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Diet Analysis of Burbot from Eastern Lake Michigan: 1999-2012

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DIET ANALYSIS OF BURBOT FROM EASTERN LAKE MICHIGAN: 1999-2012

By

Casey J. Hares

THESIS

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ABSTRACT

DIET ANALYSIS OF BURBOT FROM EASTERN LAKE MICHIGAN; 1999-2012

By

Casey J. Hares

The Lake Michigan fish community has undergone many changes due to introduction of non-native species, climate shifts, and management actions. Managers need to understand the time course of these alterations, including the time-frame of impact on the food web in the lake. It is important to understand the relationships of all the major players in the trophic system, including those that are of modest harvest interest. Burbot (*Lota lota*) is a species that most agencies neglect to include in any management plans, despite their status as a top level, native-predator in the Great Lakes. I used a collection (1999-2012) of diet samples from burbot from eastern Lake Michigan to evaluate temporal alterations in burbot diet with particular attention to non-native vs. native forage and environmental changes. Catch per unit effort (burbot/net · day) decreased from a high of 5.82 burbot/net · day (± 2.19) in 2001 to a low of 0.750 burbot/net · day (± 0.25) in 2010, which is consistent with declining burbot populations throughout the Great Lakes (Gorman and Sitar 2013; Stapanian et al. 2013). The collective contribution of sculpin (*Cottus*), alewife (*Alosa pseudoharengus*), and ninespine stickleback (*Pungitius pungitius*) to burbot diet decreased from ~80% before 2006 to ~15% in 2012. During the same time span, round goby (*Neogobius melanostomus*) contribution to burbot diet

increased from ~0% before 2006 to greater than 60% in 2012, implying nearly a complete diet shift of burbot in just six years. The diet shift suggests a change in feeding behavior from partially pelagic/benthic to almost entirely benthic, and a change in prey consumption from alewife/sculpin to round goby. This shift may prove beneficial to burbot considering the recent increase in benthic biomass due to dreissenid mussels (Nalepa et al. 2009), and serves as a potential link to move the benthos from a nutrient sink to a nutrient source by utilizing round gobies and moving nutrients up the trophic web.

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Casey J. Hares

2014

DEDICATION

This thesis is dedicated to my mother, Linda Hares.

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I thank my advisor Dr. Jill Leonard for all of the support and guidance throughout my undergraduate and graduate process. Her support in organizing my research and aiding in my protocols was invaluable. I also thank Dr. John Bruggink and Dr. Tracy Galarowicz for their guidance and for participating on my committee. I greatly appreciate the Michigan Department of Natural Resources (MDNR) Charlevoix Research Station personnel for providing me with the resources to perform my research, particularly Jory Jonas and Dave Clapp. I thank Northern Michigan University for providing equipment and necessary space to perform my research, as well as for an Excellence in Education Scholarship for funding this project. I would also like to thank my mother and sister for supporting me throughout my project. This thesis follows the format prescribed by the Journal of Great Lakes Research.

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LIST OF ABBREVIATIONS

| | | |
|---------|-------|--|
| CPUE | | Catch Per Unit Effort |
| GLFC | | Great Lakes Fishery Commission |
| LAPLMFC | | Lakewide Assessment Plan For Lake Michigan Fish Communities |
| LMFCO | | Lake Michigan Fish Community Objectives |
| MDNR | | Michigan Department of Natural Resources |
| SL | | Standard Length (mm) |
| TL | | Total Length (mm) |
| VL | | Vertebral Length (mm) |

CHAPTER 1: INTRODUCTION

The Lake Michigan fish community has undergone many changes due to introductions of non-native species, climate shifts, and management actions (Mills et al. 2003; Dobiesz et al. 2005; Gorman 2007; Bunnell 2012). Managers need to understand the time course of these alterations, including the time-frame of impact on the food web in the lake. This understanding is important for proactive management in preparation for future changes and also helps us understand the impacts of past management actions within the context of environmental change. Further, it is important to understand the relationships of all the major biota in the trophic system, even those that are of modest harvest interest. Burbot (*Lota lota*) are unique fish in the sense that although they are large native piscivores, they are not commercially fished or commonly recreationally fished in the Great Lakes. Most agencies neglect to include burbot in any management plans, leaving a gap in even knowledge of basic biology of these native fish. This project used a collection of diet samples (1999-2012) from burbot from eastern Lake Michigan to evaluate temporal alterations in burbot diet with particular attention to non-native vs. native forage and environmental changes.

