Impacts of a recovering walleye population on an altered forage fish community in Saginaw Bay, Lake Huron

by

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ABSTRACT

This study was designed to characterize the available forage base and predatory demand by walleye in Saginaw Bay to deduce impacts of their consumption on the forage fish community during May through September 2009. Walleye relied heavily age-0 yellow perch and round goby, a reflection of the fish community abundance in 2009, to achieve observed growth. In conjunction with observed growth and monthly diet data, a walleye population size range was estimated based on minimum, mean, and maximum fishing mortality rates documented by MDNR over a 23-year period and the known number of walleye harvested in 2009 to model range of predatory demands. Based upon the predatory demand range calculated for the walleye population estimates compared to the range of prey population estimates, walleye consumption did not appear to play a significant role in age-0 and -1+ yellow perch mortality in 2009. However, other species like emerald shiner, rainbow smelt, round goby, and salmonids had periods of strong predation pressure and were possibly controlled by walleye. These other prey species provided alternative forage for the walleye and buffered yellow perch from strong predation pressure that has been observed in other systems when yellow perch were abundant.

INTRODUCTION

Predators are important in structuring aquatic communities (Popova 1978; Clepper 1979; Robinson and Tonn 1989). Piscivory creates a direct effect on prey populations by lethally removing individuals (Tonn et al. 1992). Introductions of new or changes in existing piscivore populations can alter prey consumption patterns (Zaret and Paine 1973; He and Kitchell 1990; Ward et al. 2008), with impacts on forage fish community structure (He and Kitchell 1990; Goeman and Spencer 1992). Known responses in forage fish assemblages due to predation are shifts in abundance, species diversity, and recruitment strength (Forney 1974; Lyons and Magnuson 1987; Skov et al. 2002). These general effects have stimulated studies of important piscivores and their predatory demand to understand their direct effect on aquatic communities for better management (Hartman and Margraf 1992; Miller and Holey 1992; Liao et al. 2004).

Walleye *Sander vitreus* are economically important piscivores (Latta 1990). Piscivory can begin at relatively small sizes between 20mm and 30mm (Smith and Pycha 1960; Walker and Applegate 1976; Li and Ayles 1981; Mathias and Li 1982; Graeb et al. 2005) depending on available forage fish sizes (Priegel 1969; Mathias and Li 1982). Once walleye become piscivorous, they prefer to feed on soft-rayed fishes such as cyprinids, ciscoes, and clupeids (Forney 1974; Knight et al. 1984; Knight and Vondracek 1993); however, in some systems walleye have been known to be a major predator of spiny-rayed yellow perch *Perca flavescens* (Forney 1974). Walleye will also revert to consuming invertebrates to supplement their diets when forage fish abundances are low (Forney 1974; Ward et al. 2008).

When predatory demand by walleye is strong they may control prey populations (Forney 1974; Nielsen 1980; Ward et al. 2008). Predatory demand generally increases with population density, but can be strong at smaller population size depending on age-structure, age-specific consumption rates, and temperature regimes (Hartman and Margraf 1992; Kershner et al. 1999). Predatory demand by walleye controls prey populations directly, both through mortality on adult stocks and reduced recruitment potential by consuming age-0 fish (Walker and Applegate 1976; Lyons and Magnuson 1987; Hartman and Margraf 1992). Adult walleye can select and control a wide range of prey sizes and ages, while juveniles feed primarily on age-0 individuals or fish species with small terminal sizes (Lyons and Magnuson 1987; Schneider and Breck 1993). Even with greater gape limitations than adults, juveniles can exert control on prey populations due to faster growth rates and large cohort sizes (Nielsen 1980; Hartman and Margraf 1992; Ward et al. 2008).

Predatory control by walleye can cause shifts in species diversity and prey abundance and these changes in community structure are reflected in their diets (Ward et al. 2008). Conversely, variations in prey community diversity and walleye diet composition may not be driven by predation effects, but instead seasonal shifts in forage species abundance (Walker and Applegate 1976; Knight et al. 1984; Knight and Vondracek 1993). Tools are available to managers to assess whether observed variations in prey community structure are indeed impacts of predatory demand (Knight et al. 1984; Liao et al. 2004). One tool frequently utilized to evaluate predator-prey interactions is bioenergetic modeling.

Bioenergetic models are employed to assess predatory demand based on a mass-balance equation:

$$G = C - (M + U + F)$$

where G is specific growth, C is specific rate of consumption, M is metabolic demands, U *is* excretion and F is egestion (Kitchell et al. 1977; Stewart et al. 1981; Ney 1993). Bioenergetic models create estimations of predatory demand through utilization of inputs of physiological and field collected data including water temperature, predator and prey energy densities, predator metabolic parameters, mean weight change over study period, and prey proportional representation by wet weight in diets (Kitchell et al. 1977; Lyons and Magnuson 1987; Hartman and Margraf 1993; Kershner et al. 1999). Total predatory demand can be estimated by including inputs of population size and mortality rates in the model (Hartman and Margraf 1992). Analysis of total predatory demand 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 28.4-89.7%

reduction in abundance of age-0 yellow perch. Ward et al. (2008) showed introduction of age-0 walleye could suppress fathead minnow *Pimephales promelas* populations within a year by consuming up to an estimated 64% of production, and continued introduction of age-0 walleye maintained suppression. Lyons and Magnuson (1987) used bioenergetic models to conclude that walleye accounted for 100% of darter (Pericdae) mortality in Sparkling Lake, Wisconsin.

Walleye are a native predator to Saginaw Bay, Lake Huron, but the population collapsed in the 1940s and was supported by stocking until recently (Schneider and Leach 1977; Fielder 2002; Fielder et al. 2007). From 2003-2005, walleye produced three consecutive strong year classes where majority of age-0 fish (~ 80%) were wild and age-0 walleye abundances were the highest ever recorded (Fielder and Thomas 2006). Those years coincided with a combination of low abundance of alewife *Alosa pseudoharengus* (a known predator of larval walleye) and favorable weather for reproduction (Fielder and Baker 2004; Fielder et al. 2007). Multiple strong walleye year classes have been produced since 2003 and dominate Saginaw Bay as indicated by increases in catch per unit effort (CPUE) of older cohorts during fall surveys (Baker and Fielder 2007). Walleye stocking ceased in 2006 due to rearing facility disease concerns, but never resumed because natural recruitment now supports Saginaw Bay's walleye population (Baker and Fielder 2007).

Yellow perch are another economically important percid in Saginaw Bay; however, unlike walleye, yellow perch did not experience a fisheries collapse or receive stocking assistance. Instead, a general increase in perch density was observed during 1970-1990 leading to slower growth rates, high mortality rates, and a greater number of small unharvestable fish; this was likely a consequence of a lack of large benthic invertebrates that serve as their prey (Salz 1989; Schaeffer et al. 2000; Fielder and Thomas 2006). Growth conditions improved in the 1990s following a decline in abundance from 1989–1991, but there was an overall decrease in recruitment through the decade (Fielder and Thomas 2006). Yellow perch, like walleye, experienced concurrent strong recruitment during the early 2000s when average catch rate of age-0 yellow perch in trawls was 3.47 times greater than previous records (2,390 fish per ten-minute tows in 2003) while adult catch rate dropped from 321.4 to 20.7 fish per ten-minute trawl fish on average during from 1993 to 2004 (Fielder and Thomas 2006).

Strong age-0 walleye production translated into increased adult walleye density; however adult yellow perch density remained low despite several consecutive apparently strong year classes (Fielder and Thomas 2006). Yellow perch and walleye coexist in many freshwater systems and have been linked together via predator-prey interactions with walleye consuming yellow perch when yellow perch densities are high or more favorable prey are scarce (Forney 1974; Nielsen 1980; Knight et al. 1984; Hartman and Margraf 1993). Recent increases in juvenile and adult walleye abundances, increases in abundance of age-0 yellow perch, and alewife disappearance in Saginaw Bay may have created an environment similar to other studies where walleye consumption limits yellow perch recruitment.

Michigan Department of Natural Resources, Fisheries Division (MDNR) had management goals of maintaining harvestable populations of both walleye and yellow perch in Saginaw Bay because both species are preferred by recreational anglers (Latta 1990). It became imperative to know if the resurgence in walleye might be hindering yellow perch recruitment due to strong predatory demand.

This analysis sought to provide insight into predatory demand of a large and expanding walleye population on the prey fish community in Saginaw Bay, particularly yellow perch. My study objectives were to 1) characterize potential walleye population size range based on mean, minimum, and maximum estimates of fishing mortality, mean growth of age classes, monthly diets, and range of population predatory demand, and 2) determine if walleye predatory demand affected abundances of its dominant prey species in 2009.

METHODS

Study Area

Saginaw Bay, a large, shallow embayment off of the main basin of Lake Huron, is delineated into inner and outer bays that evenly divide 2,960 km^2 of total surface area (Dobiesz et al. 2005). Inner Saginaw Bay is moderately eutrophic and has a mean depth of 4.5 m with isothermic conditions due to frequent wind mixing made possible by a high surface to volume ratio (Beeton et al. 1967; Haas and Schaeffer 1992). The outer bay is deeper and reflects conditions common in Lake Huron with inputs of cooler water from Lake Huron causing surface water temperatures to be 3^{o}C to 4^{o}C cooler than the inner bay temperatures (Beeton et al. 1967).

Saginaw Bay is home to a diverse assemblage of native and exotic species of prey for walleye. Invasive alewife was an abundant prey source until its disappearance in 2003 (Fielder et al 2007). Additional soft-rayed fishes include native gizzard shad *Dorsoma cepedianum*, emerald shiner *Notropis atherinoides*, and spottail shiner *Notropis hundsonius*. Spiny-rayed forage includes trout-perch *Percopsis omiscomaycus*, age-0 freshwater drum *Aplodinotus grunniens*, non-native age-0 white perch *Morone americana*, age-0 white bass *Morone chrysops*, and age-0 yellow perch *Perca flavescens* (Fielder and Thomas 2006). Recent additions to Saginaw Bay include zebra mussel *Dreissena polymorpha*, quagga mussel *Dreissena rostriformis*, and round goby *Neogobius melanostomu* (Fielder and Thomas 2006).

Field Sampling

Predatory demand was estimated during May-September 2009 for walleye aged 1 to 6+ using bioenergetic models based on data collected from Saginaw Bay. Data from both MDNR and National Oceanic and Atmospheric Administration (NOAA) field collections were employed to provide a better spatial and temporal coverage of size classes and diets. A creel survey conducted by MNDR during May through August 2009 provided seasonal weight, diet, and population data for age-3+ walleye. MDNR surveys followed creel methods outlined initially by Ryckman (1986) and updated by Lockwood (2000). Diet contents were identified to lowest practical taxon (usually family for invertebrates and zooplankton and species for fish). Total, standard, or backbone lengths of prey items were measured during collection to back-calculate prey wet weight at capture. Fin rays and scale samples were also collected for age determination during MDNR creel surveys.

NOAA trawled Saginaw Bay from May-September (Figure 1) to collect diet, age, and weight data for age-1+ walleye while also documenting forage fish abundance. Two to four hauls were performed once a month at 15 stations for a total of 73 tows. NOAA trawling gear consisted of a semi-balloon otter bottom trawl with a headrope of 7.62 m and 32 mm stretched mesh cod-end. The net was towed on the bay bottom for ten minutes at about 4.63 km/h, with a gape width of 7.62 m sweeping an area of 0.056 hectares (ha). Captured fish were immediately identified to species, counted, and walleye were frozen for further analysis.

