of the observed dissimilarity between groups and their contribution (%) to the dissimilarity.

Comparison data source	Source of variation	ANOSIM		SIMPER (%)		
		<i>p</i> -value	<i>R</i> -value	Prey species	Contribution	Cumulative
2018 zones	May-May	<b>0.001</b>	0.169	Round goby	52	52
				Invertebrates	48	100
	June-June	0.639	-0.031			
	July-July	0.707	-0.003			
	Aug-Aug	<b>0.001</b>	0.236	Round goby	52	52
				Invertebrates	45	97
	Sept-Sept	1.000	*			
	Oct-Oct	0.156	0.096			
2018 Zone 1	May-June	0.399	0.013			
	June-July	1.000	-0.006			
	July-Aug	0.300	0.053			
	Aug-Sept	1.000	-0.012			
	Sept-Oct	1.000	-0.018			
2018 Zone 2	May-June	0.013	0.058			
	June-July	0.954	-0.044			
	July-Aug	0.021	0.052			
	Aug-Sept	1.000	-0.174			
	Sept-Oct	1.000	-0.160			
Years Zone 1	May-May	1.000	*			
	Aug-Aug	1.000	-0.005			
	Oct-Oct	0.495	0.000			
Years Zone 2	June-June	0.868	-0.050			
	July-July	1.000	-0.042			

\*Indicates lake whitefish consumed one prey category and diet compositions were identical between compared groups.

**TABLE 11.** Output from ANOSIM and SIMPER analyses of variation in Green Bay yellow perch diet compositions between zones during 2018, months within zones during 2018, and years within zones. Significance values ( $p$ -value; significant values in bold) and Rho statistics ( $R$ -value) are tabulated. Listed are taxa that cumulatively (%) explain at least 70% of the observed dissimilarity between groups and their contribution (%) to the dissimilarity.

Comparison data source	Source of variation	ANOSIM		SIMPER (%)		
		$p$ -value	$R$ -value	Prey species	Contribution	Cumulative
2018 zones	May-May	0.026	0.099			
	June-June	0.021	0.332			
	July-July	<b>0.001</b>	0.181	Round goby	49	49
				Invertebrates	47	96
	Aug-Aug	<b>0.001</b>	0.216	Invertebrates	47	47
				Round goby	36	83
	Sept-Sept	0.329	0.004			
2018 Zone 1	Oct-Oct	<b>0.001</b>	0.243	Round goby	45	45
				Invertebrates	26	71
	May-June	0.013	0.134			
	June-July	0.281	0.002			
	July-Aug	0.784	-0.008			
	Aug-Sept	<b>0.001</b>	0.728	Round goby	47	47
				Invertebrates	46	93
2018 Zone 2	Sept-Oct	0.100	0.039			
	May-June	0.333	0.011			
	June-July	0.118	0.077			
	July-Aug	0.759	-0.013			
	Aug-Sept	0.094	0.037			
	Sept-Oct	<b>0.001</b>	0.285	Round goby	46	46
Years Zone 1				Invertebrates	31	77
	May-May	0.019	0.080			
Years Zone 2	July-July	0.094	0.025			
	Aug-Aug	0.024	0.132			
	Sept-Sept	<b>0.001</b>	0.296	Invertebrates	47	47
				Round goby	35	82



**TABLE 12.** Pianka's index of niche overlap values ( $O_{jk}$ ; strong diet overlap values shown in bold) depicting the strength of diet overlap between walleye, lake whitefish, and yellow perch for each month(s) and zone collected in 2018 from Green Bay, Lake Michigan from May-October.

Zone	Month(s)	Walleye – Lake whitefish		Walleye – Yellow perch		Lake whitefish – Yellow perch	
		$O_{jk}$	Strength	$O_{jk}$	Strength	$O_{jk}$	Strength
1	May	0.082	Very weak	0.420	Moderate	<b>0.905</b>	Very strong
	June	0.105	Weak	0.113	Weak	<b>0.993</b>	Very strong
	July	0.015	Very weak	0.055	Very weak	<b>0.998</b>	Very strong
	Aug	0.004	Very weak	0.008	Very weak	<b>0.999</b>	Very strong
	Sept	0.000	No overlap	0.393	Weak	0.067	Very weak
	Oct	0.003	Very weak	0.503	Moderate	0.736	Moderate
2	May	0.653	Moderate	0.420	Moderate	<b>0.770</b>	Strong
	June	0.347	Weak	0.276	Weak	<b>0.774</b>	Strong
	July	0.222	Weak	0.448	Moderate	<b>0.815</b>	Strong
	Aug	0.500	Moderate	0.661	Moderate	<b>0.927</b>	Very strong
	Sept	0.088	Very weak	0.744	Moderate	0.471	Moderate
	Oct	0.101	Weak	0.652	Moderate	0.255	Weak
TOTAL							
1	May-Oct	0.042	Very weak	0.195	Weak	<b>0.969</b>	Very strong
2	May-Oct	0.391	Weak	0.723	Moderate	0.677	Moderate
Total		0.203	Weak	0.451	Moderate	<b>0.905</b>	Very strong

**Note:** No overlap = 0.00; Very weak = 0.001-0.099; Weak = 0.100-0.399; Moderate = 0.400-0.749; Strong = 0.750-0.900; Very strong = 0.901-0.999; and Complete overlap = 1.000. Strong overlap index values are highlighted in bold ( $O_{jk} > 0.749$ ).

**TABLE 13.** Pianka's index of niche overlap values ( $O_{jk}$ ; strong diet overlap values shown in bold) depicting the strength of diet overlap between juvenile (ages 0-3), young-adult (ages 4-6), and old-adult (ages 7-20) walleye age groups for each zone collected in 2018 (months pooled) from Green Bay, Lake Michigan from May-October.

Zone	Month(s)	Juvenile – Young adult		Juvenile – Old adult		Young adult – Old adult	
		$O_{jk}$	Strength	$O_{jk}$	Strength	$O_{jk}$	Strength
1	May-Oct	<b>0.835</b>	Strong	0.675	Moderate	0.540	Moderate
2	May-Oct	<b>0.830</b>	Strong	<b>0.835</b>	Strong	<b>0.870</b>	Strong

**Note:** No overlap = 0.00; Very weak = 0.001-0.099; Weak = 0.100-0.399; Moderate = 0.400-0.749; Strong = 0.750-0.900; Very strong = 0.901-0.999; and Complete overlap = 1.000. Strong overlap index values are highlighted in bold ( $O_{jk} > 0.749$ ).

**TABLE 14.** Zone 1 diet schedules (mean proportions; wet weight basis) for juvenile (ages 1-3), young-adult (ages 4-6), and old-adult (ages 7-20) walleye age groups collected in 2018 from Green Bay, Lake Michigan during May through October.

Ages	Day	RGB	RBS	ALW	GZS	YEP	LWF	FISH	UNIF	INVT
1-3	01-May	0.23	0.21	0.00	0.00	0.12	0.00	0.25	0.18	0.00
	16-May	0.44	0.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	19-June	0.34	0.35	0.00	0.00	0.18	0.00	0.00	0.13	0.00
	20-June	0.17	0.06	0.00	0.00	0.31	0.24	0.00	0.22	0.00
	30-June	0.18	0.04	0.30	0.07	0.00	0.00	0.00	0.41	0.00
	16-July	0.10	0.00	0.43	0.10	0.00	0.00	0.00	0.37	0.00
	15-Aug	0.00	0.00	0.10	0.50	0.00	0.00	0.15	0.25	0.00
	23-Sept	0.30	0.00	0.57	0.13	0.00	0.00	0.00	0.00	0.00
	31-Oct	0.00	0.02	0.00	0.78	0.00	0.00	0.03	0.16	0.00
4-6	01-May	0.43	0.37	0.00	0.00	0.00	0.00	0.00	0.13	0.07
	19-June	0.00	0.19	0.75	0.00	0.00	0.00	0.00	0.05	0.00
	09-July	0.16	0.00	0.76	0.00	0.00	0.00	0.00	0.07	0.00
	23-July	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.50	0.00
	09-Aug	0.00	0.02	0.53	0.45	0.00	0.00	0.00	0.00	0.00
	23-Sept	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
	30-Sept	0.02	0.03	0.00	0.89	0.00	0.00	0.02	0.04	0.00
	31-Oct	0.03	0.06	0.00	0.77	0.02	0.00	0.03	0.08	0.00
7-20	01-May	0.51	0.33	0.00	0.00	0.00	0.00	0.15	0.00	0.00
	15-May	0.52	0.25	0.00	0.00	0.00	0.00	0.23	0.00	0.00
	16-May	0.37	0.10	0.00	0.00	0.00	0.28	0.24	0.01	0.00
	06-June	0.00	0.15	0.04	0.00	0.00	0.64	0.00	0.14	0.04
	20-June	0.00	0.19	0.51	0.00	0.00	0.17	0.00	0.00	0.13
	01-July	0.00	0.14	0.39	0.38	0.00	0.00	0.00	0.00	0.09
	31-July	0.00	0.14	0.39	0.38	0.00	0.00	0.00	0.00	0.09
	16-Aug	0.00	0.00	0.00	0.50	0.50	0.00	0.00	0.00	0.00
	23-Sept	0.00	0.00	0.00	0.50	0.50	0.00	0.00	0.00	0.00
	22-Oct	0.00	0.00	0.00	0.83	0.02	0.00	0.00	0.15	0.00
	31-Oct	0.00	0.00	0.00	0.83	0.02	0.00	0.00	0.15	0.00

**Note:** Numeric table entries were rounded to the nearest hundredth and rows may not be equal to 1. Diets included round goby (RGB), rainbow smelt (RBS), alewife (ALW), gizzard shad (GZS), yellow perch (YEP), lake whitefish (LWF), other fish (FISH; freshwater drum, white perch, brown trout, emerald shiner, spottail shiner), unidentified fish (UNIF), and invertebrates (INVT; Chironomidae, Hirudinidae, and Dreissenidae).

**TABLE 15.** Zone 1 growth, abundance, and mortality estimates for walleye age classes 1-9 and pooled ages 10-20 collected from May through October in Green Bay, Lake Michigan during 2018. Observed growth (mean weight; g) was estimated for May through July (initial) and August through October (final). Nominal abundance estimates, as well as lower and upper 95% confidence limits, were obtained from statistical catch-at-age models (SCAA output). Interval total mortality rates ( $A$ ; adjusted to represent an interval of 184 simulation days) were calculated using instantaneous total mortality rates ( $Z$ ) that were first estimated from three catch-curves regressing loge abundance against age using SCAA model estimates of abundance for walleye ages 1-3 (juveniles), 4-6 (young adults), and 7-20 (old adults).