Burbot are usually characterized as piscivorous and 80% of their diet typically consists of fish (McPhail and Paragamian 2000). In North America, burbot eat a wide variety of fishes including lampreys (*Ichthyomyzon* and *Lampetra* spp.), whitefish (*Coregonus* and *Prosopium* spp.), grayling (*Thymallus arcticus*), northern pike (*Esox lucius*), suckers

(*Catostomus* spp.), many species of Cyprinidae, sticklebacks (Gasterosteidae), trout-perch (*Percopsis omiscomaycus*), yellow perch (*Perca flavescens*), sculpins (*Cottus* spp.), alewives (*Alosa pseudoharengus*) (Madenjian et al. 2002), and other burbot (McPhail and Paragamian 2000; Jacobs et al. 2010). Therefore, burbot have an important relationship with the prey fish community, and their response to the introduction of non-native prey fish has impacts on their association with the Lake Michigan food web.

Lake Michigan once boasted the largest commercial lake trout (*Salvelinus namaycush*) fishery in the Great Lakes. In the 1950's, lake trout were extirpated due to a combination of overfishing, sea lamprey (*Petromyzon marinus*) parasitism, and habitat degradation (Holey et al. 1995; Jacobs et al. 2010). During the 1950's, burbot also experienced drastic reductions (Stapanian et al. 2008), but avoided extirpation due to a lack of commercial exploitation. Burbot are functionally the only native top-predator left in Lake Michigan because rehabilitation efforts for lake trout have met with limited success (Schneeberger et al. 1998).

Burbot have historically had little commercial value in the Great Lakes, but have been recognized as an important piscivore in aquatic systems (Schram 1983.) The main commercial fisheries for burbot occur in Russia, Finland, Sweden, Estonia, and Lithuania. With a few exceptions, commercial harvest of burbot in most of North America is generally restricted to incidental catches during fishing for other species (Whitmore et al. 2008). There has also never been a serious interest in recreationally fishing burbot in the United States. Historically, there have been little to no fishing restrictions on burbot, due to the little research dedicated to understanding their biology.

Since the early 1930's, Lake Michigan's food web has been dramatically altered by aquatic invasive species. Sea lamprey (*Petromyzon marinus*) first entered Lake Michigan in the late 1930's and began impacting fish stocks by the mid 1940's (Smith and Tibbles 1980). Alewives (*Alosa pseudoharengus*) were first documented in Lake Michigan in 1949, and significantly impacted larval fishes soon after (Bunnell et al. 2006; Madenjian et al. 2008). During the 1930's and early 1960's, sea lamprey parasitism on juvenile and adult burbot, as well as predation by alewives on pelagic burbot larva, was associated with large scale burbot declines in Lake Michigan (Stapanian et al. 2008). Control of sea lamprey and alewife populations in Lake Michigan, beginning in the 1950's and 1960's, had remarkable effects on the food web (Madenjian et al. 2002). The recoveries of lake whitefish (*Coregonus clupeaformis*) and burbot populations, as well as the increase in salmonine populations, were partially attributable to sea lamprey control (Madenjian et al. 2005a). More recently, the round goby (*Neogobius melanostomus*) has spread quickly throughout the Great Lakes basin since its accidental introduction in the 1990s (Corkum et al. 2004). The round goby is a particularly threatening invasive to native fishes with similar niches (Janssen and Jude 2001) and decreases recruitment of benthic spawning fishes (Nichols et al. 2003). Round goby may replace the mottled sculpin (*Cottus bairdii*) and slimy sculpin (*C. cognatus*), which share similar habitat and spawning requirements (Cookingham and Ruetz 2008). In a recent study, Jacobs et al. (2010) found that burbot diets in northern Lake Michigan contain higher proportions of round goby than sculpin, suggesting that round goby have already replaced some of the native fauna in the food web. Though invasives of all sizes and species directly and indirectly affect burbot,

detecting a change in prey consumption through time will provide documentation of a native predator's response to an ever-changing lake.