Gill nets were deployed during September 2009 by MDNR research vessel *Chinook* to collect age-1+ walleye for diet, age, and weight data. Eighteen sites were sampled (Figure 1) using nets measuring 335 m with 30.48 m panels of 3.8, 5.1, 5.7, 6.4, 7.0, 7.6, 8.3, 8.9, 10.2, 11.3, and 12.7 cm mesh that were deployed for 24 hours. Walleye total length (mm), maturity, wet weight (g), presence of food, and gut contents were examined and recorded immediately after net lifts. Stomach contents were frozen for further analysis. Scale and fin clip samples were also collected.

September trawl surveys were conducted from the MDNR research vessel *Channel Cat.* The *Channel Cat* performed twenty-two trawls (Figure 1) with gear consisting of a 10.66 m headrope two-seam otter trawl with 4.6 m wings and 18.9 m overall length, constructed of 76 mm, 38 mm, and 32 mm graded stretched measure mesh from gape to cod-end with a 9 mm stretched mesh liner in the cod-end. The net was towed on the bottom for 10 minutes at a speed of about 3.7 km/h, sweeping an area of 0.34 ha, and catches were processed immediately. Walleye total length (mm), maturity identified from expressed gonads, wet weight (g), and presence of food were determined then gut contents were frozen for analysis. Scale and fin ray samples were removed from age-1+ walleye to determine age. Forage fish were counted and total weight of each species was recorded to determine catch per unit of effort (CPUE) and mean individual weight.

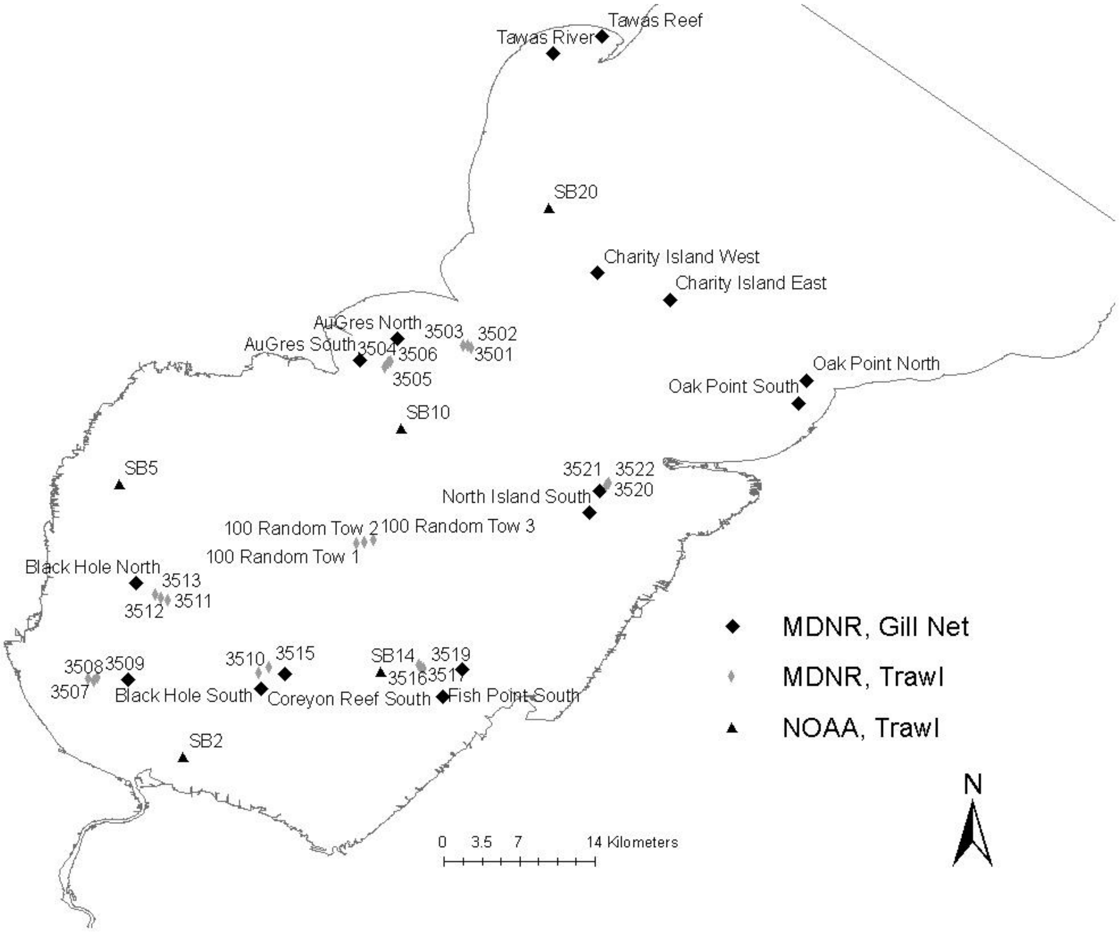

Figure 1. MDNR and NOAA sampling points utilized in 2009 for fish collections in Saginaw Bay, Lake Huron.

Modeling

Total prey consumption by an individual walleye in g from each age class was estimated using *Fish Bioenergetics 3* (Hewett and Johnson 1992) for May through September 2009, hereafter referred to as the Wisconsin model (Hewett and Johnson 1992). The model is derived from Kitchell et al.'s (1977) energetic model.

Energetic models of individual walleye require inputs of water temperature, predator and prey energy densities, predator metabolic parameters, mean weight change over the study period, and prey proportional contributions to wet weights of diets. Daily mean water temperatures were obtained from the Bay City municipal water treatment plant. Isothermic conditions are common in the bay due to the large surface-to-volume ratio that allows it to be mixed by the wind, so temperatures obtained from the water treatment plant were likely representative of the entire bay (Schaeffer 1994).

Energy densities for walleye and their prey were obtained from Schaeffer et al. (2000). Values for metabolic parameters of mature and immature walleye were those recommended by Hewett and Johnson (1992). Spawning events were not included in the model since spawning occurred prior to May.

Aging of fish was required to determine monthly mean weights and ascribe diets to particular age groups. MDNR and NOAA assigned ages to a subsample of walleyes using scales, which were cleaned then pressed onto acetate slides (Schneider 2001). All identifiable annuli were counted and totaled to estimate age (Schneider 2001).

Walleye growth was calculated from cohort-specific changes in mean weight between successive months or years depending on data available. Monthly mean weights were available during May through October for ages 1, 2, and 3, but only annual changes in mean weight were available for ages 4, 5, and 6. NOAA trawl samples were used for monthly mean weight data for age-1 and age-2 fish for May through August, while MDNR fall gillnet and trawl surveys provided mean weights for age-1 and age-2 walleye in September. Monthly mean weights were obtained from angler-caught walleye for age-3 fish for May through September and additional September weight data came from MDNR gill net and trawl samples. May 2009 mean weight data for ages 4, 5, and 6 were extrapolated from the combined September 2008 MDNR gillnet and trawl surveys.

Dietary proportions by wet weight were required inputs for a bioenergetic model. Evaluation of wet weight proportions began with identifying stomach contents to lowest possible taxon and counting the number of individuals of each taxon present in each stomach. Partially digested fish were identified using spines, vertebrae, and cleithra. Standard length or backbone length of prey fishes were measured, depending on degree of digestion, for use in regression equations to back calculate total length (Knight et al. 1984; Knight 2010). Prey total lengths were used to estimate wet weights at capture (Hartman and Margraf 1992). Benthic invertebrates were identified to lowest practical taxon, counted, and weighed.

Dietary proportions were estimated for walleye age classes 1, 2, or 3+ via partitioning to describe monthly dietary prey proportions by weight for May through September 2009. Identified prey fish lacking length data were assigned the average weight of the same species for the specific age group and month they were consumed. Unidentified fish were apportioned to a species based on the numeric proportions of identified prey species found in each age class by month and assigned the mean weight for individuals of that species. These estimated wet weights of unidentified prey fish and prey lacking wet weights were added to the initially summed prey weights to create total prey wet weight by species. Dietary proportions were estimated for each species by dividing the wet weight of each prey class by the total wet weight of prey consumed by a specific age group of walleye during a specific month.

Age groups analyzed for predatory demand were ages 1 to 6+ with specific inputs for diet and growth. All age groups were considered to be adults and fitted with adult metabolic parameters. Ages 3 to 6+ walleye were assigned pooled age 3+ diet. Age-6+ walleye were assigned growth observed for the age-6 cohort. Linear growth was assumed for walleye age-4+ due to lack of monthly data. The model calculated daily consumption of an individual walleye from each age group during May through September 2009. Each month and age group was fitted with a different proportion of maximum consumption (*P*-value) based on fitting either annual or monthly growth. Ration required to support observed growth was estimated for each age-class each month using mean weight of each group except for age classes where only annual growth was calculated.

Model predictions of consumption produced for individuals within each age class were extrapolated to model total consumption by the walleye population using the formulas:

$$N = N_{3+} + N_2 + N_1$$

$$N_{3+} = n/m_f$$

$$N_{3+} = N_3 + N_3S + N_3S^2 + N_3S^3$$

$$S = 1- m_t$$

$$m_t = m_n + m_f$$

$$N_2 = N_3/m_n$$

$$N_1 = N_3/m_n^2$$

Yearly total harvest of walleye from all sources was used to estimate the walleye population size (N) based on a fishing mortality rate (m_f). N was calculated by creating estimates of population sizes for age-3+ walleye (N_{3+}), age-2 walleye (N_2), and age-1 walleye (N_1). N_{3+} was estimated by dividing total walleye harvested (n) by the fishing mortality rate (m_f). Fishing mortality was derived from tag returns by the MDNR and only applied to age-3+ walleye. Survival (S) was calculated by subtracting the average total mortality rate (m_t) for walleye (Fielder and Thomas 2013); m_t is the sum of natural mortality (m_n) and m_f. N_2 was calculated by solving for N_3 and diving by m_n. N_1 was calculated by dividing N_3 by m_n^2. The population range of walleye was estimated via these formulas using minimum, mean, and maximum fishing mortality rates calculated from a 23-year period of annual assessments and assuming total mortality remained constant (MDNR unpublished data).

Monthly prey fish CPUE data collected during the NOAA trawls were used to estimate population size ranges of forage species in Saginaw Bay. Trawls were pooled by month and mean CPUE for emerald shiner, rainbow smelt, round goby, age-1+ yellow perch, and age-0 yellow perch were calculated. Minimum, mean, and maximum overall CPUEs for the study period of May to September 2009 were calculated for the five previously listed groups. Total area of Saginaw Bay was divided by trawl area swept then multiplied by species specific minimum, mean, or maximum CPUE to create a minimum, mean, and maximum abundance for each prey species.

The estimated range of species specific predatory demand by walleye age-classes was converted to number of fish consumed each month by dividing mass consumed by monthly mean weight of that species. Number of emerald shiner, rainbow smelt, round goby, age-1+ yellow perch, and age-0 yellow perch consumed per month by walleye were compared to the estimated range of prey populations determine the range and median percent of available prey population consumed by walleye. Total number of salmonids stocked which included lake trout *Salvelinus namaycush*, brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*, and Chinook salmon *Oncorhynchus tshawytscha* was used as a surrogate for a population range estimate for comparison to the range of walleye predatory demand to calculate percentage of the salmonid population consumed for May and June since salmonids were not collected in trawls.

Statistical Methods

Differences in walleye size caused by biases in the sampling gears were tested using one-way analysis of variance (ANOVA). Tukey's test was utilized for post-hoc group comparisons. All statistical analyses were performed using Statistical Package for Social Scientists (IBM SPSS Statistics 20.0 2011) with alpha = 0.05 to minimize rejection of a correct null hypothesis.