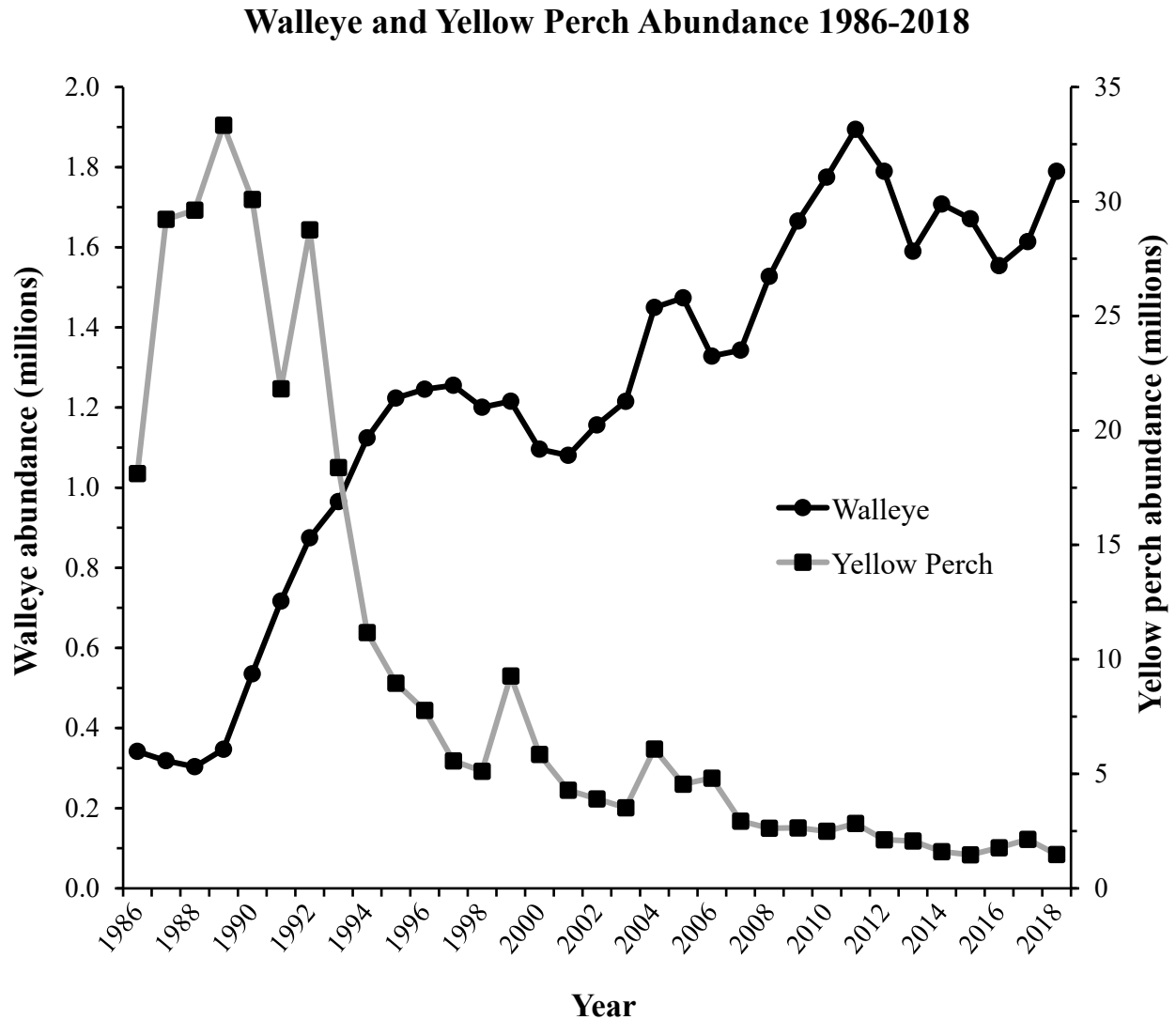
Age(s)	Growth (g)		Abundance (SCAA estimates)			Mortality
	Initial	Final	Lower 95%	Nominal	Upper 95%	$A$
1	124	304	38,260	642,570	2,178,630	0.24176
2	379	670	24,826	387,220	1,132,295	0.24176
3	793	1,162	42,323	212,390	467,786	0.24176
4	1,303	1,569	45,011	178,040	382,761	0.27794
5	1,429	1,774	46,966	156,940	332,825	0.27794
6	1,382	1,382	16,140	48,400	119,630	0.27794
7	1,966	2,113	14,989	45,520	106,370	0.16126
8	2,066	2,372	12,533	44,038	106,641	0.16126
9	2,202	2,779	8,971	28,437	71,750	0.16126
10-20	2,879	2,879	9,247	45,830	127,525	0.16126

**TABLE 16.** Zone 1 population level walleye (WAE) consumption (biomass =  $C_B$ ; number =  $C_N$ ) of lake whitefish (LWF) and yellow perch (YEP) estimated (nominal  $\pm$  upper and lower 95% confidence limits) for walleye age classes 1-9 and pooled ages 10-20 collected from Green Bay, Lake Michigan in 2018 from May-October.

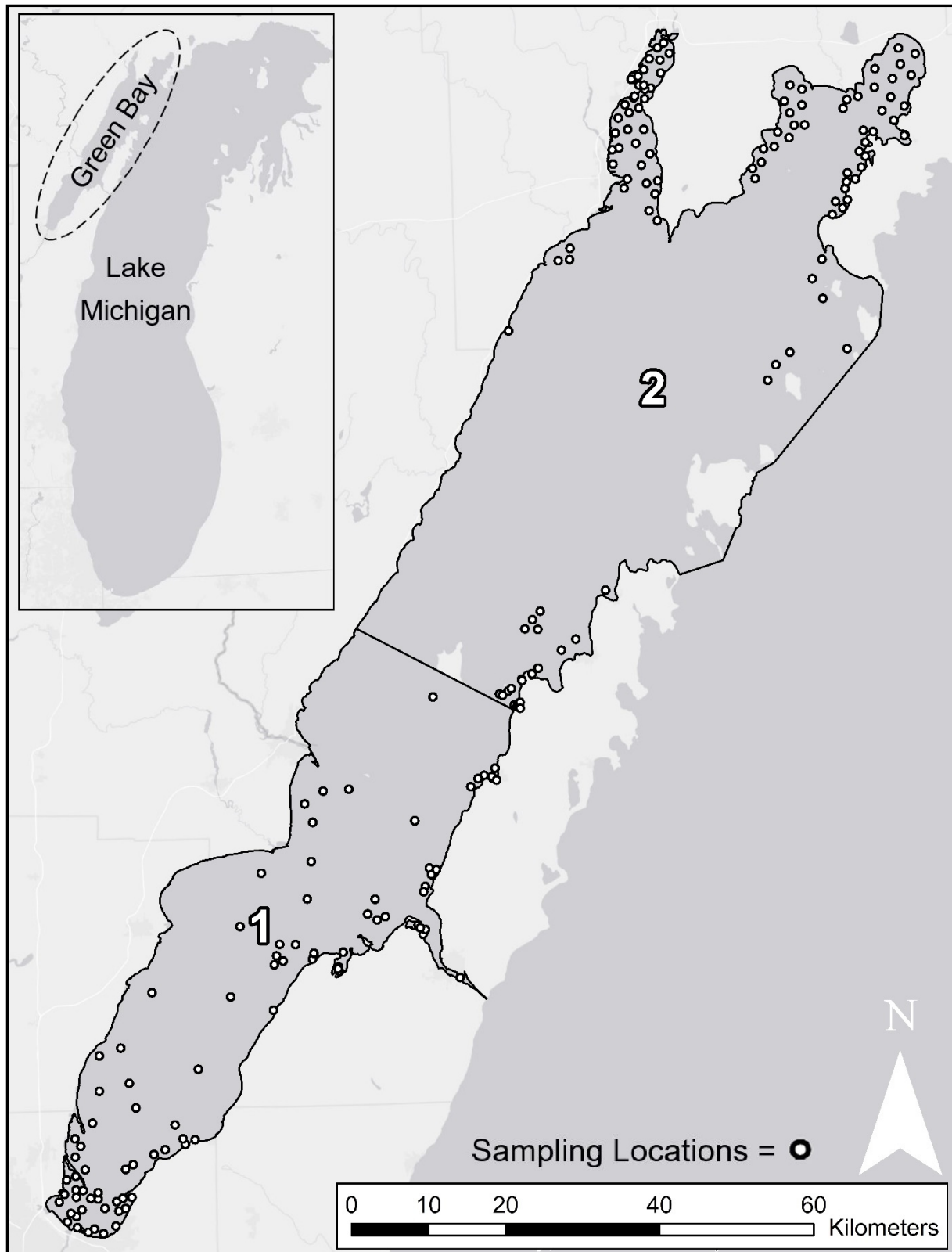
WAE		$C_B$ (kg)			$C_N$		
Age(s)	Prey (age)	Lower	Nominal	Upper	Lower	Nominal	Upper
1	LWF (0)	389	6,526	22,127	879,158	14,765,310	50,061,702
2	LWF (0)	534	8,329	24,356	1,112,516	17,352,302	50,740,988
3	LWF (0)	1,493	7,492	16,500	2,887,543	14,490,591	31,915,324
7	LWF (1)	3,358	10,197	23,828	92,372	280,523	655,518
8	LWF (1)	3,310	11,632	28,167	162,909	572,424	1,386,163
9	LWF (1)	957	3,035	7,656	43,750	138,682	349,912
	LWF (2)	1,983	6,287	15,864	21,875	69,342	174,958
10-20	LWF (1)	165	818	2,277	4,370	21,658	60,266
	LWF (2)	1,042	5,164	14,370	10,925	54,145	150,663
	LWF (3)	1,216	6,027	16,770	6,992	34,653	96,424
1	YEP (0)	1,425	23,935	81,152	4,782,372	80,319,098	272,321,452
2	YEP (1)	1,993	31,091	90,914	125,060	1,950,608	5,703,898
3	YEP (0)	634	3,184	7,013	288,523	1,447,898	3,188,975
	YEP (1)	4,991	25,049	55,169	288,555	1,448,058	3,189,328
4	YEP (0)	97	382	821	7,387	29,217	62,813
5	YEP (0)	116	389	825	8,914	29,785	63,166
6	YEP (0)	23	70	173	1,786	5,355	13,236
7	YEP (0)	676	2,052	4,795	71,532	217,235	507,630
	YEP (1)	2,857	8,677	20,277	71,532	217,235	507,630
	YEP (2)	2,828	8,589	20,070	35,766	108,618	253,815
8	YEP (0)	685	2,408	5,832	72,558	254,952	617,384
	YEP (1)	2,898	10,184	24,661	72,558	254,952	617,384
	YEP (2)	2,869	10,080	24,409	36,279	127,476	308,692
9	YEP (1)	1,954	6,195	15,632	50,818	161,086	406,440
	YEP (2)	4,018	12,737	32,138	50,817	161,085	406,438
10-20	YEP (0)	1,394	6,911	19,230	147,612	731,594	2,035,708
	YEP (1)	3,058	15,155	42,170	73,806	365,797	1,017,854
TOTAL							
	LWF (0)	2,415	22,347	62,983	4,879,217	46,608,204	132,718,014
	LWF (1)	7,790	25,681	61,928	303,400	1,013,287	2,451,858
	LWF (2)	3,025	11,452	30,233	32,800	123,487	325,622
	LWF (3)	1,216	6,027	16,770	6,992	34,653	96,424
	TOTAL	14,447	65,507	171,915	5,222,409	47,779,631	135,591,918
	YEP (0)	5,051	39,331	119,840	5,380,683	83,035,134	278,810,365
	YEP (1)	17,753	96,351	248,823	682,329	4,397,736	11,442,534
	YEP (2)	9,715	31,406	76,616	122,863	397,179	968,944
	TOTAL	32,519	167,088	445,280	6,185,874	87,830,050	291,221,843

**TABLE 17.** Zone 1 lower (lower 95% confidence limit), nominal, and upper (upper 95% confidence limit) recruitment potential estimates for lake whitefish and yellow perch age classes found in walleye diets from Green Bay, Lake Michigan during 2018.

Prey species (age)	Estimated recruitment potential (number of recruits)		
	Lower	Nominal	Upper
Lake whitefish (0)	1,003,498,692	1,435,950,595	1,868,402,498
Lake whitefish (1)	10,034,987	14,359,506	18,684,025
Lake whitefish (2)	6,020,992	8,615,704	11,210,415
Lake whitefish (3)	3,612,595	5,169,422	6,726,249
Yellow perch (0)	169,666,554	226,491,527	283,316,500
Yellow perch (1)	1,696,666	2,264,915	2,833,165
Yellow perch (2)	1,017,999	1,358,949	1,699,899

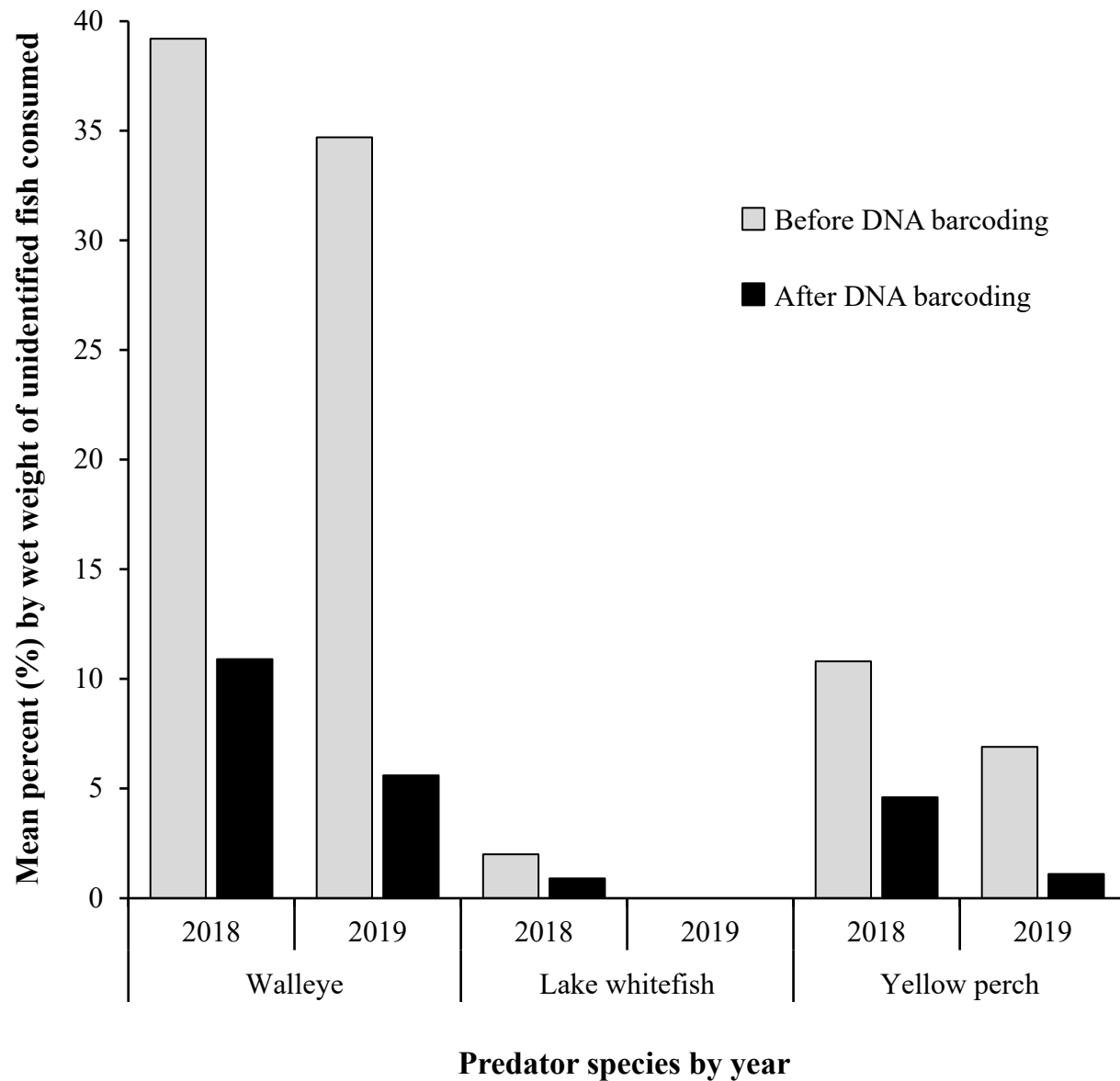


**FIGURE 1.** Zone 1 walleye (solid black line) abundance in relation to yellow perch (gray dashed line) abundance (Source: I. Tsehay, unpublished data; estimated by WIDNR using statistical catch-at-age models) from 1986 through 2018 in Green Bay, Lake Michigan.