Prior to salmonid stocking in Lake Michigan, burbot and lake trout were the top predators in this system. With the addition of Chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*) salmon and rainbow (*Oncorhynchus mykiss*) and brown (*Salmo trutta*) trout, Lake Michigan gained four new predators (Mills et al. 2003; Dobiesz et al. 2005). Adding more predators than evolved in the system can create a trophic imbalance, in which predation pressures may outweigh the recruitment of prey-fish. Brandt (1986) demonstrated clear diet similarity between lake, brown, and rainbow trout, and Chinook and coho salmon for individuals foraging in the Lake Ontario food web. Similarity in diet between these salmon predators and their stocking rates in Lake Ontario may have resulted in the overexploitation of the prey species (Rand and Stewart 1998). Most studies of trophic imbalance within the Great Lakes focus primarily on salmonid impacts on prey; however, burbot's potential impacts on forage species as well as its response to competition from non-natives needs examination.

Throughout much of the 1970s, Lake Michigan's forage base was largely dominated by alewife (Bunnell et al. 2006). After the biological control of alewives was started in the mid 1960's, a shift to a community dominated by several native species was observed during the 1980's through 1990s (Stewart et al. 1981; Bunnell et al. 2006). It is likely that the recovery of burbot, deepwater sculpin (*Myoxocephalus thompsonii*) and yellow perch (*Perca flavescens*) was aided by the alewife reduction (Bunnell et al. 2006). This forage shift away from an alewife to a more native (deepwater sculpin and yellow perch) dominated forage base shows how dynamic the Lake Michigan food web has been. An

additional community shift occurred during 1999-2004 and coincided with a reduction in species richness and total abundance (Bunnell et al. 2006). The yellow perch decline during this period has been explained by several factors including overfishing (Wilberg et al. 2005), continued alewife predation (Shroyer and McComish 2000), and low zooplankton densities (Dettmers et al. 2003). The mechanisms underlying the latest forage shift may be related to reductions in nutrients (Bunnell et al. 2006). The restoration of the native forage fish has been incomplete as emerald shiner (*Notropis atherinioides*) and cisco (*Coregonus artedii*) have yet to demonstrate recovery (Bunnell et al. 2006). Evidence indicates the forage fish populations throughout the Great Lakes continue to experience substantial fluctuations in abundance (Mills et al. 2003; Dobiesz et al. 2005; Gorman 2007). Recent data (Bunnell 2012), indicates a decrease in several prey-fish species including alewife, bloater, rainbow smelt, and deepwater sculpin. In contrast, the abundance of slimy sculpin is at its highest level in the last 32 years. It is important to determine how a native predator is affected by a very dynamic prey fish community.

The burbot is the only member of the gadiform order that lives strictly in freshwater systems. As a peripheral freshwater fish, burbot have retained many characteristics of their marine ancestors such as high fecundity, low temperature spawning, random dispersal of gametes, and a preference for cold waters (McPhail and Paragamian 2000). Burbot are unique in that they have a remarkably wide, circumpolar distribution (McPhail and Paragamian 2000). Although they are widespread and abundant throughout certain areas of their native range, many burbot populations have been extirpated, endangered, or are in serious decline due to damming of rivers, invasive species impacts, or degraded

habitat (Stapanian et al. 2010). In North America the southern limit of burbot distribution is the northern tier of the U.S. The most thorough population estimates have been conducted in Alaskan lakes, and the estimates deviate little from 10.6 fish/ha (Parker et al. 1989). The degree of variability in burbot population estimates in Lake Michigan is much more dramatic. Within Lake Michigan, densities have been estimated from 0.33 fish/ha to 139 fish/ha (Edsall et al. 1993).