RESULTS

During May through September 2009, 1068 walleye were collected from Saginaw Bay. Creel surveys collected larger fish compared to other gear types (Table 1). NOAA collected the smallest fish when compared to other gears' mean lengths. Mean lengths among gears were significantly different ($p < 0.001$), and Tukey's test indicated significant length differences between all groups except NOAA and MDNR trawls ($P = 0.083$). These differences in mean size reflect older fish taken in some of the sampling techniques.

Proportion of fish containing food varied among months with percent full increasing towards the end of the study for age-1 and -2 walleye. Age-1 walleye maintained at least 70% stomach fullness during four of five documented months (Table 2). Age-2 walleye stomachs were void during June (although only four fish were sampled); also only one stomach containing food was collected in August. The highest percentage of stomachs with food items occurred during July for age-2 walleye (79%). Age-3+ walleye had fewer void stomachs during May, and the lowest proportion of age-3+ fish with stomach contents was in June (26%).

Water temperatures for Saginaw Bay warmed from 11.6^{o}C in May to a peak of 25.0 ^{o} C during June and dropped to 18.1 ^{o} C at the end of September (Figure 2). Water temperatures varied the most during June (16.1-25.0 ^{o}C).

A subsample of 551 walleye from MDNR collections and 165 walleye from NOAA collections were aged during 2009. Monthly growth data were available for age classes 1, 2, and 3 from a combination of these data (Figure 3). Only annual growth data were estimated for age classes 4, 5, and 6. Starting weights for age classes 4-6 were taken from the fall 2008 MDNR Saginaw Bay survey. All age classes except 4 (which decreased in mean weight by 6.75%) showed positive growth. Consequently, I assumed that age-4 for fish exhibited no annual growth for bioenergetics modeling. Age-1 walleye increased 200% in weight (82.78 g) and age-3 walleye increased by 22% (79.34 g). Age-2 walleye gained less total weight (76 g) than age-3, but increased by a greater percentage of body weight (29%).

Walleye frequently contained age-0 and 1+ yellow perch, emerald shiner, round goby, rainbow smelt, salmonids, zooplankton, and macroinvertebrates in their stomachs, and diet composition varied among months and age classes. Based on weight, age-1 walleye consumed large amounts of round goby in all months, followed by age-0 yellow perch, and emerald shiner (Figure 4). Sufficient age-2 walleye stomachs were collected to provide data to describe only July and September diets and large quantities of age-0 yellow perch were consumed at those times followed by round goby (Figure 5). August diet proportions were estimated to be an average between age-2 July and September data while June diet was an average of age-1 and age-3+ diets for June. Age-3+ walleye stomachs contained a greater prey variety than younger age classes, with round goby, emerald shiner, salmonids, age-1+ yellow perch, age-0 yellow perch, rainbow smelt, gizzard shad, and other fish which included white perch *Morone americana*, white bass *Morone chrysops*, freshwater drum *Aplodinotus grunniens*, walleye, mottled sculpin *Cottus bairdii*, and bloater *Coregonus hoyi* (Figure 6).

I used the Wisconsin bioenergetic model to estimate consumption needed to account for observed growth during May-September 2009 for an individual walleye from each age group. P-values (proportion of maximum consumption) varied from 0.15 to 0.64 and differed among age groups and months (Table 3). P-values were estimated for walleye age-groups 1-4 based on monthly growth data. There was not a consistent temporal trend for each age class of walleye. P-values for age-1 walleye increased from June to July then decreased thereafter. Age-2 walleye reached their maximum p-value in July, and then decreased in value during August and September. P-values for age-3 walleye steadily decreased until July then increased in August and September. Age-4 walleye showed a slight temporal increase in P-values among months.

An individual age-1 walleye required approximately 328 g of prey to achieve observed growth from May through September. The majority of biomass it consumed was obtained from round goby (48%) and age-0 yellow perch (31%) (Table 4). An age-1 walleye consumed 157 g of round goby and 116 g of age-0 and 1+ yellow perch. Cannibalism accounted for 30 g of their consumption, emerald shiner 20 g, while macroinvertebrates and other species made minor contributions.

An individual age-2 walleye consumed 636 g of biomass over four months (Table 4). It relied heavily on age-0 yellow perch (55%) followed by round goby (29%). Age-2 walleye consumed 19 g of emerald shiner and salmonids compromised 42 g. Macroinvertebrates made a larger contribution (4%) to biomass consumed than rainbow smelt (2%).

Table 1. Mean lengths of walleye collected in Saginaw Bay, Lake Huron by gear during 2009.

		Length (mm)		
Gear	**N**	**Mean**	**Minimum**	**Maximum**
MDNR Creel	653	474.5	375.0	1104.9
MDNR Gill Net	251	408.1	239.0	605.0
MDNR Trawl	13	349.9	217.0	483.0
NOAA Trawl	137	301.1	154.0	541.0

Table 2. Percent of fish with food in their stomachs by age group for walleye collected during May-September 2009 from Saginaw Bay.

	Age-1		**Age-2**		**Age-3+**	
Month	**Total Fish Collected**	**Percent with Food (%)**	**Total Fish Collected**	**Percent with Food (%)**	**Total Fish Collected**	**Percent with Food (%)**
May	5	40	2	50	129	43
June	7	71	4	0	199	26
July	37	81	14	79	144	33
August	5	100	1	100	156	29
September	17	76	49	65	293	39

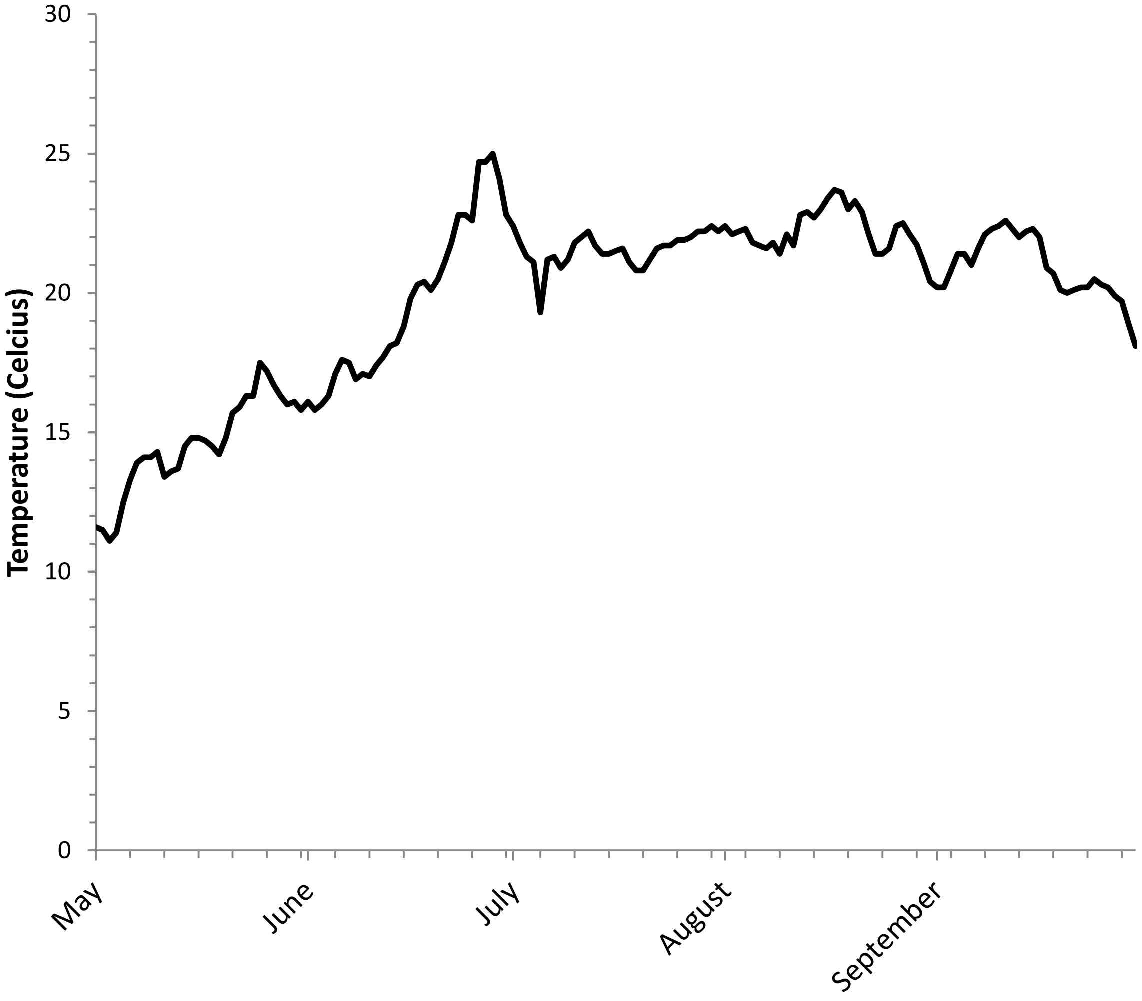

Figure 2. Daily mean water temperatures for Saginaw Bay, Lake Huron from May-September 2009 taken at the Bay City water treatment plant.

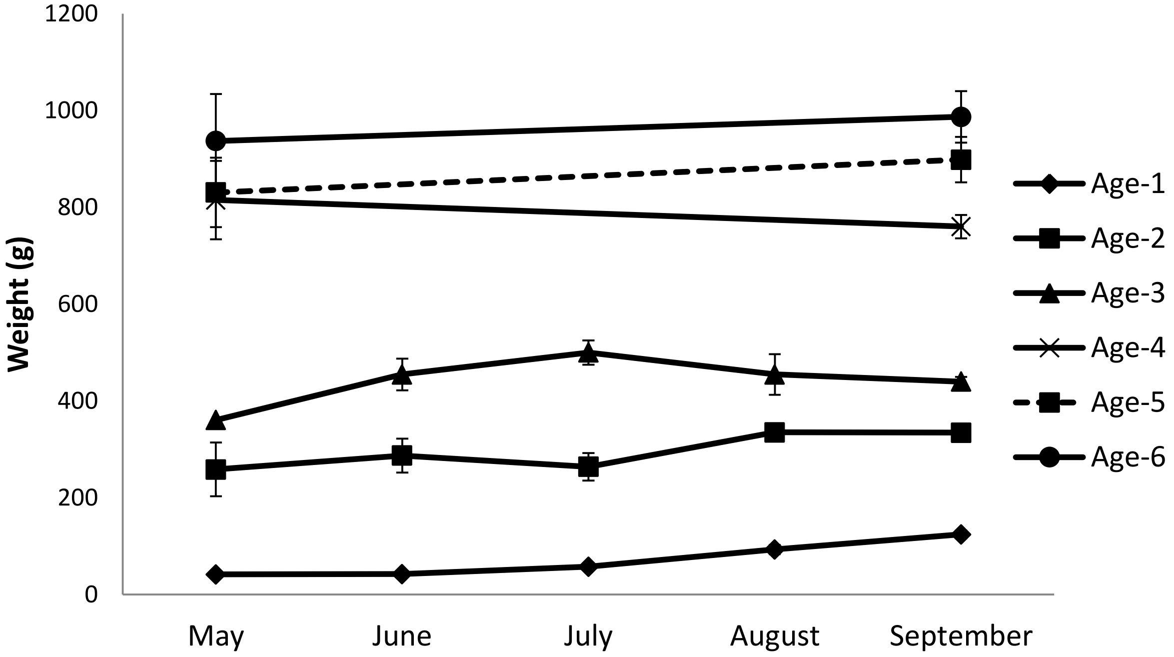

Figure 3. Mean weight of each walleye age-class with standard error bars by month during May-September 2009, Saginaw Bay, Lake Huron.