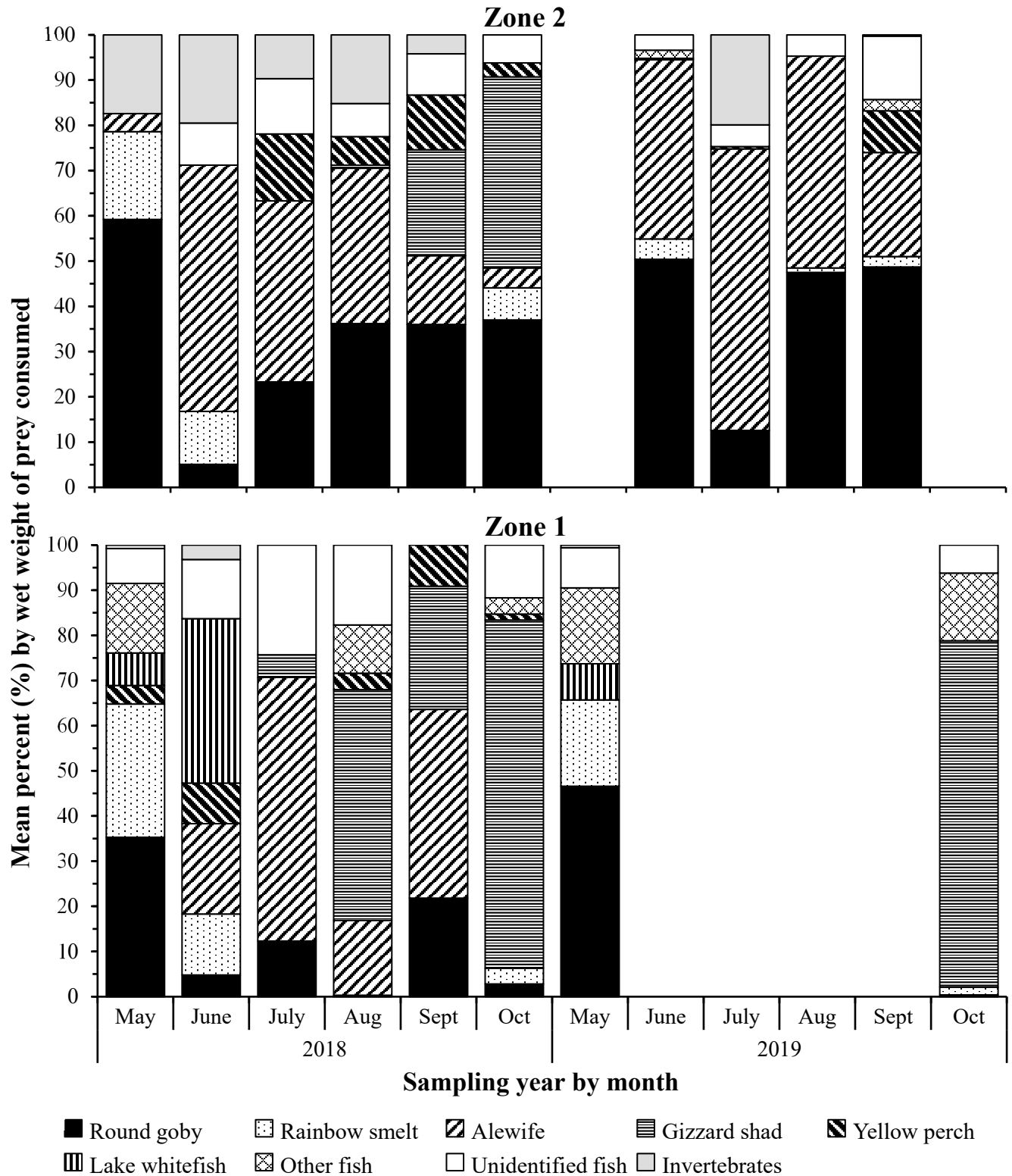


**FIGURE 2.** Map of Green Bay, Lake Michigan study area with zone boundaries (outlined in black and numbered) and sampling locations (white and black circles) used to assess the diets of walleye, lake whitefish, and yellow perch from May through October during 2018 and 2019.

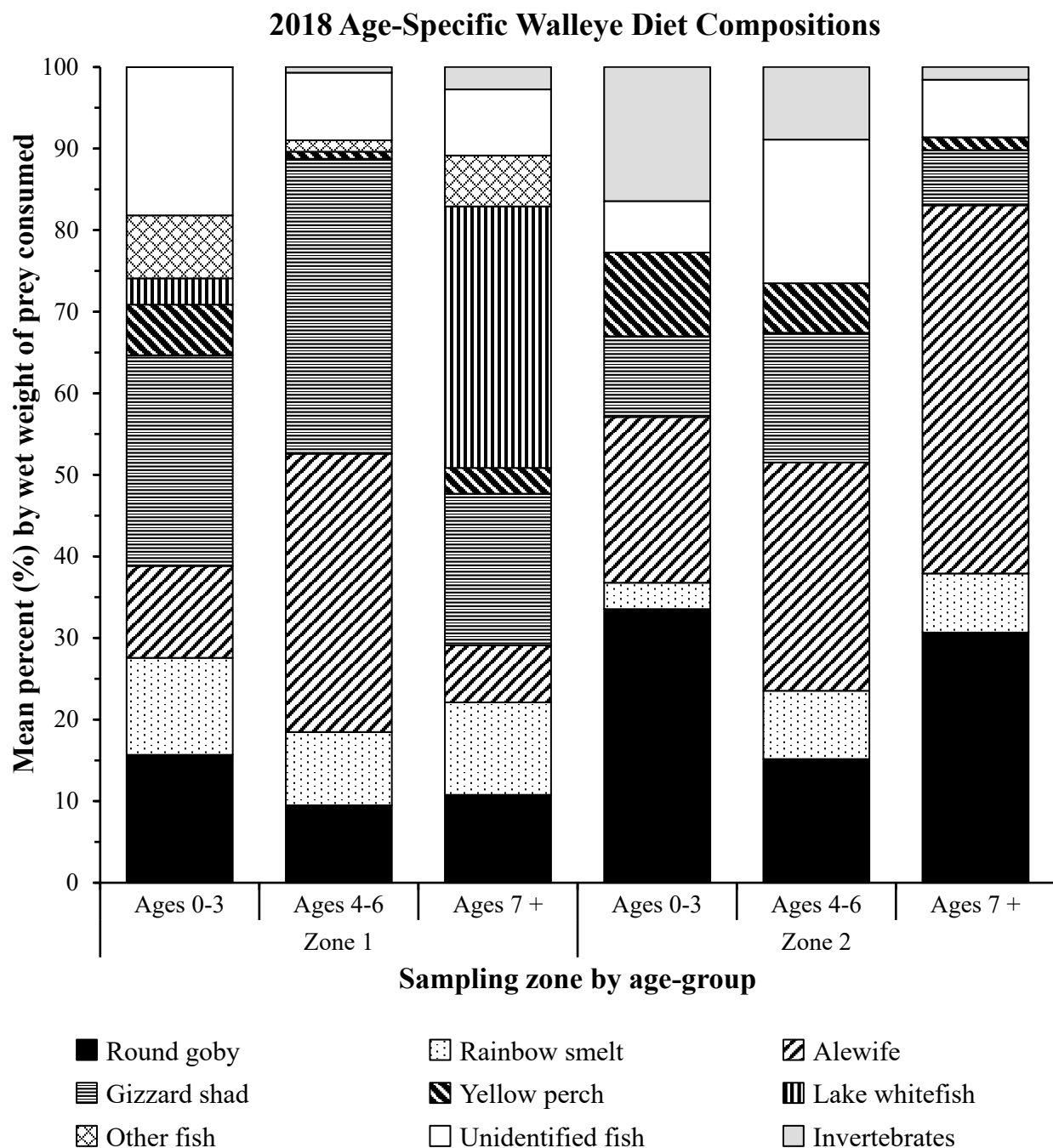




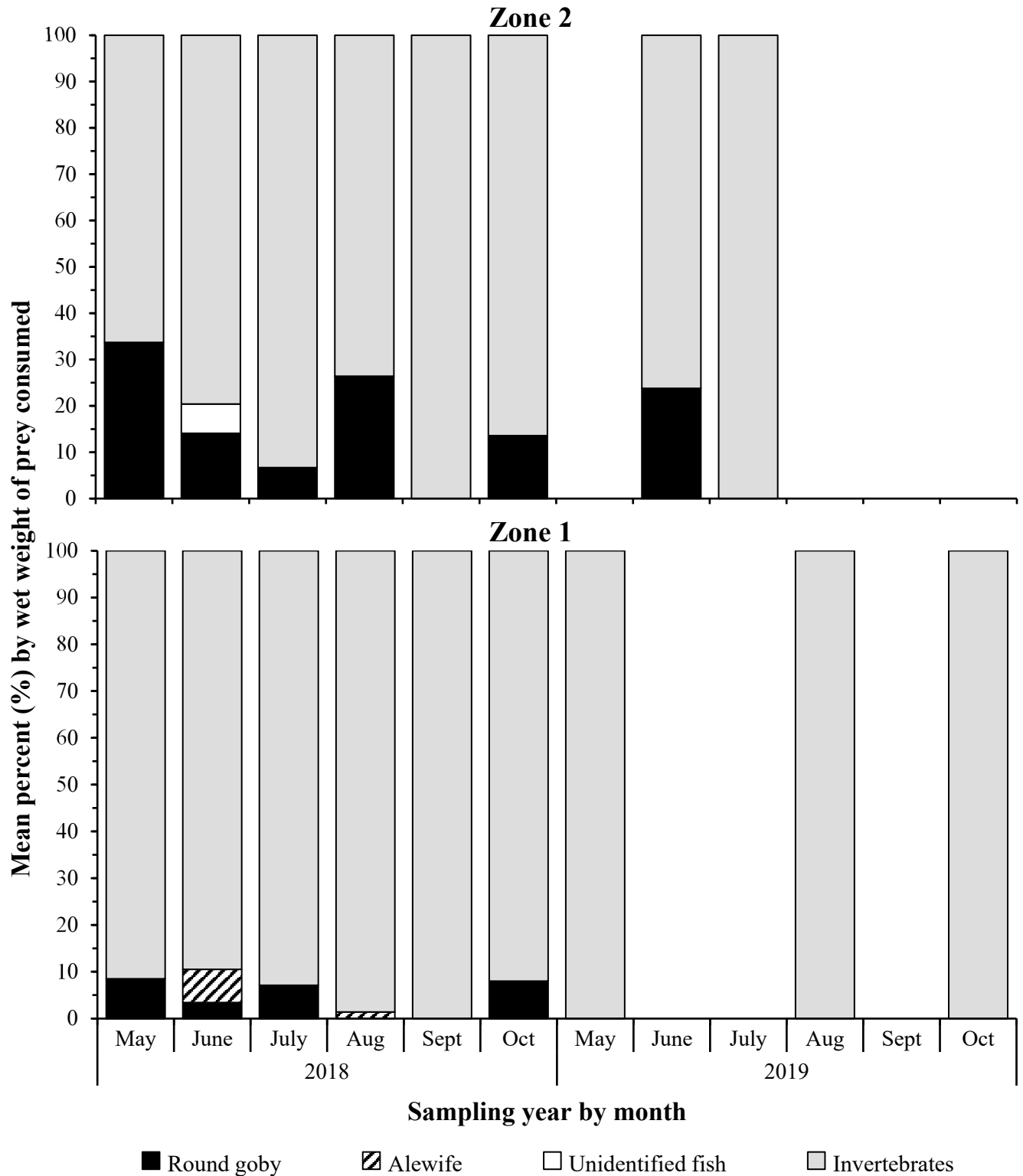
**FIGURE 3.** Mean percent (%) by wet weight of unidentified prey fish before and after DNA barcoding during 2018 and 2019. Percent's represent portions of the overall diet compositions (pooled zones and months) for walleye, lake whitefish, and yellow perch in Green Bay, Lake Michigan from May through October.