The body of a burbot is elongated and almost eel-shaped with long, soft-rayed dorsal and anal fins that join a rounded caudal fin (McPhail and Paragamian 2000). The burbot is smooth to the touch, but the skin is embedded with tiny cycloid scales that make aging scales nearly impossible. Aging is therefore accomplished using otolith analysis. Burbot have extraordinarily large livers that take up about one third of their peritoneal cavity (McPhail and Paragamian 2000). When burbot are tested in a lab, they have historically been relatively low in mercury and PCBs, most likely due to their high liver detoxification capacity (Fisher et al. 1995). Adult burbot are benthic predators and inhabit large cool rivers of the north temperate region as well as the hypolimnion of large lakes. Burbot prefer temperatures of 10-14°C (Cooper and Fuller 1945; Hackney 1973; Hoffman and Fischer 2002). In some Finnish and Swedish populations, sub-adult burbot have been found in estuaries and brackish lagoons. Residence in these areas is transitory, and adults in these areas have been found to be sterile or fail to reach maturity, suggesting that burbot can tolerate brackish conditions, but it should be considered a marginal environment (Pullianinen and Korhonen 1990). Like other members of the Lotidae family, potential annual fecundity of burbot is enormous and estimates of eggs per female vary from 6,300 (Miller 1970) to 3,477,699 (Roach and Evenson 1993). For

the majority of the northern tier of the United States, the burbot is the only fish that spawns under the ice (December to early March: McPhail and Paragamian 2000; Evenson 2000), with the spawning season being highly synchronized and relatively short (Boag 1989; McPhail and Paragamian 2000). Burbot eggs sometimes hatch under the ice, and in eastern North America, larvae are usually exogenously feeding by mid-April (Ghan and Sprules 1993). Shortly after hatching, larval densities can be high (up to 15/m²), but within a month drop to less than 1/m² due to high larval mortality (Ghan and Sprules 1991). In lakes, newly hatched larvae are limnetic and drift passively in the water column, but as they grow and their swimming abilities improve, they become more mobile (Fischer 1999).

The Great Lakes Fishery Commission's (GLFC) Lake Michigan Fish Community Objectives (LMFCO) state that the goal for managing burbot populations in Lake Michigan is to maintain and preserve the current stock abundance (Schneeberger et al. 1996). This goal is important for burbot because prior management actions did not include burbot in most plans. Similarly, the Michigan Department of Natural Resources (MDNR) initiated their Lakewide Assessment Plan for Lake Michigan Fish Communities (LAPLMFC) to determine the relative abundance of three key predators: lake trout, Chinook salmon, and burbot in 1998. The assessment done by the MDNR is quite comprehensive; however, support for assessment of burbot diet samples has been lacking. The objectives of the lake wide assessment are to determine growth, population mortality, age-specific diet, juvenile recruitment, and general physical health of burbot. This study focused on age-specific diet of burbot in Lake Michigan in support of these management priorities.

CHAPTER TWO: DIET ANALYSIS OF BURBOT FROM EASTERN LAKE MICHIGAN: 1999:2012

CHAPTER SUMMARY: Burbot diet was analyzed from eastern Lake Michigan using 553 burbot stomach samples collected from 1999 to 2012. Non-native round gobies replaced sculpins (Cottidae) and alewives (*Alosa pseudoharengus*) as the main diet item during the period. With the invasion of Lake Michigan by round gobies (*Neogobius melanostomus*), there was potential for dramatic shifts in the food web supporting large, native predators such as burbot (*Lota lota*). Round gobies appeared in the diet in 1999 and became frequent in 2003. Round goby relative contribution to burbot diet, based on abundance, increased from 1% (± 1.05) in 1999 to 64% (± 4.94) in 2012 with abundance increasing from 0.02 (± 0.02) to 2.8 (± 0.35) goby/burbot in 2012. Conversely, cottid sculpin contribution to burbot diet decreased from 32% (± 3.49) in 1999 to 14% (± 3.47) in 2012 and abundance decreased from 2.36 (± 0.34) to 0.74 (± 0.20) sculpin/burbot in 2012. This shift in diet was coincident with a decrease in burbot relative abundance in the samples with a decrease in catch per effort from 1999 (4.73 burbot / standard gill net) (± 0.64) to 2012 (2.12 burbot/ net · day) (± 0.45), mirroring declining burbot populations in Lake Superior (Gorman and Sitar 2013). These data help characterize the striking food web shift linked to non-native species that has taken place in Lake Michigan since 2000 and highlight its impact on native predator ecology.