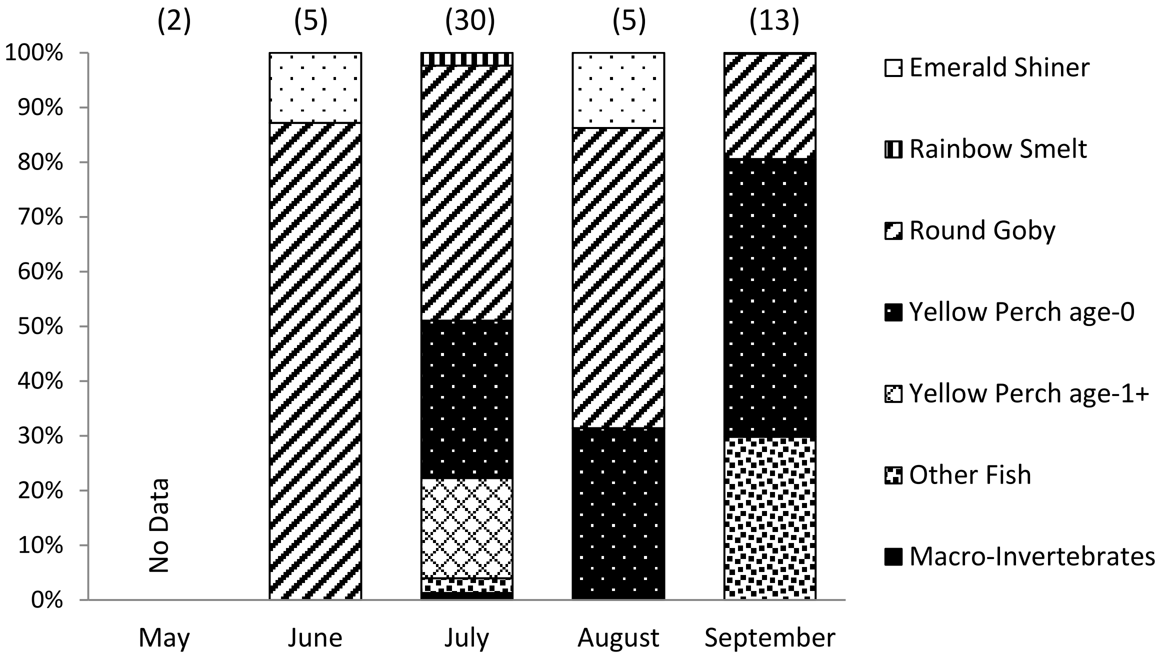

Figure 4. Percent contribution by wet weight of individual prey types to age-1 walleye diets. Number above each bar is total sample size.

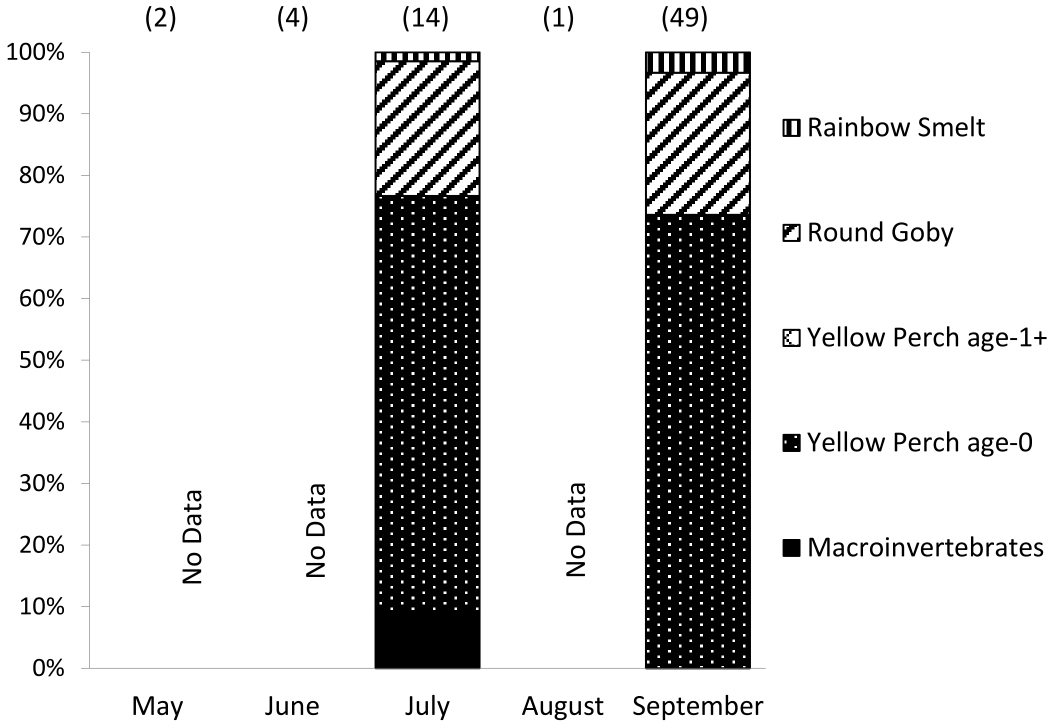

Figure 5. Percent contribution by wet weight of individual prey types to age-2 walleye diets. Number above each bar is total sample size.

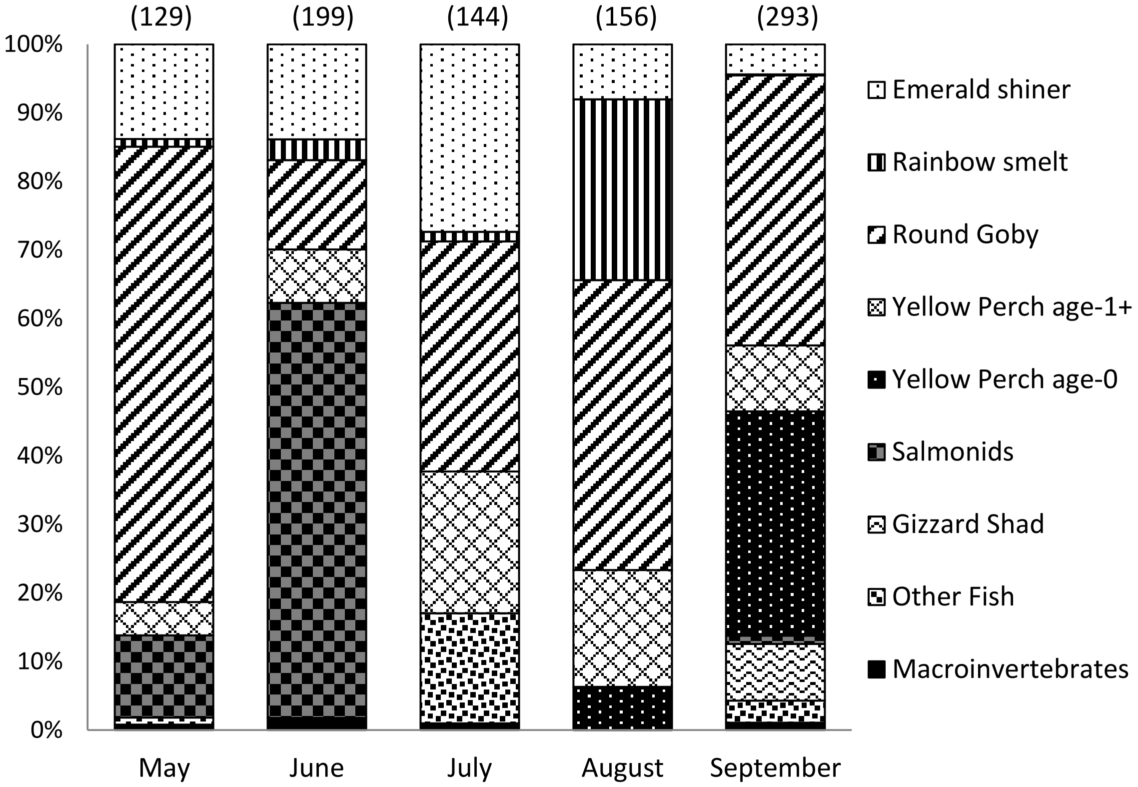

Figure 6. Percent contribution by wet weight of individual prey types to age-3+ walleye diets. Number above each bar is total sample size.

Table 3. P-values for walleye age classes 1-4 during 2009.

Age group	**May**	**June**	**July**	**August**	**September**
Age 1	-	0.46	0.64	0.51	0.26
Age 2	-	0.27	0.55	0.29	0.28
Age 3	0.50	0.34	0.15	0.21	0.24
Age 4	0.24	0.25	0.30	0.32	0.30

Age-3, -4, -5, and -6 walleye individuals were assumed to consume the same diet proportions, but showed differences in total biomass consumed due to differences in observed weights. An age-3, -4, -5 and - 6 walleye consumed 885 g, 1337 g, 1509 g, and 1605 g of biomass, respectively, over the simulation period (Table 4). Age-3 to -6 individual predatory demand consisted of 36% round goby, 13% age-1+ yellow perch, 9% age-0 yellow perch, 13% salmonids, and 14% emerald shiner.

The three total mortality rates for walleye were 45%, 50%, and 55% and were calculated based on the minimum, mean, and maximum fishing mortality rates plus the natural mortality rate. The three different fishing mortality rates were derived from low, mean, and high rates from the MDNR dataset covering the years 1986 to 2009 (Table 5). Natural mortality was assumed to be 40% based on MDNR observations (unpublished data 2009).

A population range for walleye was estimated based on the total harvest of 288,243 walleye during 2009 and the three mortality rates estimated previously (Figure 7). Based on the minimum mortality rate of 45% an estimated 17,669,917 walleye existed in the bay. Using the mean fishing mortality rate of 10% plus the natural mortality rate of 40% the estimated population was 9,512,894 walleye. The maximum mortality rate led to an estimated population with 6,819,768 individuals.

Bioenergetic models using the same inputs for diet, temperature, and growth were used to create a range of consumption estimates based on the walleye population range calculated from different mortality rates. The walleye population consumed at a minimum 8,192,226 kg of prey (Table 6). Mean predatory demand for the walleye population was 4,273,270 kg of prey (Table 7). A total consumption of 3,026,803 kg of prey was the maximum estimated predatory demand exhibited by the walleye population (Table 8). Total biomass consumed was composed of about 39% round goby, 25% age-0 yellow, 10% salmonids, 9.5% emerald shiner, 7% age-1+ yellow perch, and 4% rainbow smelt. Age-2 walleye consumed the most prey biomass (28%) with age-1 walleye consuming slightly more than 23% while age-3 walleye accounted for 22% of the total.

Prey species composition was determined from data collected during monthly trawls performed by NOAA with MDNR September trawl data added for comparison. Total fish density collected during each period was apportioned to estimate species composition.

Trout-perch were the most abundant species collected during remained abundant through June-September (Figure 8). Age-1+ yellow perch were second in abundance during May and remained abundant over the summer, while round goby increased during June. Age-0 yellow perch were recruited to the trawl and comprised the largest proportion of prey collected during July and August followed by round goby which became the most abundant fish in September hauls. MDNR trawls differed from NOAA trawls during September, with MDNR trawls having smaller proportions of age-0 yellow perch, rainbow smelt, and round goby, but larger proportions of trout perch, spottail shiner, and white bass.

No trend in mortality could be determined for a given prey species to estimate a total population and some monthly CPUE data was lacking for specific prey species. Therefore, an overall minimum, mean, and maximum CPUEs were calculated (Table 9). Rainbow smelt had the highest maximum CPUE of all the prey species while emerald shiner had the lowest minimum CPUE. The minimum, mean, and maximum CPUEs for each prey species were used to calculate minimum, mean, and maximum prey population abundance for a single month (Figure 9). Age-0 and -1+ rainbow smelt population sizes were pooled resulting in the largest estimated population using the maximum CPUE. Using the mean and minimum CPUEs, age-0 yellow perch were estimated to have the largest population abundance followed by rainbow smelt and round goby.