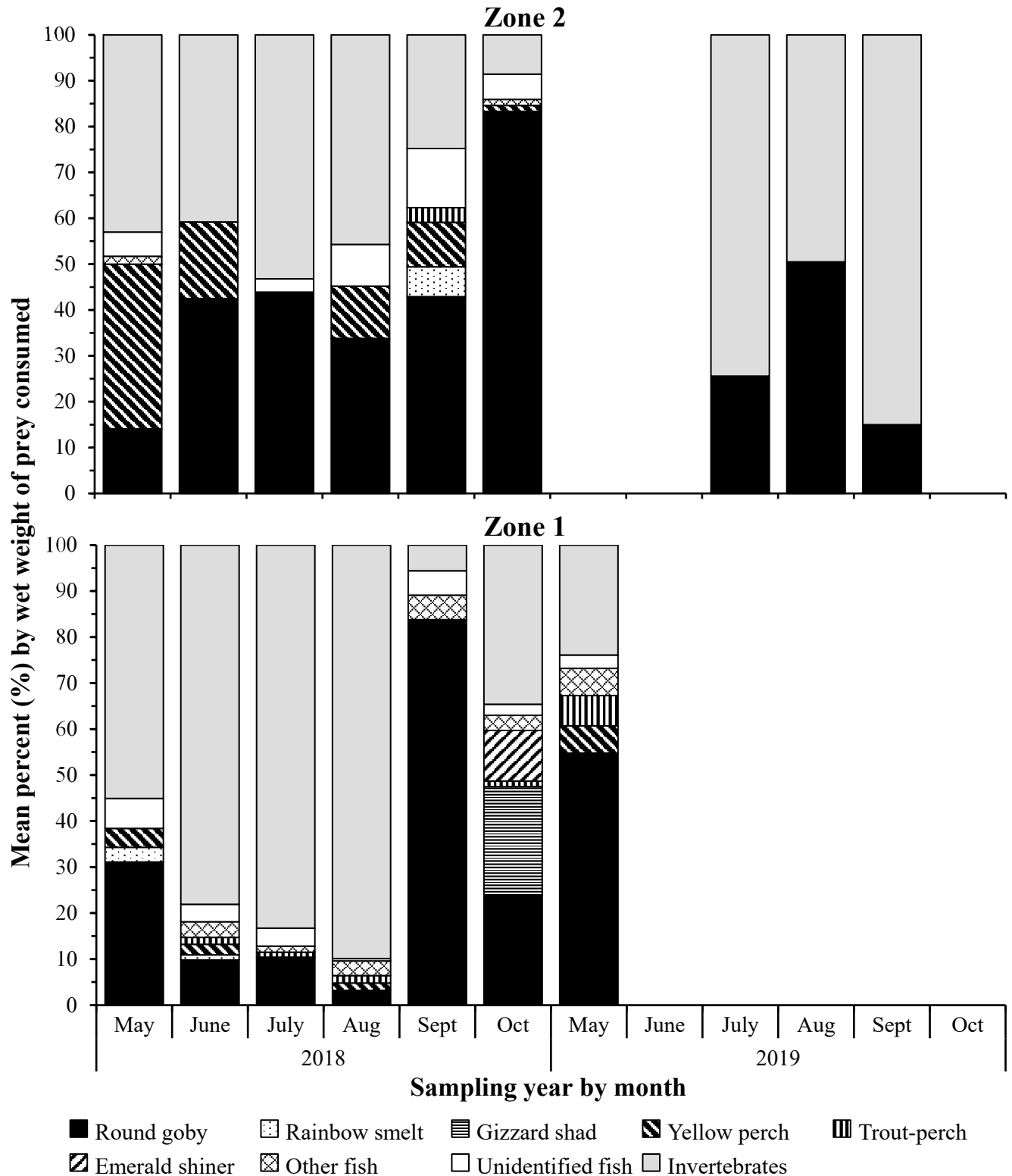
**FIGURE 4.** Walleye diet compositions expressed as the mean percent (%) by wet weight of major prey taxa consumed in Zone 1 (bottom figure) and Zone 2 (top figure) from May through October in Green Bay, Lake Michigan during 2018 and 2019. Other fish include freshwater drum, white perch, white bass, brown trout, emerald shiner, spottail shiner, and pumpkinseed.



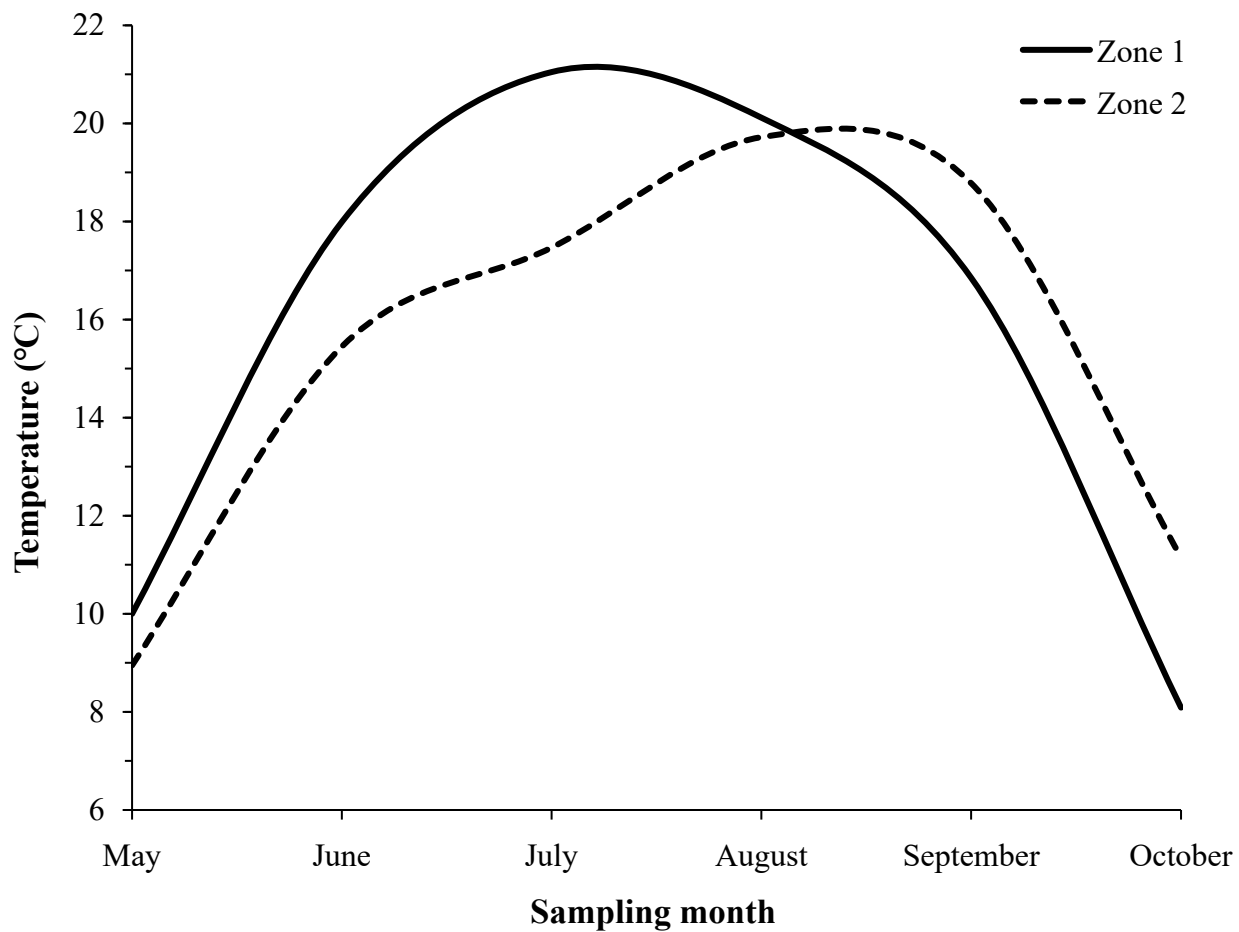
**FIGURE 5.** Walleye diet compositions expressed as the mean percent (%) by wet weight of major prey taxa consumed by juvenile (ages 0-3), young-adult (ages 4-6), and old-adult (ages 7-20) age groups for each zone collected in 2018 (months pooled) from Green Bay, Lake Michigan from May-October. Other fish include freshwater drum, white perch, brown trout, emerald shiner, and spottail shiner.



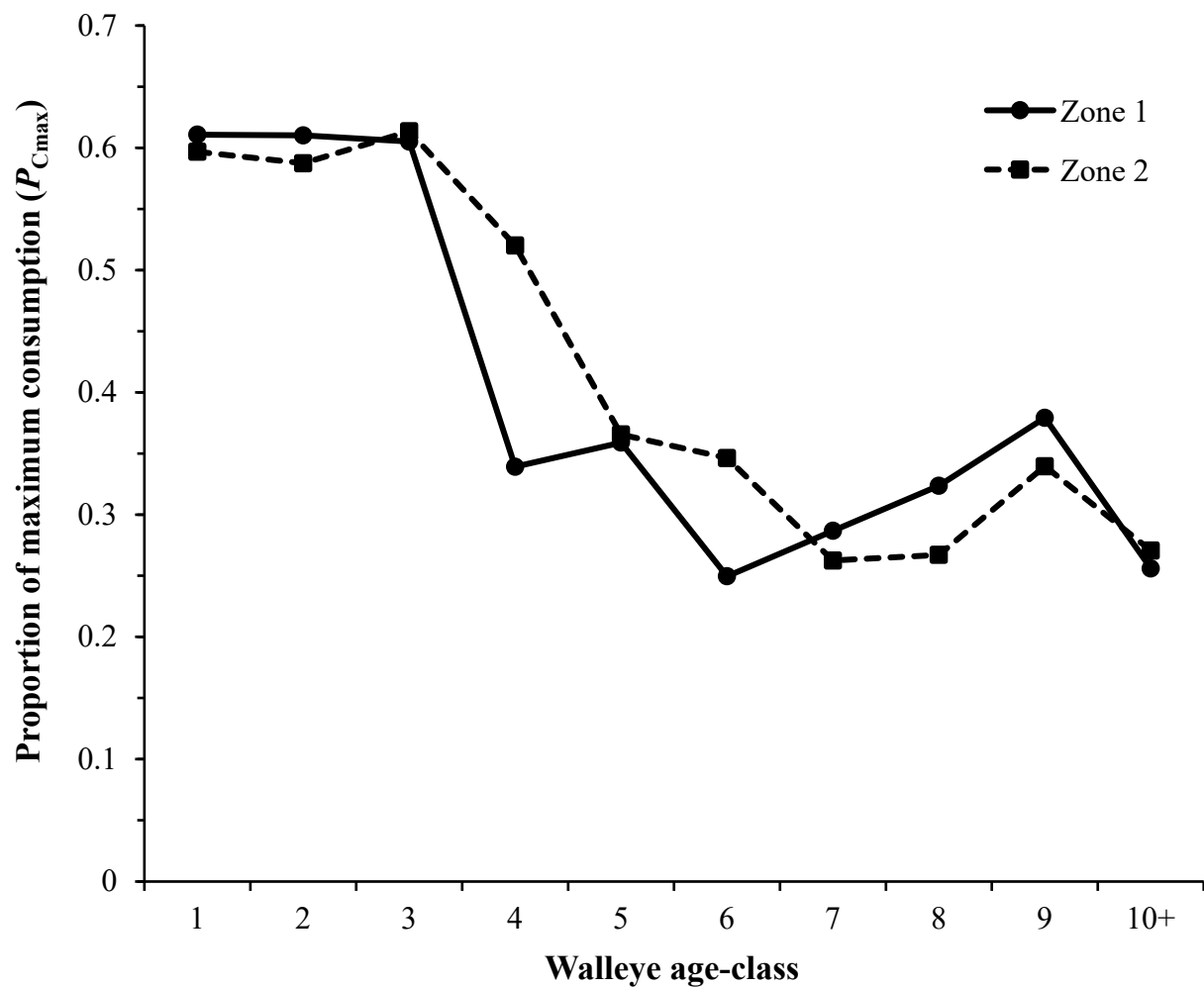
**FIGURE 6.** Lake whitefish diet compositions expressed as the mean percent (%) by wet weight of major prey taxa consumed in Zone 1 (bottom figure) and Zone 2 (top figure) from May through October in Green Bay, Lake Michigan during 2018 and 2019.