INTRODUCTION: Burbot (*Lota lota*) are usually characterized as piscivorous and 80% of their diet typically consists of fish (McPhail and Paragamian 2000). In North

America, burbot eat a wide spectrum of fishes including lampreys (*Ichthyomyzon* and *Lampetra* spp.), whitefish (*Coregonus* and *Prosopium* spp.), grayling (*Thymallus arcticus*), northern pike (*Esox lucius*), suckers (*Catostomus* spp.), many species of Cyprinidae, sticklebacks (Gasterosteidae), trout-perch (*Percopsis omiscomaycus*), yellow perch (*Perca flavescens*), sculpins (*Cottus* spp.), alewife (*Alosa pseudoharengus*) (Madenjian et al. 2002), and other burbot (McPhail and Paragamian 2000).

Burbot have historically had limited commercial value in the Great Lakes, but have been recognized as an important native piscivore in aquatic systems (Schram 1983). With a few exceptions, commercial harvest of burbot in most of North America is generally restricted to incidental catches during fishing for other species (Whitmore et al. 2008). Historically, there have been few or no fishing restrictions on burbot in the Great Lakes (Stapanian et al. 2010).

Since the early 1930's, Lake Michigan's food-web has been heavily altered by aquatic invasive species. Alewives were first documented in Lake Michigan in 1949, and began significantly impacting native larval fishes soon after (Bunnell et al. 2006; Madenjian et al. 2008). During the 1930's, sea lamprey (*Petromyzon marinus*) parasitism on juvenile and adult burbot as well as alewife predation on pelagic burbot larva in the early 1960's were associated with large scale burbot declines in Lake Michigan (Stapanian et al. 2008). Control of sea lamprey and alewife populations in Lake Michigan, beginning in the 1950's and 1960's, had remarkable effects on the food web (Madenjian et al. 2002). The recoveries of lake whitefish (*Coregonus clupeaformis*) and burbot populations, as well as the increase in salmonine populations, were partially attributable to sea lamprey control (Madenjian et al. 2005a).

Throughout much of the 1970s, Lake Michigan's forage base was largely dominated by alewife (Bunnell et al. 2006). After the biological control of alewives was started in the mid 1960's, a shift to a community dominated by several native species was observed during the 1980's and 1990s (Stewart et al. 1981; Bunnell et al. 2006). It is likely that the recovery of burbot, deepwater sculpin (*Myoxocephalus thompsonii*) and yellow perch (*Perca flavescens*) was aided by the alewife reduction (Bunnell et al. 2006). This forage shift away from an alewife to a more native (deepwater sculpin and yellow perch) dominated forage base shows how dynamic the Lake Michigan food web has been. An additional community shift occurred during 1999-2004 and coincided with a reduction in species richness and total fish (Bunnell et al. 2006). The yellow perch decline during this period has been explained by several factors including overfishing (Wilberg et al. 2005), continued alewife predation (Shroyer and McComish 2000), and low zooplankton densities (Dettmers et al. 2003). The mechanisms underlying that forage shift may be related to reductions in nutrients (Bunnell et al. 2006). The restoration of the native forage fish assemblage has been incomplete as emerald shiner (*Notropis atherinioides*) and cisco (*Coregonus artedii*) have yet to demonstrate recovery (Bunnell et al. 2006). Evidence indicates the forage fish populations throughout the Great Lakes continue to experience substantial fluctuations in abundance (Mills et al. 2003; Dobiesz et al. 2005; Gorman 2007).

Most recently, the round goby (*Neogobius melanostomus*) has spread quickly throughout the Great Lakes basin since its accidental introduction in the 1990s (Corkum et al. 2004). The round goby is a particularly threatening invasive for native fishes with similar niches (Janssen and Jude 2001) and decreases recruitment of benthic spawning fishes (Nichols et

al. 2003). Round goby may replace the mottled sculpin (*Cottus bairdii*) and slimy sculpin (*C. cognatus*), which share similar habitat and spawning requirements (Cookingham and Ruetz 2008). In a recent study, Jacobs et al. (2010) found that burbot diets in northern Lake Michigan contained higher proportions of round gobies than sculpins, suggesting that gobies have already replaced some of the native fauna in the food web. Though invasive species directly and indirectly affect burbot, detecting a change in prey consumption through time will provide an important clue to this native predator's response to an ever-changing lake. Depth of catch, condition factor, and relative abundance will be determined to assess behavioral and biological changes in burbot.