Monthly data for abundances of each prey species and the maximum, minimum, and mean estimates of the number of each prey species consumed by the walleye population were compared to determine the mean and range of the percentage of the estimated prey population consumed by walleye (Figure 10, Appendix Tables 1-3). Assuming mean prey densities and mean predatory demands were correct, walleyes consumed 38% of the emerald shiner population, 9% of the round goby population, 5% of the age-0 yellow perch population,1% of the age-1+ yellow perch population, and1% of the rainbow smelt population. Large variances were observed for percentage of prey populations consumed. Emerald shiner was predicted experience a population consumption range of 1-13,630% while the ranges for rainbow smelt and round goby were 0.02-235% and 2.5-305%, respectively. Yellow perch had smaller ranges and lower maximums than the other prey species: consumption range for age-1 yellow perch was 0.1-22%, and consumption range for age-0 yellow perch was 0.8-29%.

Consumption of stocked salmonids greatly exceeded 100% of the number stocked in every comparison for May and June (Table 10). September percent consumption of salmonids was not analyzed due to lack of population data because none were trawled.

Table 4. Estimated biomass consumed by an individual walleye from each age group in Saginaw Bay for May-September 2009.

	Biomass (g) consumed							
Prey Type	age-1	age-2	age-3	age-4	age-5	age-6+	Total Consumed	Percent of Total
Emerald Shiner	20.1	18.7	120.3	184.0	206.6	220.1	769.7	12.2
Rainbow Smelt	2.1	14.1	62.4	92.6	105.2	111.6	387.9	6.2
Round Goby	156.9	182.1	332.8	504.1	568.4	604.7	2348.9	37.3
Yellow Perch Age-1+	14.3	5.4	112.7	169.0	191.2	203.1	695.7	11.0
Yellow Perch Age-0	101.9	349.6	76.0	109.5	126.0	133.2	896.1	14.2
Salmonids	0.0	42.0	116.9	183.6	204.0	218.1	764.7	12.1
Gizzard Shad	0.0	0.0	16.0	23.0	26.5	28.0	93.5	1.5
Walleye	29.8	0.0	3.8	5.7	6.4	6.8	52.5	0.8
White Perch	2.1	0.0	3.0	4.3	4.9	5.2	19.5	0.3
White Bass	0.0	0.0	3.8	5.7	6.4	6.8	22.7	0.4
Freshwater Drum	0.0	0.0	1.6	2.3	2.7	2.8	9.5	0.2
Mottled Sculpin	0.0	0.0	15.7	23.8	26.9	28.6	95.0	1.5
Bloater	0.0	0.0	10.2	15.3	17.3	18.3	61.1	1.0
Macroinvertebrates	1.0	23.6	8.0	12.2	13.7	14.6	73.2	1.2
Dressenids	0.0	0.0	1.6	2.6	2.9	3.1	10.2	0.2
Zooplankton	0.0	0.0	0.0	0.0	0.1	0.1	0.2	0.0
Total	328.2	635.5	884.8	1337.6	1509.1	1605.2	6300.2	99.8
Percent of total	5.2	10.1	14.0	21.2	24.0	25.5		

Table 5. Fishing mortality rates derived by the MDNR for walleye in Saginaw Bay from 1986 to 2009.

Year	Exploitation Rate
1986	0.11
1987	0.13
1988	0.11
1989	0.09
1990	0.08
1991	0.07
1992	0.15
1993	0.13
1994	0.07
1995	0.06
1996	0.07
1997	0.09
1998	0.10
1999	0.11
2000	0.09
2001	0.05
2002	0.12
2003	0.08
2004	0.07
2005	0.09
2006	0.10
2007	0.13
2008	0.14
2009	0.15
Mean	0.10
Minimum	0.05
Maximum	0.15

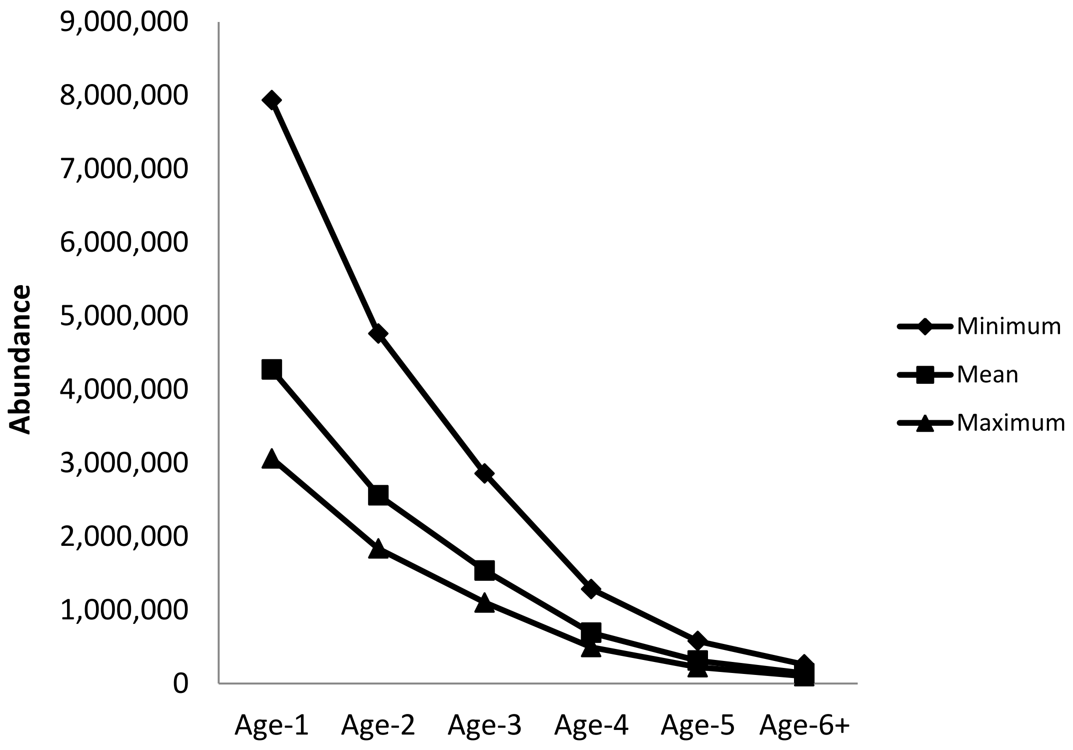

Figure 7. Walleye population size range estimated by different total and fishing mortality rates based on the number harvested in 2009.

Table 6. Estimated biomass consumed to satisfy maximum predatory demand of the walleye population in Saginaw Bay for May-September 2009.

	Biomass (kg) consumed							
Prey Type	age-1	age-2	age-3	age-4	age-5	age-6+	Total Consumed	Percent of Total
Emerald Shiner	120,594	75,948	264,034	182,524	92,055	44,159	779,315	9.5
Rainbow Smelt	12,795	47,583	121,427	81,290	41,526	19,834	324,454	4.0
Round Goby	945,674	660,233	703,759	483,711	244,623	117,257	3,155,257	38.5
Yellow Perch Age-1+	88,106	22,075	229,068	155,288	78,925	37,761	611,224	7.5
Yellow Perch Age-0	550,869	1,165,896	129,461	83,971	43,482	20,680	1,994,359	24.3
Salmonids	0	171,341	281,644	199,287	99,604	47,928	799,805	9.8
Gizzard Shad	0	0	26,738	17,260	8,957	4,257	57,212	0.7
Walleye	149,281	0	7,968	5,434	2,754	1,319	166,756	2.0
White Perch	0	0	4,974	3,211	1,666	792	10,643	0.1
White Bass	12,896	0	7,968	5,434	2,754	1,319	30,371	0.4
Freshwater Drum	0	0	2,713	1,751	909	432	5,805	0.1
Mottled Sculpin	0	0	33,383	22,766	11,537	5,524	73,209	0.9
Bloater	0	0	20,830	14,107	7,170	3,430	45,537	0.6
Zooplankton	0	0	74	53	26	13	165	0.0
Macroinvertebrates	6,111	84,995	17,348	11,986	6,047	2,901	129,388	1.6
Dresseinids	0	0	3,917	2,762	1,382	665	8,726	0.1
Total	1,886,327	2,228,071	1,855,307	1,270,835	643,417	308,270	8,192,226	100
Percent of total	23.0	27.2	22.6	15.5	7.9	3.8		

Table 7. Estimated biomass consumed to satisfy mean predatory demand of the walleye population in Saginaw Bay for May-September 2009.

	Biomass (kg) consumed							
Prey Type	age-1	age-2	age-3	age-4	age-5	age-6+	Total Consumed	Percent of Total
Emerald Shiner	64,924	40,888	136,512	88,978	47,616	22,844	401,761	9.4
Rainbow Smelt	6,888	25,617	61,545	38,836	21,053	10,056	163,995	3.8
Round Goby	509,119	355,448	362,238	234,900	126,017	60,416	1,648,137	38.6
Yellow Perch Age-1+	47,433	11,885	117,000	74,783	40,330	19,297	310,728	7.3
Yellow Perch Age-0	296,569	627,679	64,195	39,235	21,562	10,255	1,059,497	24.8
Salmonids	0	92,244	147,628	98,439	52,216	25,126	415,654	9.7
Gizzard Shad	0	0	13,212	8,036	4,426	2,104	27,778	0.7
Walleye	80,368	0	4,091	2,629	1,414	677	89,179	2.1
White Perch	6,943	0	2,458	1,495	823	391	12,110	0.3
White Bass	0	0	4,091	2,629	1,414	677	8,811	0.2
Freshwater Drum	0	0	1,341	815	449	213	2,819	0.1
Mottled Sculpin	0	0	17,140	11,014	5,924	2,836	36,914	0.9
Bloater	0	0	10,643	67,93	3,664	1,753	22,852	0.5
Zooplankton	0	0	39	26	14	7	85	0.0
Macroinvertebrates	3,290	45,759	8,959	5,838	3,125	1,499	68,469	1.6
Dresseinids	0	0	2,049	1,361	723	348	4,481	0.1
Total	1,015,535	1,199,519	953,141	615,806	330,769	158,499	4,273,270	100.0
Percent of total	23.8	28.1	22.3	14.4	7.7	3.7		

Table 8. Estimated biomass consumed to satisfy minimum predatory demand of the walleye population in Saginaw Bay for May-September 2009.