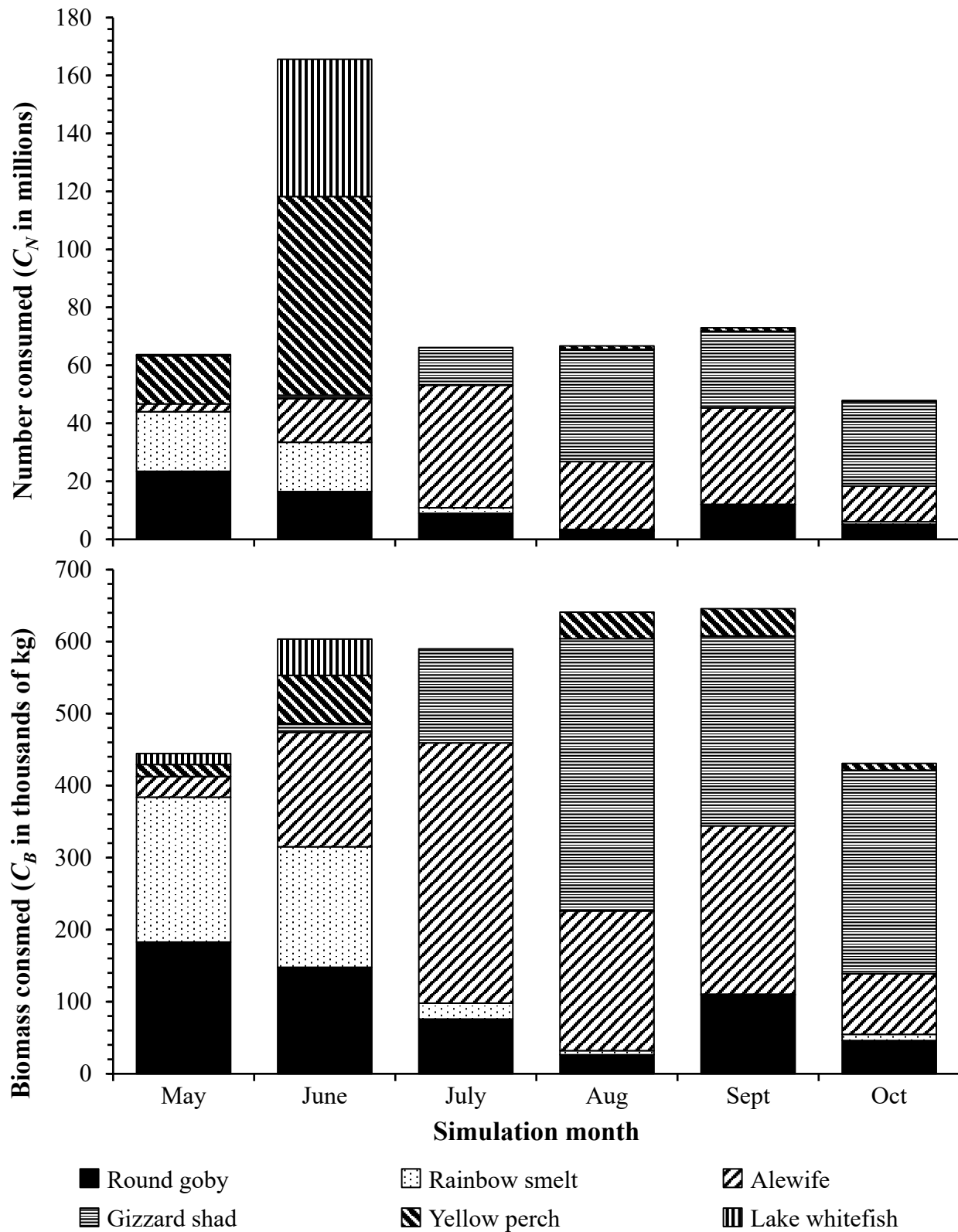
**FIGURE 7.** Yellow perch diet compositions expressed as the mean percent (%) by wet weight of major prey taxa consumed in Zone 1 (bottom figure) and Zone 2 (top figure) from May through October in Green Bay, Lake Michigan during 2018 and 2019. Other fish include alewife, white bass, smallmouth bass, fathead minnow, and bluegill.



**FIGURE 8.** Thermal conditions (mean monthly temperatures) experienced by walleyes in Zone 1 (solid line) and Zone 2 (dashed line) of Green Bay, Lake Michigan from May through October during 2018.

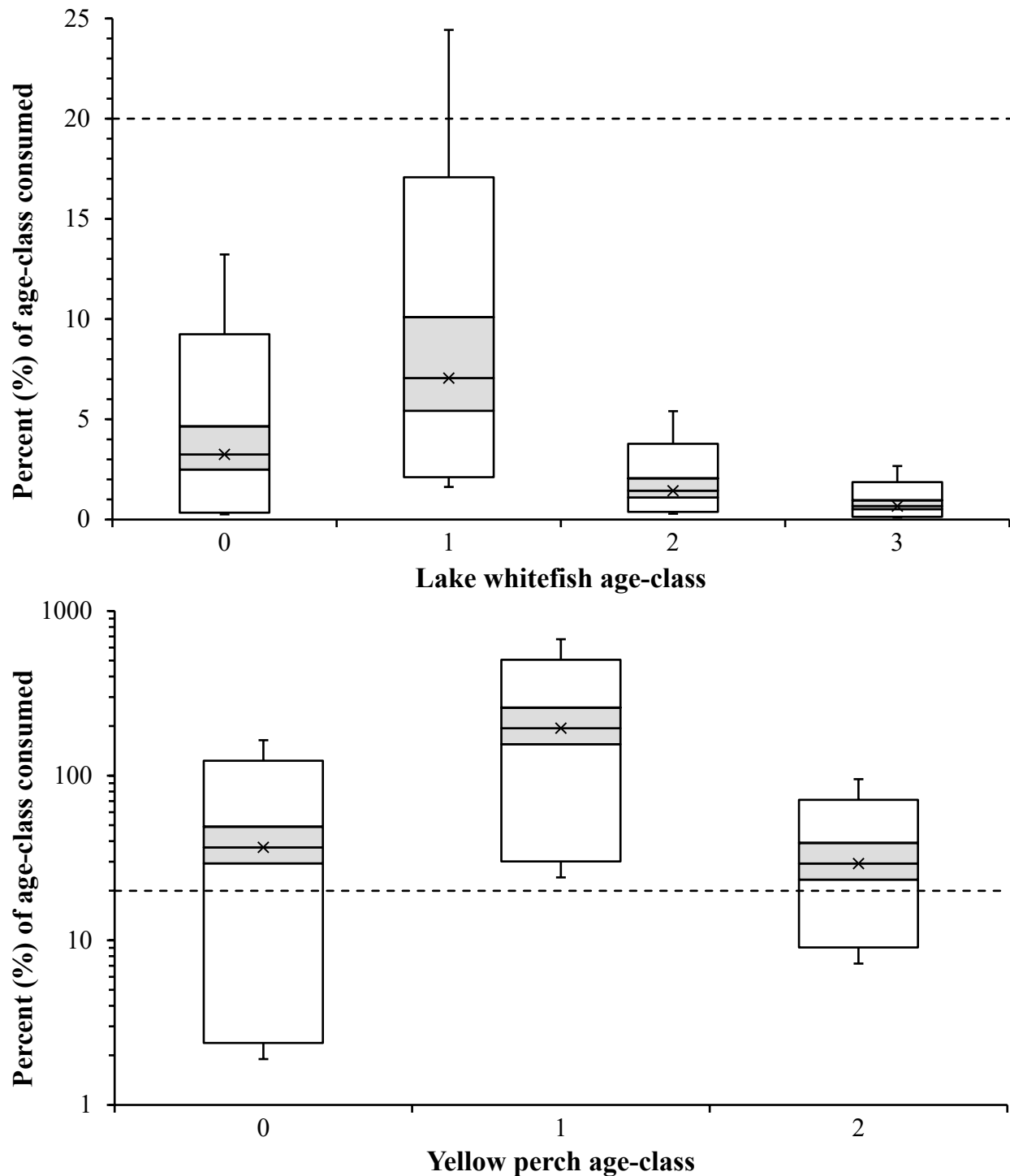


**FIGURE 9.** Proportion of maximum consumption ( $P_{Cmax}$ ) experienced by an individual walleye for age classes 1-9 and pooled ages 10-20 in Zone 1 (solid black line) and Zone 2 (dashed gray line) of Green Bay, Lake Michigan from May through October during 2018.



**FIGURE 10.** Monthly consumption of major prey species comparing biomass (lower panel) and number (upper panel) consumed by the walleye population in Zone 1 of Green Bay, Lake Michigan from May through October during 2018.





**FIGURE 13.** Estimated percent of lake whitefish (upper panel) and yellow perch (lower panel; log<sub>10</sub> scaled) age classes consumed by the walleye population in Zone 1 of Green Bay, Lake Michigan from May-October during 2018. Estimates depicted in the figures include: nominal consumption of nominal recruits (x); nominal consumption of nominal  $\pm$  95% confidence limit (CL) recruits (gray box region); nominal  $\pm$  95% CL consumption of nominal recruits (white box region); nominal  $\pm$  95% CL consumption of nominal  $\pm$  95% CL recruits (vertical bars); and the horizontal dashed line depicts 20% consumption of lake whitefish and yellow perch cohorts.

**Appendix A.** Walleye diet compositions (mean percent by wet weight of each prey encountered in the diets of walleye) from May-October during 2018-2019 in Green Bay, Lake Michigan.