METHODS: Burbot stomach samples were collected by the Michigan Department of Natural Resources (MDNR) Charlevoix Research Station in accordance with the MDNR's Lakewide Assessment Plan for Lake Michigan Fish Communities (LAPLMFC). Bottom gill nets were used to sample all burbot for this study. The nets were 2m deep and had eight 30m panels of different mesh sizes (range= 64 – 152mm stretched mesh) arranged from smallest to largest mesh size. Two nets were combined for each set, creating a total of 488m of net. Nets were left in the water for 24 hours for each set. Sampling was conducted each year (1999 – 2012) at 17 sites (Figure 1) in the Michigan waters of Lake Michigan, although not all sites were sampled every year. Sampling locations were grouped into diet districts within regions consistent with the Elliot et al. (1996) protocol of conducting diet studies of Lake Michigan piscivores. There were three regions examined in this study (Southeast, Northeast, and North) that

were composed of districts MM7 and MM8, MM5 and MM6, and MM2 and MM3, respectively.

Set locations at each sample site were randomly selected. Sampling was performed during early spring when the water column was not stratified and bottom temperatures at fishing depths were greater than 4°C.

When possible, 10 fish stomachs per size group per day per location were collected for stomach content analysis from assessment nets. Burbot were sorted into the following size groups: <200mm, 200-399mm, 400-599mm, 600-799mm, and ≥800mm.

Variation in sampling depth ranged from 6.1m to 132.3m. Burbot were assigned to depth bins of 0-19.99m, 20-39.99m, 40-59.99m, 60-79.99m, and 80-99.99m if the range of depth covered by their gill net was no greater than 20m. Of the 553 fish in this study, 468 could be assigned to a depth bin; for the remaining fish there was insufficient information to determine their capture depth and they were not used for depth analysis. Linear regression was used to determine if there was a temporal trend in depth of burbot catch.

Catch rates from bottom gill nets were adjusted for net length and set duration to provide a relative abundance. Adjusted net length was calculated by dividing 609.6 meters (2000 feet) by reported net lengths to establish a standard net length at 609.6 meters. Adjusted net set duration was calculated to establish standard net set duration to one day. Fish abundance per netting event was corrected to create a standardized CPUE value (fish/net · day). The year 2002 was removed from the CPUE analysis because no fish were caught. Linear regression was used to test for significant changes in average CPUE from 1999-2012.

Fish condition (K) is the relative robustness of a fish and is commonly used as an indicator of energetic stores. Condition factor was calculated as $K = (100,000 * W) / (L^3)$, where weight (W) = grams and total length (L) = mm. Condition of female and male burbot were assessed over time using a linear regression. A Kruskal-Wallis one way analysis of variance on ranks was used to assess differences in condition between female and male burbot.

A Mann-Whitney test was used to assess differences in depth-specific frequency of catch of female (N= 262) and male (N= 264) burbot. True gill-net depths that met net depth criteria were used in this analysis.

Prey items within the stomachs were identified to the lowest possible taxonomic classification. Through use of diagnostic bones and identification keys, even severely digested prey were identified (Elliot et al. 1996; MDNR Charlevoix). Cleithrum (Traynor et al. 2010) and otolith (MDNR Charlevoix) identification were most commonly used to identify prey items. Length (Total length (TL), Standard length (SL), or Vertebral length (VL)) of all prey items, and wet mass of complete prey items were determined. All prey items that were only measured for (VL) or (SL) were later converted to TL using published conversion coefficients (Elliot et al. 1996). Length-weight regressions were then used to estimate weight of partially digested prey items. All identifying bones and calcareous structures (otoliths) were oven dried for 24 hours and stored.

Dominant prey items were determined as percent of overall prey items found. This excludes all assumed non-intentional diet items including rocks, wood, tapeworms, and dreissenid mussels; lack of evidence in the literature supported burbot predation on

dreissenid mussels. These items were assumed to have been either incidentally ingested or to have been consumed by a prey item (i.e. zebra mussels from round gobies). Most prey items were identified to species, but others could only be identified to genus.

Sculpins of the genus *Cottus* were collectively identified as one group, because cleithrum and otolith distinction between slimy sculpin (*Cottus cognatus*) and mottled sculpin (*C. bairdii*) is difficult (Traynor et al. 2010). A Spearman correlation was used to identify if dreissenid mussel appearance was correlated with round goby appearance.