	Biomass (kg) consumed							
Prey Type	age-1	age-2	age-3	age-4	age-5	age-6+	Total Consumed	Percent of Total
Emerald Shiner	46,544	29,312	93,631	64,826	34,140	15,678	284,130	9.4
Rainbow Smelt	4,938	18,365	41,286	27,664	14,760	6,748	113,761	3.8
Round Goby	36,4986	254,819	247,344	170,496	89,986	41,300	1,168,932	38.6
Yellow Perch Age-1+	34,005	8,520	79,175	53,755	28,528	13,066	217,050	7.2
Yellow Perch Age-0	21,2610	449,982	42,024	27,264	14,749	6,714	753,342	24.9
Salmonids	0	66,130	102,765	72,745	37,982	17,493	297,115	9.8
Gizzard Shad	0	0	8,615	5,562	3,015	1,372	18,564	0.6
Walleye	57,616	0	2,783	1,898	1,005	461	63,763	2.1
White Perch	4,977	0	1,603	1,035	561	255	8,430	0.3
White Bass	0	0	2,783	1,898	1,005	461	6,147	0.2
Freshwater Drum	0	0	874	564	306	139	1,884	0.1
Mottled Sculpin	0	0	11,661	7,953	4,211	1,930	25,754	0.9
Bloater	0	0	7,203	4,881	2,591	1,186	15,861	0.5
Zooplankton	0	0	27	19	10	5	61	0.0
Macroinvertebrates	2,359	32,804	6,138	4,250	2,238	1,028	48,817	1.6
Dresseinids	0	0	1,423	1,004	525	242	3,193	0.1
Total	728,035	859,932	649,335	445,814	235,611	108,077	3,026,803	100.0
Percent of total	24.1	28.4	21.5	14.7	7.8	3.6		

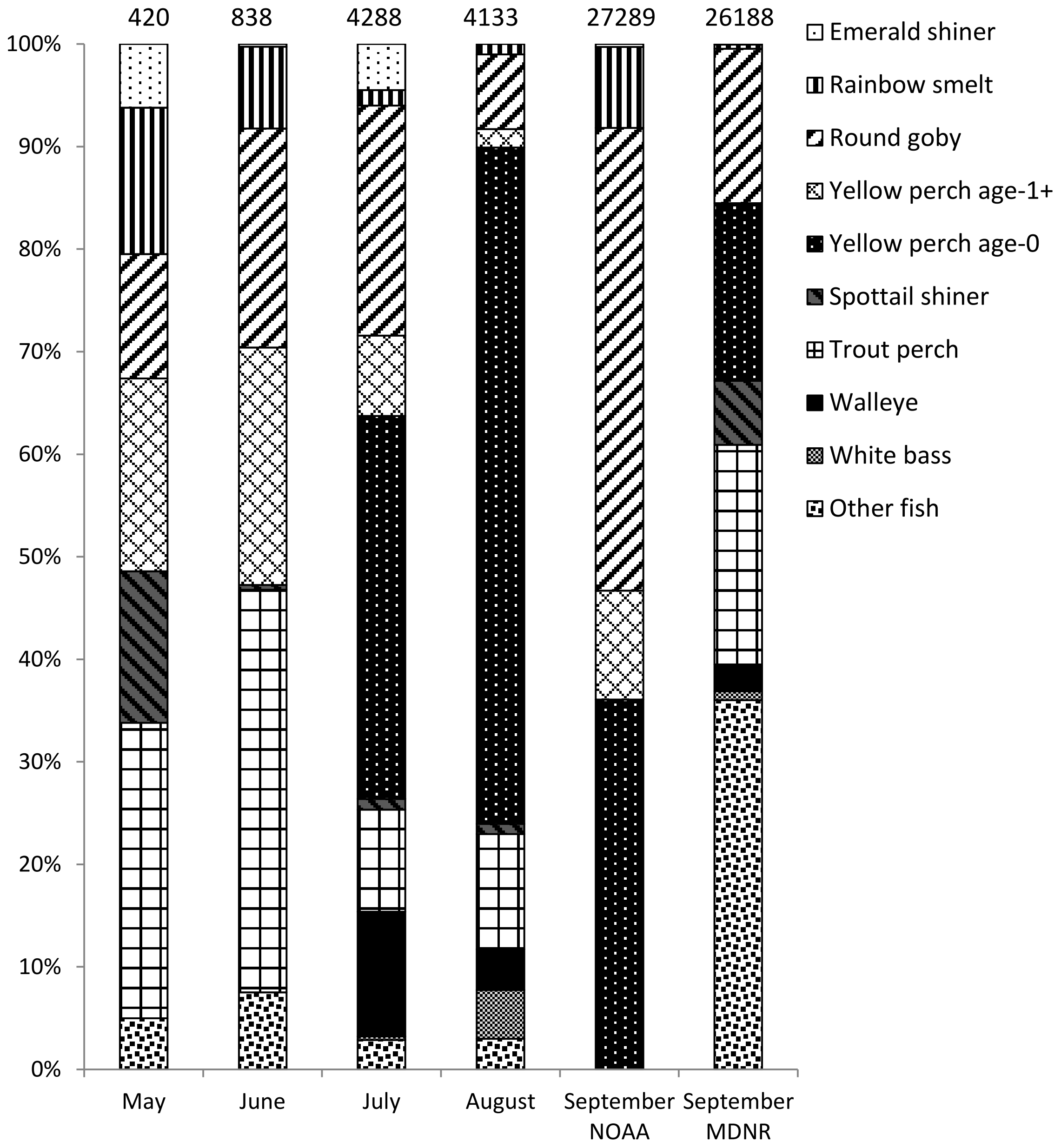

Figure 8. Trawl composition for prey species by number from 2009 NOAA trawls used in May through September, or MDNR trawls used in September 2009 in Saginaw Bay. Number above each bar is total sample size.

Table 9. NOAA trawl CPUEs for the six most common species in walleye diets.

Species	May Mean CPUE	June Mean CPUE	July Mean CPUE	August Mean CPUE	September Mean CPUE	Overall Mean CPUE	Overall Maximum CPUE	Overall Minimum CPUE
Emerald Shiner	1.73	0.02	7.91	0.00	1.06	2.14	7.91	0.02
Rainbow Smelt (age-1+)	4.20	0.59	2.54	1.74	176.56	37.13	176.56	0.59
Rainbow Smelt (age-0)	-	-	0.13	0.47	2.68	1.09	2.68	0.13
Round Goby	3.67	1.38	39.89	15.84	33.67	18.89	39.89	1.38
Yellow Perch (age-1+)	5.40	0.79	13.95	3.89	2.04	5.22	13.95	0.79
Yellow Perch (age-0)	-	-	65.57	143.47	80.19	96.41	143.47	65.57
Salmonids	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

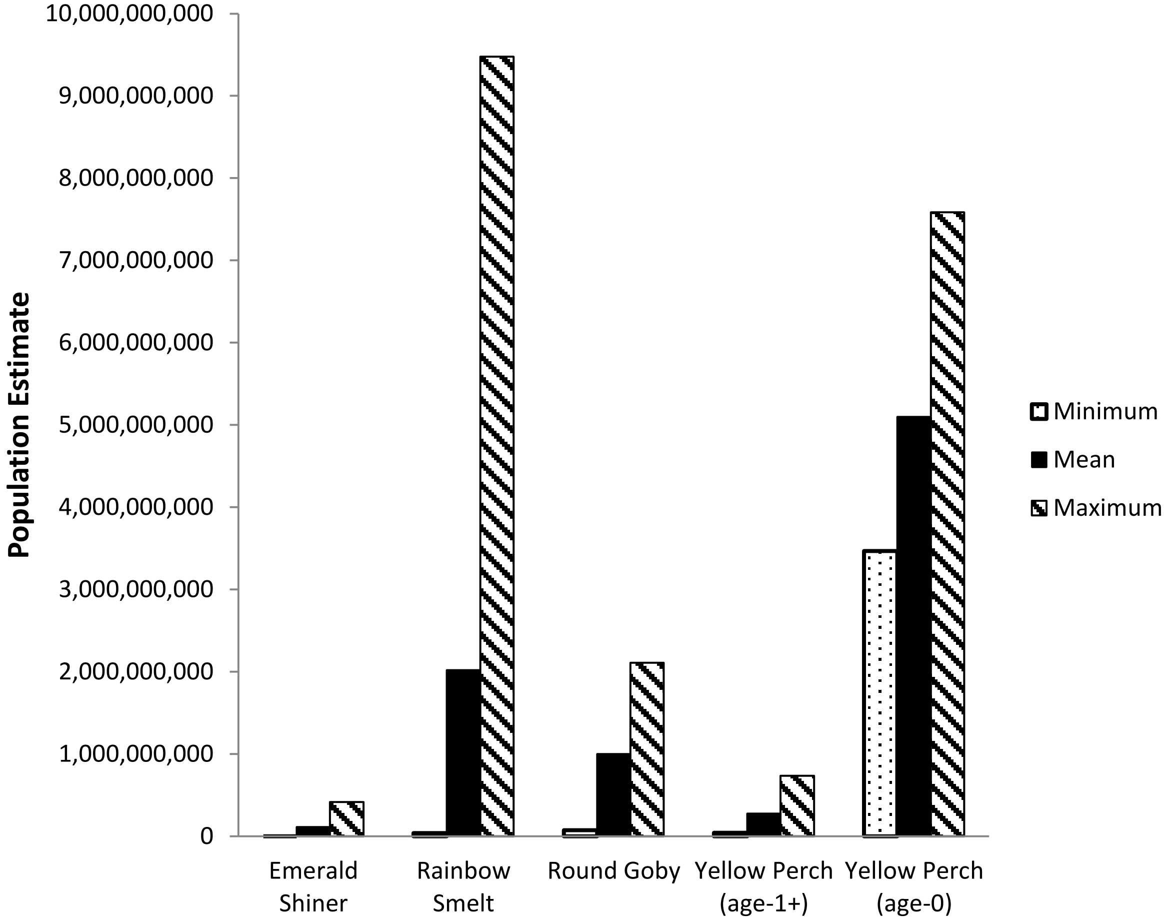

Figure 9. Prey fish population size range of the five most common species in walleye diets estimated using minimum, mean, and maximum CPUEs.

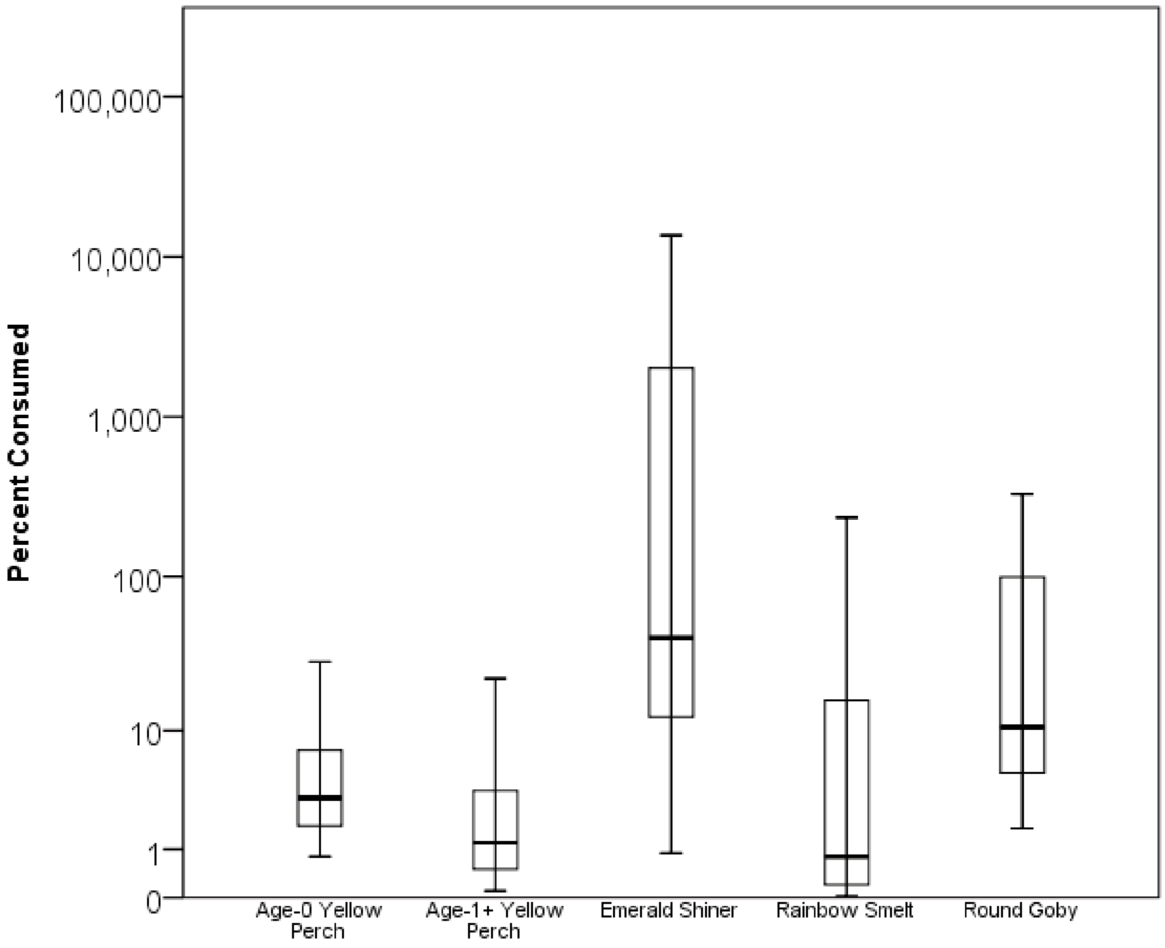

Figure 10. Box plot of percent of prey population consumed by walleye for the five most common species found in their diet in 2009. The dark horizontal bar represents the median, the bottom and top of the box are the 1st and 3rd quartiles, and the vertical bars depict the upper and lower value for 1.5 times the interquartile range.