YEAR	ZONE/MONTH	RGB	RBS	ALW	GZS	YEP	LWF	FWD	WHP	WHB	BNT	EMS	SPS	PKS	UNIF	INVT	
2018	2018 Total	20.25	8.46	21.63	19.34	5.35	5.57	0.78	0.39	-	0.09	0.77	1.18	-	10.93	5.25	
	Zone 1 Total	12.80	10.99	16.09	26.63	4.03	9.88	1.38	0.70	-	0.16	1.36	2.09	-	13.00	0.89	
	Zone 2 Total	29.89	5.20	28.81	9.89	7.06	-	-	-	-	-	-	-	-	8.25	10.90	
	May Total	41.38	26.88	1.03	-	3.05	5.33	4.32	0.23	-	0.51	-	6.51	-	5.76	5.00	
	June Total	4.90	12.85	33.15	-	5.53	22.51	-	-	-	-	-	-	-	11.63	9.42	
	July Total	18.72	-	47.74	2.11	8.54	-	-	-	-	-	-	-	-	17.29	5.61	
	Aug Total	20.11	0.14	26.42	23.10	5.09	-	-	1.59	-	-	3.17	-	-	11.92	8.46	
	Sept Total	32.46	-	21.81	24.36	11.36	-	-	-	-	-	-	-	-	6.84	3.16	
	Oct Total	13.32	4.58	1.34	66.37	1.87	-	-	0.72	-	-	1.75	-	-	10.05	-	
	Zone 1	May	35.25	29.47	-	-	4.10	7.16	5.80	0.31	-	0.68	-	8.75	-	7.74	0.75
		June	4.76	13.56	20.02	-	8.96	36.44	-	-	-	-	-	-	-	13.07	3.17
		July	12.35	-	58.37	5.00	-	-	-	-	-	-	-	-	-	24.28	-
		Aug	-	0.31	16.59	51.10	3.57	-	-	3.57	-	-	7.14	-	-	17.72	-
		Sept	21.84	-	41.79	27.27	9.09	-	-	-	-	-	-	-	-	-	-
	Zone 2	Oct	2.78	3.47	-	77.13	1.32	-	-	1.05	-	-	2.52	-	-	11.73	-
		May	59.25	19.35	4.01	-	-	-	-	-	-	-	-	-	-	-	17.39
		June	5.13	11.70	54.36	-	-	-	-	-	-	-	-	-	-	9.29	19.51
		July	23.35	-	40.00	-	14.76	-	-	-	-	-	-	-	-	12.21	9.69
		Aug	36.20	-	34.29	0.71	6.30	-	-	-	-	-	-	-	-	7.29	15.22
	2019	Sept	36.00	-	15.15	23.39	12.12	-	-	-	-	-	-	-	-	9.12	4.22
Oct		37.05	7.06	4.35	42.17	3.13	-	-	-	-	-	-	-	-	6.25	-	
2019 Total		37.57	5.48	28.84	7.30	2.24	1.61	2.31	1.43	1.06	-	0.05	-	0.87	7.58	3.65	
Zone 1 Total		31.78	13.51	-	24.65	-	5.44	7.81	4.83	3.57	-	0.05	-	-	7.96	0.39	
Zone 2 Total		40.00	2.10	40.99	-	3.19	-	-	-	-	-	0.05	-	1.24	7.41	5.02	
Zone 1		May	46.66	19.12	-	-	-	8.02	11.50	-	5.26	-	0.08	-	-	8.78	0.57
		Oct	0.37	1.66	-	76.69	-	-	-	15.03	-	-	-	-	-	6.25	-
Zone 2		June	50.42	4.44	39.58	-	0.33	-	-	-	-	-	-	-	1.79	3.43	-
		July	12.62	-	62.23	-	0.45	-	-	-	-	-	-	-	-	4.80	19.90
		Aug	47.47	0.96	46.81	-	-	-	-	-	-	-	-	-	-	4.76	-
		Sept	48.66	2.33	23.03	-	9.24	-	-	-	-	-	0.14	-	2.33	14.04	0.24
2018 + 2019	Grand Total	25.01	7.64	23.62	16.03	4.50	4.48	1.20	0.68	0.29	0.07	0.57	0.85	0.24	10.01	4.81	
	Zone 1 Total	15.95	11.41	13.41	26.30	3.36	9.14	2.45	1.38	0.59	0.14	1.14	1.74	-	12.17	0.81	
	Zone 2 Total	33.74	4.02	33.44	6.13	5.59	-	-	-	-	-	0.02	-	0.47	7.93	8.67	
	May Total	42.95	24.58	0.72	-	2.14	6.13	6.45	0.16	1.56	0.36	0.02	4.58	-	6.66	3.69	
	June Total	16.78	10.66	34.83	-	4.18	16.64	-	-	-	-	-	-	0.47	9.49	6.96	
	July Total	17.14	-	51.47	1.56	6.46	-	-	-	-	-	-	-	-	14.07	9.29	
	Aug Total	26.95	0.34	31.52	17.33	3.81	-	-	1.19	-	-	2.38	-	-	10.13	6.34	
	Sept Total	40.47	1.15	22.41	12.32	10.31	-	-	-	-	-	0.07	-	1.15	10.40	1.72	
	Oct Total	11.41	4.15	1.14	67.90	1.60	-	-	2.83	-	-	1.49	-	-	9.49	-	
	Zone 1	May	39.38	25.72	-	-	2.61	7.47	7.86	0.20	1.90	0.44	0.03	5.58	-	8.11	0.69
		June	4.76	13.56	20.02	-	8.96	36.44	-	-	-	-	-	-	-	13.07	3.17
		July	12.35	-	58.37	5.00	-	-	-	-	-	-	-	-	-	24.28	-
		Aug	-	0.31	16.59	51.10	3.57	-	-	3.57	-	-	7.14	-	-	17.72	-
		Sept	21.84	-	41.79	27.27	9.09	-	-	-	-	-	-	-	-	-	-
	Zone 2	Oct	2.30	3.11	-	77.04	1.05	-	-	3.84	-	-	2.02	-	-	10.64	-
		May	59.25	19.35	4.01	-	-	-	-	-	-	-	-	-	-	-	17.39
		June	26.87	8.22	47.27	-	0.16	-	-	-	-	-	-	-	0.86	6.48	10.15
		July	19.32	-	48.33	-	9.39	-	-	-	-	-	-	-	-	9.43	13.52
		Aug	40.42	0.36	38.98	0.44	3.94	-	-	-	-	-	-	-	-	6.34	9.51
	Zone 2	Sept	43.16	1.32	19.61	10.16	10.49	-	-	-	-	0.08	-	1.32	11.90	1.97	-
		Oct	37.05	7.06	4.35	42.17	3.13	-	-	-	-	-	-	-	-	6.25	-

**Note:** Prey; round goby (RGB), rainbow smelt (RBS), alewife (ALW), gizzard shad (GZS), yellow perch (YEP), lake whitefish (LWF), freshwater drum (FWD), white perch (WHP), white bass (WHB), brown trout (BNT), emerald shiner (EMS), spottail shiner (SPS), pumpkinseed (PKS), unidentified fish (UNIF), and invertebrates (INVT).

**Appendix B.** Lake whitefish diet compositions (mean percent by wet weight prey encountered in diets) from May-October during 2018-2019 in Green Bay, Lake Michigan.

YEAR	ZONE/MONTH	RGB	ALW	UNIF	INVT
2018	2018 Total	10.88	0.50	0.93	87.69
	Zone 1 Total	4.62	0.87	.	94.50
	Zone 2 Total	19.12	.	2.16	78.71
	May Total	17.01	.	.	82.99
	June Total	12.05	1.35	5.08	81.52
	July Total	6.82	.	.	93.18
	Aug Total	6.92	1.01	.	92.07
	Sept Total	.	.	.	100.00
	Oct Total	9.71	.	.	90.29
	Zone 1 May	8.47	.	.	91.53
	June	3.40	7.11	.	89.48
	July	7.14	.	.	92.86
	Aug	.	1.37	.	98.63
	Sept	.	.	.	100.00
	Oct	8.00	.	.	92.00
	Zone 2 May	33.70	.	.	66.30
	June	14.06	.	6.27	79.67
	July	6.67	.	.	93.33
	Aug	26.35	.	.	73.65
	Sept	.	.	.	100.00
	Oct	13.61	.	.	86.39
2019	2019 Total	1.83	.	.	98.17
	Zone 1 Total	.	.	.	100.00
	Zone 2 Total	10.34	.	.	89.66
	Zone 1 May	.	.	.	100.00
	Aug	.	.	.	100.00
	Oct	.	.	.	100.00
	Zone 2 June	23.78	.	.	76.22
	July	.	.	.	100.00
	Grand Total	8.68	0.37	0.71	90.24
	Zone 1 Total	3.15	0.59	.	96.25
2019	Zone 2 Total	18.10	.	1.91	79.99
	May Total	13.17	.	.	86.83
	June Total	13.44	1.19	4.48	80.89
	July Total	5.26	.	.	94.74
	Aug Total	4.60	0.67	.	94.73
	Sept Total	.	.	.	100.00
	Oct Total	6.25	.	.	93.75
	Zone 1 May	5.88	.	.	94.12
	June	3.40	7.11	.	89.48
	July	7.14	.	.	92.86
	Aug	.	0.81	.	99.19
	Sept	.	.	.	100.00
	Oct	4.44	.	.	95.56
	Zone 2 May	33.70	.	.	66.30
	June	15.45	.	5.37	79.17
	July	4.65	.	.	95.35
	Aug	26.35	.	.	73.65
	Sept	.	.	.	100.00
	Oct	13.61	.	.	86.39

**Note:** Prey; round goby (RGB), alewife (ALW), unidentified fish (UNIF), and invertebrates (INVT).

**Appendix C. Yellow perch diet compositions (mean percent by wet weight of prey encountered in diets) from May-October during 2018-2019 in Green Bay, Lake Michigan.**

YEAR	ZONE/MONTH		RGB	RBS	ALW	GZS	YEP	WHB	SMB	TRP	EMS	FAT	BLG	UNIF	INVT
2018	2018 Total		31.51	0.67	0.77	3.65	3.76	0.18	0.18	0.87	1.68	0.24	0.50	4.55	51.44
	Zone 1 Total		18.15	0.51	0.96	5.91	1.12	0.29	0.29	1.12	2.71	0.29	0.81	3.19	64.64
	Zone 2 Total		53.09	0.95	0.47	-	8.02	-	-	0.47	-	0.16	-	6.73	30.11
	May Total		24.62	2.00	-	-	16.19	-	-	-	-	0.66	-	6.00	50.53
	June Total		12.45	0.99	1.75	-	3.50	-	-	1.37	-	1.37	-	3.50	75.07
	July Total		20.63	-	0.89	0.17	0.08	-	-	0.72	-	-	-	3.60	73.89
	Aug Total		15.78	-	0.93	-	5.61	0.93	-	0.93	-	-	-	4.03	71.78
	Sept Total		58.48	4.00	-	-	6.00	-	2.00	2.00	-	-	-	10.00	17.52
	Oct Total		52.04	-	0.63	12.47	0.63	-	-	0.63	5.78	-	1.73	3.87	22.23
	Zone 1	May	31.10	3.23	-	-	4.09	-	-	-	-	-	-	6.45	55.13
		June	9.75	1.08	1.90	-	2.32	-	-	1.49	-	1.49	-	3.81	78.14
		July	10.16	-	1.30	0.25	-	-	-	1.05	-	-	-	3.94	83.30
		Aug	3.17	-	1.59	-	1.59	1.59	-	1.59	-	-	-	0.49	89.98
		Sept	83.83	-	-	-	-	-	5.26	-	-	-	-	5.26	5.65
		Oct	23.77	-	-	23.75	-	-	-	1.19	11.01	-	3.29	2.38	34.61
	Zone 2	May	14.06	-	-	-	35.92	-	-	-	-	1.73	-	5.26	43.03
		June	42.57	-	-	-	16.67	-	-	-	-	-	-	-	40.77
		July	43.67	-	-	-	0.27	-	-	-	-	-	-	2.86	53.20
		Aug	33.84	-	-	-	11.36	-	-	-	-	-	-	9.09	45.71
		Sept	42.95	6.45	-	-	9.68	-	-	3.23	-	-	-	12.90	24.79
		Oct	83.30	-	1.32	-	1.32	-	-	-	-	-	-	5.53	8.54
2019	2019 Total		32.15	-	-	-	1.39	1.39	-	1.56	-	-	-	0.69	62.82
	Zone 1 Total		54.81	-	-	-	5.88	5.88	-	6.59	-	-	-	2.94	23.90
	Zone 2 Total		25.15	-	-	-	-	-	-	-	-	-	-	-	74.85
	Zone 1	May	54.81	-	-	-	5.88	5.88	-	6.59	-	-	-	2.94	23.90
	Zone 2	July	25.61	-	-	-	-	-	-	-	-	-	-	-	74.39
		Aug	50.51	-	-	-	-	-	-	-	-	-	-	-	49.49
		Sept	14.99	-	-	-	-	-	-	-	-	-	-	-	85.01
2018 + 2019	Grand Total		31.64	0.54	0.61	2.89	3.27	0.43	0.14	1.01	1.33	0.19	0.40	3.75	53.79
	Zone 1 Total		21.47	0.46	0.87	5.37	1.55	0.80	0.27	1.61	2.47	0.27	0.74	3.17	60.95
	Zone 2 Total		43.52	0.62	0.31	-	5.27	-	-	0.31	-	0.10	-	4.42	45.44
	May Total		36.84	1.19	-	-	12.02	2.38	-	2.67	-	0.39	-	4.76	39.75
	June Total		12.45	0.99	1.75	-	3.50	-	-	1.37	-	1.37	-	3.50	75.07
	July Total		21.82	-	0.68	0.13	0.06	-	-	0.55	-	-	-	2.74	74.01
	Aug Total		21.48	-	0.78	-	4.69	0.78	-	0.78	-	-	-	3.37	68.12
	Sept Total		35.90	1.92	-	-	2.88	-	0.96	0.96	-	-	-	4.81	52.56
	Oct Total		52.04	-	0.63	12.47	0.63	-	-	0.63	5.78	-	1.73	3.87	22.23
	Zone 1	May	43.50	1.54	-	-	5.03	3.08	-	3.45	-	-	-	4.62	38.79
		June	9.75	1.08	1.90	-	2.32	-	-	1.49	-	1.49	-	3.81	78.14
		July	10.16	-	1.30	0.25	-	-	-	1.05	-	-	-	3.94	83.30
		Aug	3.17	-	1.59	-	1.59	1.59	-	1.59	-	-	-	0.49	89.98
		Sept	83.83	-	-	-	-	-	5.26	-	-	-	-	5.26	5.65
		Oct	23.77	-	-	23.75	-	-	-	1.19	11.01	-	3.29	2.38	34.61
	Zone 2	May	14.06	-	-	-	35.92	-	-	-	-	1.73	-	5.26	43.03
		June	42.57	-	-	-	16.67	-	-	-	-	-	-	-	40.77
		July	34.64	-	-	-	0.13	-	-	-	-	-	-	1.43	63.79
		Aug	39.22	-	-	-	7.69	-	-	-	-	-	-	6.15	46.93
		Sept	25.18	2.35	-	-	3.53	-	-	1.18	-	-	-	4.71	63.05
		Oct	83.30	-	1.32	-	1.32	-	-	-	-	-	-	5.53	8.54

**Note:** Prey; round goby (RGB), rainbow smelt (RBS), alewife (ALW), gizzard shad (GZS), yellow perch (YEP), white bass (WHB), smallmouth bass (SMB), trout-perch (TRP), emerald shiner (EMS), fathead (FAT), bluegill (BLG), unidentified fish (UNIF), and invertebrates (INVT).

**Appendix D.** Frequency of occurrence (%) for dominant invertebrate taxa found in the diets of walleye (WAE), lake whitefish (LWF), and yellow perch (YEP) from May through October in each zone of Green Bay, Lake Michigan during 2018.

Species Zone	Month	Frequency of Occurrence (%)											
		CHIR	EPHE	BYTH	DREI	PISI	DAPH	TRIC	AMPH	ASEL	TROM	OSTR	HIRU
WAE													
1	May	1.5	·	·	1.5	·	·	·	·	·	·	·	1.5
	June	1.6	·	·	·	·	·	·	·	·	·	·	·
2	May	·	13.0	·	·	·	·	4.4	4.4	·	·	·	·
	June	7.7	15.4	·	·	·	·	·	·	·	·	·	·
	July	·	12.7	·	·	·	·	·	·	·	·	·	·
	Aug	·	14.3	2.9	·	·	·	·	2.9	·	·	·	·
	Sept	·	3.0	·	6.1	·	·	·	·	·	·	·	·
LWF													
1	May	72.3	·	8.0	16.1	24.1	24.1	·	8.0	·	·	·	·
	June	31.0	·	·	·	15.5	61.9	·	·	·	·	·	·
	July	31.0	·	15.5	·	46.4	·	·	·	·	15.5	·	·
	Aug	80.7	·	35.9	9.0	71.7	9.0	·	·	·	9.0	17.9	·
	Sept	75.0	·	25.0	·	75.0	·	·	·	·	·	12.5	·
	Oct	61.3	10.2	71.6	20.4	61.3	10.2	·	20.4	·	61.3	10.2	·
2	May	69.8	·	10.0	29.9	49.8	·	·	·	10.0	29.9	·	·
	June	47.6	·	13.6	20.4	27.2	34.0	·	·	·	13.6	·	·
	July	56.0	·	·	65.3	18.7	·	·	·	·	·	18.7	·
	Aug	84.6	14.1	14.1	28.2	14.1	·	·	·	·	·	28.2	·
	Sept	·	·	100.0	·	·	·	·	·	·	·	·	·
	Oct	55.6	11.1	22.2	22.2	33.3	·	·	·	·	22.2	22.2	·
YEP													
1	May	54.8	3.2	·	·	·	·	·	·	·	·	·	3.2
	June	29.9	4.5	26.9	37.3	·	1.5	25.4	3.0	3.0	4.5	·	·
	July	53.2	10.4	63.6	19.5	·	1.3	31.2	15.6	6.5	1.3	·	1.3
	Aug	42.9	1.6	74.6	12.7	·	3.2	22.2	15.9	17.5	6.3	·	·
	Sept	·	·	5.3	5.3	·	·	·	·	·	·	·	·
	Oct	17.9	·	7.1	2.4	·	2.4	1.2	3.6	6.0	·	·	1.2
2	May	15.8	10.5	·	·	·	·	·	·	·	·	·	·
	June	16.7	16.7	50.0	·	·	·	·	·	·	·	·	·
	July	·	37.1	14.3	5.7	2.9	2.9	2.9	·	·	·	·	·
	Aug	11.4	20.5	31.8	2.3	·	·	·	2.3	·	·	·	·
	Sept	·	3.2	16.1	6.5	·	·	3.2	·	·	·	·	·
	Oct	·	7.9	·	1.3	·	·	·	·	·	·	·	1.3

**Note:** Invertebrates included Chironomidae (CHIR), Ephemeroptera (EPHE), Bythotrephes spp. (BYTH), Dreissenidae (DREI), Pisidiidae (PISI), Daphniidae (DAPH), Trichoptera (TRIC), Amphipoda (AMPH), Asellidae (ASEL), and Hirudinidae (HIRU).

**Appendix E.** Zone 1 individual level walleye consumption estimates for age classes 1-9 and pooled ages 10-20 during May 1 through October 31 collected from Green Bay, Lake Michigan in 2018. Biomass ( $C_B$ ; g) of each prey category consumed was used to calculate the percent of total  $C_B$  within each walleye age-class. The mean weight (g) of prey includes all individuals within each prey category consumed by the respective age-class of walleye, which was used to convert  $C_B$  to the number of individuals consumed ( $C_N$ ).

WAE age	Prey category (age-class)	$C_B$ (g)	Percent (%) of total $C_B$	Mean weight of prey (g)	$C_N$
1	Lake whitefish (0)	11.000	0.7	0.442	24.9
	Yellow perch (0)	39.591	2.5	0.298	132.9
	Round goby	268.714	17.1	8.569	31.4
	Rainbow smelt	133.304	8.5	10.363	12.9
	Alewife	384.952	24.5	4.108	93.7
	Gizzard shad	378.340	24.1	5.498	68.8
	Other fish	69.430	4.4		
	Unidentified fish	284.204	18.1		
	Invertebrates	0.015	0.0		
	TOTALS	1,569.552	100.0		364.5
2	Lake whitefish (0)	23.297	0.8	0.480	48.5
	Yellow perch (1)	85.304	2.7	15.939	5.4
	Round goby	544.382	17.5	6.297	86.5
	Rainbow smelt	290.373	9.4	8.063	36.0
	Alewife	740.832	23.9	10.462	70.8
	Gizzard shad	715.908	23.1	15.890	45.1
	Other fish	136.272	4.4		
	Unidentified fish	568.844	18.3		
	Invertebrates	0.034	0.0		
	TOTALS	3,105.244	100.0		292.2
3	Lake whitefish (0)	38.202	0.8	0.517	73.9
	Yellow perch (0)	15.923	0.3	2.199	7.2
	Yellow perch (1)	125.268	2.6	17.298	7.2
	Round goby	872.333	17.8	24.233	36.0
	Rainbow smelt	483.480	9.9	11.628	41.6
	Alewife	1,151.944	23.5	10.027	114.9
	Gizzard shad	1,102.072	22.5	12.007	91.8
	Other fish	214.358	4.4		
	Unidentified fish	904.660	18.4		
	Invertebrates	0.056	0.0		
	TOTALS	4,908.299	100.0		372.6

**Appendix E.** (continued).

WAE age	Prey category (age-class)	$C_B$ (g)	Percent (%) of total $C_B$	Mean weight of prey (g)	$C_N$
4	Yellow perch (0)	2.907	0.1	13.067	0.2
	Round goby	157.740	6.4	4.943	31.9
	Rainbow smelt	204.009	8.3	18.163	11.2
	Alewife	946.253	38.6	10.287	92.0
	Gizzard shad	893.531	36.4	10.172	87.8
	Other fish	8.126	0.3		
	Unidentified fish	224.203	9.1		
	Invertebrates	17.607	0.7		
	TOTALS	2,454.377	100.0		223.2
5	Yellow perch (0)	3.362	0.1	13.067	0.3
	Round goby	179.321	6.4	6.653	27.0
	Rainbow smelt	232.025	8.3	13.308	17.4
	Alewife	1,080.415	38.4	10.095	107.0
	Gizzard shad	1,029.389	36.6	9.269	111.1
	Other fish	9.394	0.3		
	Unidentified fish	256.093	9.1		
	Invertebrates	19.960	0.7		
	TOTALS	2,809.959	100.0		262.7
6	Yellow perch (0)	1.960	0.1	13.067	0.2
	Round goby	118.032	6.7	14.362	8.2
	Rainbow smelt	152.258	8.6	2.017	75.5
	Alewife	690.069	39.2	17.051	40.5
	Gizzard shad	617.409	35.0	24.662	25.0
	Other fish	5.495	0.3		
	Unidentified fish	163.139	9.3		
	Invertebrates	13.392	0.8		
	TOTALS	1,761.754	100.0		149.4
7	Lake whitefish (1)	231.536	8.6	36.350	6.4
	Yellow perch (0)	50.912	1.9	9.446	5.4
	Yellow perch (1)	215.289	8.0	39.945	5.4
	Yellow perch (2)	213.085	7.9	79.072	2.7
	Round goby	123.857	4.6	4.941	25.1
	Rainbow smelt	244.744	9.1	10.338	23.7
	Alewife	419.882	15.6	19.938	21.1
	Gizzard shad	961.264	35.6	10.752	89.4
	Other fish	59.743	2.2		
	Unidentified fish	69.939	2.6		
	Invertebrates	109.315	4.0		
	TOTALS	2,699.565	100.0		179.0

**Appendix E.** (continued).

WAE age	Prey category (age-class)	$C_B$ (g)	Percent (%) of total $C_B$	Mean weight of prey (g)	$C_N$
8	Lake whitefish (1)	273.007	8.4	20.320	13.4
	Yellow perch (0)	61.767	1.9	9.446	6.5
	Yellow perch (1)	261.194	8.1	39.945	6.5
	Yellow perch (2)	258.519	8.0	79.072	3.3
	Round goby	145.289	4.5	7.809	18.6
	Rainbow smelt	290.195	9.0	19.790	14.7
	Alewife	500.467	15.5	25.532	19.6
	Gizzard shad	1,162.980	35.9	11.153	104.3
	Other fish	70.111	2.2		
	Unidentified fish	84.045	2.6		
	Invertebrates	130.205	4.0		
	TOTALS	3,237.778	100.0		186.9
9	Lake whitefish (1)	110.301	2.7	21.881	5.0
	Lake whitefish (2)	228.541	5.5	90.672	2.5
	Yellow perch (1)	246.098	6.0	38.460	6.4
	Yellow perch (2)	505.963	12.3	79.072	6.4
	Round goby	178.964	4.3	3.010	59.5
	Rainbow smelt	363.146	8.8	11.207	32.4
	Alewife	631.015	15.3	19.938	31.6
	Gizzard shad	1,498.287	36.4	14.606	102.6
	Other fish	86.417	2.1		
	Unidentified fish	107.264	2.6		
	Invertebrates	164.005	4.0		
	TOTALS	4,120.000	100.0		246.4
10-20	Lake whitefish (1)	18.451	0.6	37.775	0.5
	Lake whitefish (2)	116.462	3.8	95.376	1.2
	Lake whitefish (3)	135.920	4.4	173.923	0.8
	Yellow perch (0)	170.282	5.5	9.446	18.0
	Yellow perch (1)	373.416	12.0	41.430	9.0
	Round goby	145.716	4.7	6.660	21.9
	Rainbow smelt	284.569	9.2	11.156	25.5
	Alewife	485.392	15.7	19.938	24.3
	Gizzard shad	1,093.667	35.3	10.480	104.4
	Other fish	70.253	2.3		
	Unidentified fish	80.171	2.6		
	Invertebrates	126.467	4.1		
	TOTALS	3,100.767	100.0		205.6

**Note:** Numeric table entries were rounded and may not equal the totals within each age-class.



**Appendix F.** Zone 1 population level walleye (WAE) consumption estimates of major prey groups for age classes 1-9 and pooled ages 10-20 during May 1 through October 31 collected from Green Bay, Lake Michigan in 2018. Lower (lower 95% confidence limit), nominal, and upper (upper 95% confidence limit) consumption estimates are provided. Total biomass ( $C_B$ , kg) and number ( $C_N$ ) of major prey groups consumed are shown at the bottom.