Table 10. Comparison of number of stocked salmonids to predatory demand range of walleye for May and June 2009 in Saginaw Bay.

	May			June		
Walleye Predatory Demand	**Number Stocked**	**Number Consumed**	**Percent Consumed**	**Number Stocked**	**Number Consumed**	**Percent Consumed**
Maximum	255,839	10,626,502	4,154	434,523	11,705,870	2,694
Mean	255,839	5559,463	2,173	434,523	6,011,670	1,384
Minimum	255,839	404,5903	1,581	434,523	5,748,556	1,323

DISCUSSION

This study was designed to characterize the available forage base, diet, growth, population size range, and predatory demand range by walleye in Saginaw Bay, and to deduce impacts of their consumption on the forage fish community during May through September 2009. Walleye relied heavily on round goby and age-0 yellow perch to achieve observed growth, a reflection of the relative abundance of those prey species in 2009. In conjunction with observed growth and monthly diet data, the walleye population was estimated based on minimum, mean, and maximum fishing mortality rates documented by MDNR over a 23-year period and the known number of walleye harvested in 2009 to model potential range of predatory demands. Based upon the predatory demand range calculated for the walleye population estimate and the range of prey population estimates, walleye consumption did not appear to play a significant role in age-0 and -1+ yellow perch mortality in 2009. Age-1 and -2 walleye consumption in July may have been sufficient at the maximum level to control age-0 yellow perch population size if it continued at that rate, but strong predatory demand did not persist through the remainder of the summer. However, emerald shiner and salmonids were possibly controlled by walleye.

Saginaw Bay's prey base has dramatically changed since a walleye diet study was conducted during 1986-1988 and these changes were reflected in walleye diets in 2009. Changes from 1986-1988 to the 2009 forage fish community include loss of the alewife population, invasion of round goby, and greatly increased abundance of age-0 yellow perch. Alewife were previously abundant and were a major component of walleye diets (Schaeffer 1994), but they have been absent in MDNR annual surveys since 2003 (Fielder and Thomas 2006). Walleye diets reflected alewife absence in the bay. Round goby greatly increased in abundance since invading in 1999 (Fielder and Thomas 2006) and were an average of 25% of NOAA trawl composition in 2009. The large population of round goby was also the dominant species consumed by walleye, averaging 40% of biomass consumed. Age-0 yellow perch have been documented in record numbers since 2003 by MDNR and were a significant component of the forage fish community in 2009 as estimated by NOAA bottom trawls. Age-0 and 1+ yellow perch accounted for 32% of biomass consumed by walleye, another increase from the 22% observed by Schaeffer (1994) for 1988. Other species that contributed 2% or less to total biomass consumed by walleye in 2009 were gizzard shad and white perch. Gizzard shad had previously accounted for 33% of biomass consumed by walleye (Schaeffer 1994).

Additional prey species consumed by walleye in 2009 remained similar to previous observations in Saginaw Bay, but changed slightly with inclusion of salmonids, the exclusion of trout-perch, and shifts in proportions of prey biomass consumed compared to previous studies. Consistent components of walleye diets both in 2009 and 1986-1988 were emerald shiner and rainbow smelt. Emerald shiner accounted for 10% of biomass consumed by walleye in 2009, an increase from the observed 3% cyprinid biomass contribution in 1988 (Schaeffer 1994). Rainbow smelt contributed 4% to total biomass consumed by walleye in 2009, similar to their contribution of 5% in 1988 (Schaeffer 1994). Salmonids were 10% of biomass consumed by walleye in 2009; however they were not documented in the diets for 1986-1988 (Schaeffer 1994). Trout-perch were very abundant in Saginaw Bay, but were avoided as a prey source in 2009 unlike data from 1988 (Schaeffer 1994), when they compromised 2% of the diet.

In addition to changes in diets over decades due to invasions and extirpations of prey species, walleye diets varied also seasonally in Saginaw Bay. Primary forage fish for walleye during spring were cyprinids, round goby, age-0 salmonids, and age-1+ yellow perch. Summer saw shifts to age-0 forage fish and heavy predation directed at age-0 yellow perch and round goby. Walleye were reported to have seasonal changes in diet in Saginaw Bay in the 1980s, but based upon a different forage base consisting of abundant alewife, gizzard shad, and rainbow smelt (Schaeffer 1994). Walleye in Saginaw Bay behaved similarly to Lake Erie’s walleye population that switched from cyprinids during spring to available age-0 forage fish during summer and fall (Knight et al. 1984).

Saginaw Bay’s prey forage base has declined in abundance since 2003, which coincided with increased walleye abundance (Fielder and Thomas 2013). A typical predation effect on the prey base includes a decrease in prey abundance (Hartman and Margraf 1993; Pierce et al. 2006). However, walleye predatory demand was not strong enough to be a significant factor in age-0 or -1+ yellow perch mortality during May through September 2009 in Saginaw Bay. Walleye consumed a maximum of 29% of the estimated age-0 yellow perch population; with a mean percentage consumed of only 3%. Age-1+ yellow perch were estimated to have a population consumption percentage maximum of 22%, but a mean of only 1%. All ages of walleye increased consumption of age-0 yellow perch from July to September. MDNR has observed a decline in growth of age-0 yellow perch since 2003 (Fielder and Thomas 2013) indicating that greater numbers of age-0 yellow perch will need to be consumed to satisfy similar levels of predatory demand. Intense predatory demand by walleye on yellow perch has been demonstrated in other systems when age-0 yellow perch were abundant and cyprinids and clupeids were rare or absent (Forney 1974, 1977, 1980; Nielsen 1980, Lyons and Magnuson 1987; Hartman and Margraf 1993), but this was not the case in Saginaw Bay in 2009.

Alternative species of prey were available for walleye in Saginaw Bay throughout the study, including consistently abundant round goby and abundant rainbow smelt in September. NOAA trawl data showed the rainbow smelt population was estimated to be 45% more abundant than the age-0 yellow perch population during September. Emerald shiner and salmonids were also consumed in large quantities by walleye even though they were not collected in large quantities by NOAA bottom trawls. Additionally, 690,362 salmonids were stocked as fingerlings in Saginaw Bay. These alternative sources of prey buffered walleye predatory control on yellow perch in 2009.

Strong walleye predation pressure on fish populations, specifically yellow perch, has been observed to result in decreases in age-0 abundance and recruitment (Hartman and Margraf 1993; Pierce et al. 2006). Pierce et al. (2006) noted once lake stocking was resumed for walleye, there was a significant decrease in small yellow perch abundance. Forney (1974) observed age-0 yellow perch abundance per haul from August 1968 to May 1969 decrease by 99% due to rapid exploitation by walleye in Oneida Lake. The proportion of the age-0 yellow perch population consumed by walleye in Saginaw Bay generally was lower than the range (28.4-89.7%) observed by Hartman and Margraf (1993) when they concluded yellow perch recruitment was controlled by walleye predation in Lake Erie during June-July 1988. The only month with a high apparent predation impact was July. However, consumption percentages for emerald shiner (28/45 comparisons), round goby (15/45 comparisons), rainbow smelt (11/45 comparisons), and salmonids (6/6 comparisons) exceeded the minimum noted for population control of yellow perch in the study conducted by Hartman and Margraf (1993).

Emerald shiner experienced strong predation by walleye. All levels of predatory demand at the minimum emerald shiner population estimate resulted in overconsumption for all months. Overall predatory demand compared to mean emerald shiner population estimate also showed a strong and consistent predation pressure for May-August. I expected, from these data, emerald shiner would decrease in population size due to strong walleye predation as shown in Lake Erie in the late 1980s (Knight and Vondracek 1993). However, emerald shiner in the main basin Lake Huron have been increasing in density due to two strong year classes in 2005-2006 (Schaeffer et al. 2008). Emerald shiner population estimates based on bottom trawls likely underestimated their abundance in Saginaw Bay, since they are a pelagic species (Schaeffer et al. 2000; Fielder and Thomas 2013) and would explain why a majority of the comparisons greatly exceeded 100% consumption. Better estimates of emerald shiner population would more clearly elucidate predation effects.

Walleye exhibited potential to control the rainbow smelt population by consumption during July-September. Abundance of rainbow smelt has been at its lowest since 2003, which coincided with increased abundance of walleye (Fielder and Thomas 2013). Even with a decrease in rainbow smelt abundance, their contribution to walleye biomass consumed remained the same as when they were a dominant forage fish in 1988 (Schaeffer 1994).

Round goby were the main species contributing to walleye diets and walleye consumption exhibited potential to impact their abundance. The round goby population plateaued since 2003 and remained a consistent 14% of the total catch of MDNR fall survey trawls from 2005-2011 (Fielder and Thomas 2013). This study suggests the plateau could be the result of predation control exerted by walleye. Walleye diets were comprised of 32% round goby, and walleye consumed an estimated 11% of the round goby population. In Lake Erie, a similar trend was observed by Madenjian et al. (2011), after round goby became an important component of burbot *Lota Lota* diets, the round goby population decreased.

Estimated walleye consumption greatly exceeded the known number of stocked salmonids during May and June, and additional salmonids were consumed during September when none were stocked in Saginaw Bay. Wild juvenile lake trout *Salvelinus namaycush* are typically collected in low numbers during main basin bottom trawl surveys performed by the United States Geological Survey USGS in fall, but were absent in Au Sable Point after walleye increased in abundance (Riley et al. 2010). The replacement of salmonids by walleye at Au Sable Point may be a result of walleye feeding on salmonids and decreasing their abundance. Lake Huron also supported a Chinook salmon *Oncorhynchus tshawytscha* population consisting of 80% wild fish during 2000-2003 (Johnson et al. 2010) so population estimates for salmonids would have been greatly underestimated based solely on stocked numbers. Better estimates of the salmonid population are needed to accurately calculate effects of predator consumption; however, walleye predation may be a factor in explaining recent low harvest returns from stocked fish (Johnson et al. 2010).

Age-1, -2, and -3 walleye cohorts accounted for 74% of prey consumption indicating they have the most potential to control prey recruitment and shift aquatic communities. These three groups are important due to large walleye cohort sizes, greater observed growth rates than older fish, and increasing gape allowing for larger prey sizes to be consumed (Werner 1974; Mittlebach and Persson 1998). Age-1 walleye were estimated to be the most abundant cohort and consume 23% of prey biomass. Age-2 walleye were the second most abundant cohort, but were estimated to consume more prey biomass (28%). Consecutive months of strong predatory demand by age-1, -2, and -3 walleye has the potential to control recruitment and were likely affecting abundances of round goby, emerald shiner, rainbow smelt, and salmonids in Saginaw Bay.

Growth of age-4 walleye was assumed to be negligible during the study period, due to observed decrease between start and end weights from MDNR fall trawl samples in 2008 and 2009. This decrease in weight was likely due to bias arising from a small sample size of age-4 walleye (4 fish) in 2009 compared to the sample of 52 age-3 fish collected in 2008 (MDNR unpublished data). Total predatory demand would be underestimated if growth did occur, leading to underestimation of age-4 walleye impact on the forage fish community. This would not change my conclusions substantially because estimates with no growth suggest walleye predatory demand impacted the emerald shiner population, and the inclusion of positive growth for age-4 walleye would increase demand and strengthen that conclusion.

The lack of diet samples or small sample sizes required diets to be estimated at times from other age groups or months. This was the case for age-2 walleye for June and August. This approach was based on the findings of Knight et al. (1984) who observed high diet overlap between age-1 and age-2 and older Lake Erie walleye during all seasons. This suggests that age-2 walleye diets for June could be calculated with confidence from age-1 and age-3+ age groups.

Small samples sizes of stomachs containing prey could also have skewed diet proportions. In Saginaw Bay during May, it is unlikely age-1 and age-2 walleye survived on only one prey type while age-3 and older walleye consumed a variety of species, as did younger cohorts during following months. Small sample size of age-2 walleye would have led to the conclusion that age-2 walleye excluded age-1 yellow perch from their diet. This was unrealistic considering younger and older walleye both consumed age-1 yellow perch during the study. Bioenergetics models for age-1 and -2 walleye were created to explain demand from June to September 2009, excluding diet and growth data for May. The inclusion of modeled predatory demand for May for age-1 and -2 walleye would have increased the percent consumed of prey populations, but would not have affected the general conclusions.

Considerable bias may exist in estimates of predator consumption due to population estimation techniques. I assumed Saginaw Bay was a closed system with no emigration or immigration of walleye. The total harvest of 288,243 walleye in 2009, total mortality, and fishing mortality as calculated by MDNR were used to estimate the range of population sizes (MDNR unpublished data). To overcome biases in the calculations of mortality rates, a population estimate was created using minimum, mean, and maximum fishing mortality rates to describe a range of possible populations to analyze walleye predatory impact.

Diet data were not collected following September 2009, and it is likely that predation on common prey species continued, further depleting their abundances and increasing percentage of the population consumed. This was observed with yellow perch in Lake Oneida, New York (Forney 1974) and age-0 bluegill *Lopomis macrochirus* during overwintering in Michigan lakes (Schneider and Breck 1993). If the majority of yellow perch consumption occurred from September through April, this would be a major bias. Further investigation of walleye diets over winter and prey abundances at those times would reveal if this bas is significant.

Monthly mean CPUEs could not be used to estimate prey population size since no mortality trend could be discerned and some species were not collected regularly. Some prey populations were probably underestimated due to poor recruitment to bottom trawls, especially pelagic species like emerald shiner and rainbow smelt, and especially salmonids

(Trautman 1981; Argyle 1982; Schaeffer et al. 2000; Warner et al. 2009). Trawls could not sample in preferred habitats like rocky areas leading to possible underestimation of round goby abundance and overestimating predatory impact (Johnson et al. 2005).

Understanding diets and bioenergetics of a naturally reproducing and larger than historic walleye population in Saginaw Bay can assist fisheries managers interested in achieving management goals. One management goal for Saginaw Bay was to establish and maintain a productive yellow perch and walleye fishery. Historically, both species coexisted in Saginaw Bay (Baldwin and Saalfeld 1962). Strong production of age-0 yellow perch has occurred since 2003, but adult recruitment has been low (Fielder and Thomas 2006). This coincides with yellow perch becoming a greater part of walleye diets than observed in the late 1980s when alewives and gizzard shad were most important (Schaeffer 1994). However, this study suggests that walleye consumption did not play a major role in regulating age-0 and age-1 yellow perch mortality in 2009. Alternative prey like round goby, emerald shiner, rainbow smelt, and salmonids provided a substitute forage source and buffered yellow perch from predation (Forney 1974; Kaufman et al. 2006). Further investigation into trends in walleye predation pressure on yellow perch over multiple years, throughout the entire year including winter, and observations of predation pressure from other predators in Saginaw Bay would help to better understand predation as a possible cause of poor yellow perch recruitment.

Increased utilization of the forage base was the second goal of predator restoration in Saginaw Bay (Fielder and Thomas 2013). Abundance of soft-rayed forage species has declined since 2003, which coincided with strong production and recruitment of walleye (Fielder and Thomas 2006; Fielder and Thomas 2013). This increased walleye population utilized available forage species and exerting consistent and strong predation pressure on select prey populations in 2009. Strong and consistent predation pressure has been identified as the cause of prey population decline and stabilization as observed in predator-prey relationships between walleye-yellow perch and burbot-round goby (Forney 1974; Knight and Vondracek 1993; Madenjian et al. 2011). This study supports that strong and consistent walleye predation pressure on emerald shiner, rainbow smelt, and round goby occurred in 2009, consistent with management goals.

Walleye diets consisted of 40% round goby and 32% yellow perch in 2009 and this reliance by walleye on round goby and yellow could pose a problem for fisheries managers if either population crashed. The void left by round goby or yellow perch would need to be filled by remaining forage species and this increased predation pressure could affect potential recovery of species like emerald shiner, a preferred prey species, may have experienced. Typically, a lack of forage abundance would cause the predator population and predatory demand to decline (Kershner et al. 1999). However, walleye would likely not show any negative effects on abundance due to loss of one main forage species as long as alternative prey were available.

The minimum size limit for walleye in Saginaw Bay is 350 mm. However, the two walleye cohorts (age-1 and -2) which account for 50% of the estimated biomass consumed by the walleye population fall under harvest size limit in 2009, therefore management through increased angler harvest currently harvestable walleyes would not decrease their impact on the forage base. Strong predation pressure by these two cohorts on the forage fish community may be a phase that must be endured as suggested by Hartman and Margraf (1992) until age-1 and -2 walleye become susceptible to harvest.

Predation by walleye was likely not the cause of poor yellow perch recruitment in 2009 based on a diet study conducted from May-September. Other studies have linked yellow perch year class failures to unusually small pre-winter size structure as observed in 2003 and 2004 (Fielder and Thomas 2013). Ivan et al. (2011) surmised that smaller size likely increased overwinter mortality. Further study of mechanisms underlying poor growth of age-0 yellow perch and overwinter mortality would better define mechanisms underlying yellow perch year class failures.

Walleye accounted for over 100% consumption of the known number of stocked salmonids in Saginaw Bay for 2009. Lower returns of hatchery marked fish have been observed in the central and southern main basin of Lake Huron (Johnson et al. 2010). Walleye are known to prey on age-0 salmonids (Fielder et al. 2007) and they have been observed to overlap spatially (Riley et al. 2010). Our results represent only a conservative estimate of walleye predation on salmonids because we could not estimate abundance of wild fish; however, our results suggest that walleye predation was likely reducing (at least regionally) the effectiveness of the salmonid stocking program in Saginaw Bay, and walleye could be important predators on salmonids throughout Lake Huron should their population expand beyond Saginaw Bay.

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APPENDICES

Appendix Table 1**.** Percent of prey population range consumed to satisfy maximum predatory demand of walleye population in 2009.

	Minimum Prey Population	**Mean Prey Population**	**Maximum Prey Population**
Species	**May**		
Emerald Shiner	5304	49.5	13.4
Rainbow Smelt	11	0.2	0.0
Round Goby	126	9.2	4.4
Yellow Perch (age-1+)	10	1.5	0.5
Yellow Perch (age-0)	-	-	-
	June		
Emerald Shiner	11866	110.7	30.0
Rainbow Smelt	43	0.8	0.2
Round Goby	328	24.0	11.4
Yellow Perch (age-1+)	20	3.1	1.2
Yellow Perch (age-0)	-	-	-
	July		
Emerald Shiner	13630	127.2	34.5
Rainbow Smelt	86	1.6	0.3
Round Goby	267	19.6	9.3
Yellow Perch (age-1+)	22	3.4	1.3
Yellow Perch (age-0)	29	19.4	13.1
	August		
Emerald Shiner	7589	70.8	19.2
Rainbow Smelt	234	4.4	0.9
Round Goby	305	22.3	10.6
Yellow Perch (age-1+)	11	1.7	0.6
Yellow Perch (age-0)	7	4.8	3.2
	September		
Emerald Shiner	1044	9.7	2.6
Rainbow Smelt	77	1.5	0.3
Round Goby	165	12.1	5.7
Yellow Perch (age-1+)	3	0.4	0.2
Yellow Perch (age-0)	5	3.2	2.1

Appendix Table 2. Percent of prey population range consumed to satisfy mean predatory demand of walleye population in 2009.

	Minimum Prey Population	**Mean Prey Population**	**Maximum Prey Population**
Species		**May**	
Emerald Shiner	2775	25.9	7.0
Rainbow Smelt	6	0.1	0.0
Round Goby	66	4.8	2.3
Yellow Perch (age-1+)	5	0.8	0.3
Yellow Perch (age-0)	-	-	-
		June	
Emerald Shiner	6122	57.1	15.5
Rainbow Smelt	23	0.4	0.1
Round Goby	176	12.9	6.1
Yellow Perch (age-1+)	10	1.6	0.6
Yellow Perch (age-0)	-	-	-
		July	
Emerald Shiner	7003	65.3	17.7
Rainbow Smelt	45	0.8	0.2
Round Goby	141	10.3	4.9
Yellow Perch (age-1+)	12	1.8	0.7
Yellow Perch (age-0)	15	10.5	7.0
		August	
Emerald Shiner	3559	33.2	9.0
Rainbow Smelt	118	2.2	0.5
Round Goby	145	10.6	5.0
Yellow Perch (age-1+)	6	0.8	0.3
Yellow Perch (age-0)	4	2.5	1.7
		September	
Emerald Shiner	837	7.8	2.1
Rainbow Smelt	40	1.0	0.2
Round Goby	99	7.2	3.4
Yellow Perch (age-1+)	2	0.3	0.1
Yellow Perch (age-0)	2	1.5	1.0

Appendix Table 3. Percent of prey population range consumed to satisfy minimum predatory demand of walleye population in 2009.

	Minimum Prey Population	**Mean Prey Population**	**Maximum Prey Population**
Species		**May**	
Emerald Shiner	2020	18.8	5.1
Rainbow Smelt	4	0.1	0.0
Round Goby	48	3.5	1.7
Yellow Perch (age-1+)	4	0.6	0.2
Yellow Perch (age-0)	-	-	-
		June	
Emerald Shiner	4376	40.8	11.1
Rainbow Smelt	16	0.3	0.1
Round Goby	126	9.2	4.4
Yellow Perch (age-1+)	7	1.1	0.4
Yellow Perch (age-0)	-	-	-
		July	
Emerald Shiner	4886	45.6	12.4
Rainbow Smelt	33	0.6	0.1
Round Goby	102	7.4	3.5
Yellow Perch (age-1+)	8	1.3	0.5
Yellow Perch (age-0)	11	7.5	5.0
		August	
Emerald Shiner	2715	25.3	6.9
Rainbow Smelt	81	1.5	0.3
Round Goby	113	8.3	3.9
Yellow Perch (age-1+)	4	0.6	0.2
Yellow Perch (age-0)	3	1.9	1.3
		September	
Emerald Shiner	339	3.2	0.9
Rainbow Smelt	28	0.5	0.1
Round Goby	72	5.3	2.5
Yellow Perch (age-1+)	1	0.1	0.1
Yellow Perch (age-0)	2	1.1	0.8