WAE		$C_B$ (kg)			$C_N$		
Age	Prey	Lower	Nominal	Upper	Lower	Nominal	Upper
1	RGB	9,106	152,930	518,508	1,062,642	17,846,891	60,509,785
	RBS	4,860	81,616	276,720	468,939	7,875,743	26,702,662
	ALW	12,394	208,155	705,749	3,017,043	50,670,705	171,798,743
	GZS	11,955	200,778	680,738	2,174,386	36,518,427	123,815,522
	FISH	2,288	38,429	130,293			
	UNIF	9,519	159,873	542,050			
	INVT	1	10	32			
2	RGB	12,045	187,876	549,380	1,912,875	29,835,802	87,244,795
	RBS	6,877	107,265	313,660	852,924	13,303,356	38,901,202
	ALW	15,517	242,018	707,700	1,483,137	23,133,023	67,644,766
	GZS	14,710	229,436	670,908	925,734	14,439,009	42,222,039
	FISH	2,925	45,622	133,407			
	UNIF	12,396	193,337	565,350			
	INVT	1	13	37			
3	RGB	33,020	165,704	364,960	1,362,596	6,837,929	15,060,443
	RBS	19,533	98,022	215,893	1,679,816	8,429,841	18,566,607
	ALW	41,193	206,720	455,298	4,108,222	20,616,339	45,407,198
	GZS	38,653	193,973	427,223	3,219,208	16,154,991	35,581,141
	FISH	7,861	39,450	86,888			
	UNIF	33,656	168,897	371,993			
	INVT	2	11	25			
4	RGB	6,635	26,243	56,419	1,342,225	5,309,143	11,413,912
	RBS	8,524	33,717	72,486	469,306	1,856,330	3,990,849
	ALW	37,559	148,564	319,392	3,651,121	14,441,927	31,048,116
	GZS	31,637	125,139	269,031	3,110,191	12,302,289	26,448,194
	FISH	272	1,078	2,317			
	UNIF	8,858	35,039	75,329			
	INVT	768	3,037	6,528			
5	RGB	7,867	26,290	55,753	1,182,543	3,951,545	8,380,100
	RBS	10,112	33,789	71,657	759,822	2,538,995	5,384,485
	ALW	44,737	149,491	317,029	4,431,595	14,808,469	31,404,542
	GZS	38,025	127,065	269,468	4,102,435	13,708,558	29,071,944
	FISH	329	1,098	2,329			
	UNIF	10,554	35,268	74,794			
	INVT	908	3,034	6,435			
6	RGB	1,783	5,348	13,219	124,176	372,375	920,396
	RBS	2,286	6,856	16,946	1,133,520	3,399,157	8,401,676
	ALW	9,835	29,491	72,894	576,771	1,729,597	4,275,036
	GZS	7,845	23,524	58,145	318,090	953,874	2,357,686
	FISH	66	198	490			
	UNIF	2,316	6,944	17,164			
	INVT	209	628	1,552			

**Appendix F.** (continued).

WAE		$C_B$ (kg)			$C_N$		
Age	Prey	Lower	Nominal	Upper	Lower	Nominal	Upper
7	RGB	1,833	5,568	13,010	371,047	1,126,831	2,633,150
	RBS	3,494	10,612	24,798	338,018	1,026,524	2,398,755
	ALW	5,890	17,888	41,800	295,427	897,181	2,096,511
	GZS	12,855	39,040	91,228	1,195,613	3,630,949	8,484,711
	FISH	882	2,680	6,262			
	UNIF	954	2,897	6,771			
	INVT	1,537	4,667	10,906			
8	RGB	1,798	6,318	15,300	230,270	809,113	1,959,322
	RBS	3,464	12,170	29,472	175,021	614,981	1,489,219
	ALW	5,870	20,625	49,945	229,898	807,809	1,956,164
	GZS	13,000	45,679	110,615	1,165,609	4,095,674	9,917,953
	FISH	866	3,042	7,367			
	UNIF	957	3,364	8,147			
	INVT	1,530	5,377	13,022			
9	RGB	1,585	5,026	12,680	526,715	1,669,625	4,212,667
	RBS	3,101	9,831	24,805	276,742	877,238	2,213,377
	ALW	5,297	16,790	42,364	265,662	842,118	2,124,766
	GZS	11,982	37,983	95,835	820,374	2,600,488	6,561,347
	FISH	764	2,421	6,110			
	UNIF	873	2,768	6,983			
	INVT	1,380	4,373	11,034			
10-20	RGB	1,331	6,595	18,351	199,798	990,242	2,755,412
	RBS	2,507	12,426	34,577	224,742	1,113,865	3,099,402
	ALW	4,201	20,822	57,938	210,711	1,044,328	2,905,912
	GZS	9,026	44,736	124,481	861,289	4,268,723	11,878,003
	FISH	640	3,173	8,828			
	UNIF	676	3,349	9,317			
	INVT	1,097	5,437	15,129			
TOTAL							
	RGB	77,004	587,897	1,617,581	8,314,888	68,749,495	195,089,982
	RBS	64,758	406,305	1,081,013	6,378,849	41,036,029	111,148,233
	ALW	182,492	1,060,565	2,770,108	18,269,589	128,991,497	360,661,753
	GZS	189,689	1,067,353	2,797,672	17,892,929	108,672,983	296,338,540
	FISH	16,894	137,192	384,291			
	UNIF	80,760	611,737	1,677,898			
	INVT	7,433	26,587	64,700			

**Note:** Major prey species included round goby (RGB), rainbow smelt (RBS), alewife (ALW), gizzard shad (GZS), other fish (FISH), unidentified fish (UNIF), and invertebrates (INVT).

**Appendix G.** Zone 2 diet schedules (mean proportions; wet weight basis) for juvenile (ages 1-3), young-adult (ages 4-6), and old-adult (ages 7-20) walleye age groups collected from Green Bay, Lake Michigan during May through October in 2018.

Ages	Day	RGB	RBS	ALW	GZS	YEP	UNIF	INVT
1-3	01-May	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	30-May	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	14-June	0.10	0.20	0.10	0.00	0.00	0.00	0.60
	30-June	0.19	0.11	0.27	0.00	0.00	0.05	0.38
	17-July	0.25	0.00	0.39	0.00	0.18	0.08	0.10
	14-Aug	0.40	0.00	0.07	0.00	0.16	0.08	0.29
	31-Aug	0.40	0.00	0.60	0.00	0.00	0.00	0.00
	11-Sept	0.52	0.00	0.09	0.22	0.00	0.12	0.06
	31-Oct	0.43	0.12	0.02	0.43	0.00	0.00	0.00
4-6	01-May	0.50	0.50	0.00	0.00	0.00	0.00	0.00
	18-June	0.13	0.22	0.28	0.00	0.00	0.17	0.20
	18-July	0.00	0.00	0.33	0.00	0.00	0.50	0.17
	15-Aug	0.17	0.00	0.50	0.04	0.00	0.24	0.05
	31-Aug	0.10	0.00	0.57	0.17	0.00	0.14	0.03
	13-Sept	0.00	0.00	0.50	0.25	0.25	0.00	0.00
	08-Oct	0.29	0.00	0.00	0.57	0.14	0.00	0.00
	31-Oct	0.29	0.00	0.00	0.57	0.14	0.00	0.00
7-20	01-May	0.70	0.19	0.05	0.00	0.00	0.00	0.06
	18-June	0.00	0.04	0.86	0.00	0.00	0.11	0.00
	16-July	0.40	0.00	0.60	0.00	0.00	0.00	0.00
	15-Aug	0.29	0.00	0.71	0.00	0.00	0.00	0.00
	31-Aug	0.16	0.00	0.55	0.25	0.00	0.04	0.00
	07-Sept	0.00	0.00	0.25	0.43	0.25	0.07	0.00
	01-Oct	0.19	0.02	0.21	0.41	0.00	0.17	0.00
	31-Oct	0.33	0.04	0.11	0.29	0.00	0.22	0.00

**Note:** Numeric table entries were rounded to the nearest hundredth and rows may not be equal to 1. Diets included round goby (RGB), rainbow smelt (RBS), alewife (ALW), gizzard shad (GZS), yellow perch (YEP), unidentified fish (UNIF), and invertebrates (INVT; Chironomidae, Ephemeroptera, Amphipoda, Zygoptera, Trichoptera, Dreissenidae, and *Bythotrephes spp.*).

**Appendix H.** Zone 2 individual level walleye consumption estimates for age classes 1-9 and pooled ages 10-20 during May 1 through October 31 collected from Green Bay, Lake Michigan in 2018. Biomass ( $C_B$ ; g) of each prey category consumed was used to calculate the percent of total  $C_B$  within each walleye age-class. The mean weight (g) of prey includes all individuals within each prey category consumed by the respective age-class of walleye, which was used to convert  $C_B$  to the number of individuals consumed ( $C_N$ ).

WAE age	Prey category (age-class)	$C_B$ (g)	Percent (%) of total $C_B$	Mean weight of prey (g)	$C_N$
1	Yellow perch (0)	50.131	4.9	1.313	38.2
	Round goby	323.826	31.5	5.083	63.7
	Rainbow smelt	40.565	3.9	0.433	93.7
	Alewife	176.729	17.2	4.817	36.7
	Gizzard shad	103.359	10.0	17.027	6.1
	Unidentified fish	52.068	5.1		
	Invertebrates	282.850	27.5		
	TOTALS	1,029.529	100.0		238.3
2	Yellow perch (0)	130.944	4.9	1.286	101.8
	Round goby	805.333	30.4	11.269	71.5
	Rainbow smelt	105.042	4.0	15.717	6.7
	Alewife	456.053	17.2	13.334	34.2
	Gizzard shad	244.256	9.2	15.986	15.3
	Unidentified fish	131.469	5.0		
	Invertebrates	778.057	29.3		
	TOTALS	2,651.153	100.0		229.5
3	Yellow perch (0)	181.847	4.9	1.286	141.4
	Round goby	1,127.101	30.6	4.512	249.8
	Rainbow smelt	145.845	4.0	15.359	9.5
	Alewife	634.583	17.2	16.162	39.3
	Gizzard shad	344.530	9.3	18.353	18.8
	Unidentified fish	183.549	5.0		
	Invertebrates	1,069.304	29.0		
	TOTALS	3,686.759	100.0		458.7
4	Yellow perch (1)	86.032	3.0	22.783	3.8
	Yellow perch (2)	94.573	3.3	50.091	1.9
	Round goby	440.211	15.2	13.566	32.4
	Rainbow smelt	219.360	7.6	5.397	40.6
	Alewife	869.701	30.1	7.467	116.5
	Gizzard shad	501.313	17.3	13.976	35.9
	Unidentified fish	467.589	16.2		
	Invertebrates	211.924	7.3		
	TOTALS	2,890.703	100.0		231.1

**Appendix H.** (continued).

WAE age	Prey category (age-class)	$C_B$ (g)	Percent (%) of total $C_B$	Mean weight of prey (g)	$C_N$
5	Yellow perch (2)	143.268	5.8	50.091	2.9
	Round goby	380.817	15.3	9.510	40.0
	Rainbow smelt	209.273	8.4	7.308	28.6
	Alewife	748.141	30.1	6.921	108.1
	Gizzard shad	396.942	16.0	8.727	45.5
	Unidentified fish	415.008	16.7		
	Invertebrates	192.146	7.7		
	TOTALS	2,485.594	100.0		225.1
6	Yellow perch (1)	151.806	5.7	22.783	6.7
	Round goby	408.917	15.3	11.876	34.4
	Rainbow smelt	227.778	8.5	13.043	17.5
	Alewife	802.467	30.1	8.854	90.6
	Gizzard shad	420.483	15.8	13.961	30.1
	Unidentified fish	447.125	16.8		
	Invertebrates	207.648	7.8		
	TOTALS	2,666.225	100.0		179.3
7	Yellow perch (1)	22.903	1.0	20.667	1.1
	Yellow perch (2)	31.862	1.4	57.502	0.6
	Round goby	532.690	24.2	17.085	31.2
	Rainbow smelt	69.169	3.1	6.505	10.6
	Alewife	1,070.663	48.6	7.729	138.5
	Gizzard shad	311.037	14.1	20.075	15.5
	Unidentified fish	153.017	6.9		
	Invertebrates	11.366	0.5		
	TOTALS	2,202.707	100.0		197.5
8	Yellow perch (1)	25.594	1.0	20.667	1.2
	Yellow perch (2)	35.606	1.4	57.502	0.6
	Round goby	594.696	24.2	5.819	102.2
	Rainbow smelt	77.179	3.1	7.458	10.3
	Alewife	1,195.233	48.6	12.263	97.5
	Gizzard shad	347.625	14.1	20.369	17.1
	Unidentified fish	170.937	6.9		
	Invertebrates	12.675	0.5		
	TOTALS	2,459.544	100.0		228.9

**Appendix H.** (continued).

WAE age	Prey category (age-class)	$C_B$ (g)	Percent (%) of total $C_B$	Mean weight of prey (g)	$C_N$
9	Yellow perch (1)	29.780	1.1	20.667	1.4
	Yellow perch (2)	41.429	1.5	57.502	0.7
	Round goby	672.177	24.0	15.505	43.4
	Rainbow smelt	85.731	3.1	14.788	5.8
	Alewife	1,348.127	48.2	16.728	80.6
	Gizzard shad	407.316	14.6	19.348	21.1
	Unidentified fish	197.585	7.1		
	Invertebrates	13.794	0.5		
	TOTALS	2,795.939	100.0		153.0
10-20	Yellow perch (1)	32.478	1.0	20.667	1.6
	Yellow perch (2)	45.184	1.4	57.502	0.8
	Round goby	755.064	24.2	10.187	74.1
	Rainbow smelt	98.029	3.1	10.906	9.0
	Alewife	1,517.655	48.6	18.277	83.0
	Gizzard shad	440.994	14.1	18.546	23.8
	Unidentified fish	216.898	6.9		
	Invertebrates	16.108	0.5		
	TOTALS	3,122.410	100.0		192.3

**Note:** Numeric table entries were rounded and may not equal the totals within each age-class.