Changes in burbot diet composition were analyzed overall and by three grouped regions (Southeast, Northeast, and North) and among all regions. Individual diet districts within each region were combined to improve statistical power while maintaining regional integrity. Relative prey contribution to burbot diet (by abundance) was calculated for main prey items for each of the three regions over time to assess changes in prey contribution. Relative prey contribution to burbot diet was also assessed by depth.

RESULTS: Netting effort (net (609.6m gill net) · day) ranged from 22.32 net · days in 2001 to 79.88 net · days in 2012. Standardized sampling was not put into effect until 2002, but thereafter remained relatively consistent (Figure 2). Catch per unit effort (burbot/net · day) decreased significantly from 1999 through 2012 ($P= 0.003$, $R^2= 0.571$, $CPUE= 520.215 - (0.258 * YEAR)$). Catch per unit effort ranged from a low of 0.750 burbot/net · day (± 0.25) in 2010 to a high of 5.82 burbot/net · day (± 2.19) in 2001 (Figure 3). Catch per unit effort was highest in the first three study years with the lowest netting effort, and lowest in the last six years of the study, despite having higher netting efforts associated with later years.

Female burbot condition factor (K) did not change throughout the time series ($P= 0.179$) (Figure 4). Similarly, male burbot K did not change throughout the time series ($P= 0.707$) (Figure 4). K of female ($P= 0.186$) and male ($P= 0.225$) burbot did not vary significantly with capture depth (Figure 5). Female ($n=222$) K (median 0.840; mean 0.846 ± 0.007) was significantly greater than male ($n=223$) K (median 0.791; mean 0.801 ± 0.008) ($P < 0.001$).

Male burbot were caught in significantly deeper water than female burbot ($P= 0.004$, U Statistic= 20881.500). Median catch depths of female and male burbot were 22.71m and 32.92m, respectively. Average catch depth of female burbot was 28.25m (± 0.87), while average catch depth of male burbot was 31.55m (± 0.86) (Figure 6).

There were 5042 prey items found in 553 burbot stomachs (Table 1) and 4377 were deemed intentional prey items. Of the 17 prey taxa identified as intentional prey items, six of those accounted for 98.2% of all prey items found in the burbot stomachs in the entire study (Figure 7). Alewives were the most common prey item and accounted for 53.5% of all prey items. Sculpins of the genus *Cottus* were the second most common prey item (21.73%) followed by round goby (8.18%), ninespine sticklebacks (6.92%), bloaters (5.48%), and crayfish (2.42%).

Alewife and cottid sculpin average proportion of contribution to burbot diet decreased over time, while round goby contribution increased. Average percent alewife contribution to burbot diet by abundance did not differ over time ($P= 0.121$); however, the average abundance of alewives per burbot stomach decreased ($P= 0.027$, $R^2= 0.372$, Average abundance= $1097.167 - (0.545 * \text{YEAR})$) (Figure 8). Average proportion of cottid sculpin contribution to burbot diet decreased from 1999 through 2012 ($P= 0.027$,

$R^2 = 0.372$, Average % Contribution = $50.324 - (0.0250 * \text{YEAR})$ (Figure 9). Similarly, the average abundance of sculpin per burbot stomach decreased significantly ($P = 0.009$, $R^2 = 0.479$, Average Abundance = $298.803 - (0.148 * \text{YEAR})$) (Figure 9). Round goby average proportion of contribution to burbot diet increased from 1999 through 2012 ($P < 0.001$, $R^2 = 0.923$, Average % Contribution = $23255.5837 + (-23.2388 * \text{YEAR}) + (0.0058 * (\text{YEAR}^2))$) (Figure 10). From 1999 to 2005, round goby contribution was minimal and was near 0. During 2006-2012, round goby contribution to burbot diet went from ~20% to over 60% of the burbot diet items (Figure 10). Round gobies were found in burbot from shallow water (<39.99m) in 1999 and not until 2006 in burbot from deeper water (>39.99m). Average proportion of ninespine stickleback contribution to burbot diet did not change from 1999 to 2012 ($P = 0.833$). However, in burbot stomachs containing ninespine sticklebacks (NSP), there was a significant decrease in average abundance of NSP from 1999 through 2012 ($P = 0.009$, $R^2 = 0.473$, Average abundance of NSP = $795.732 - (0.396 * \text{Year})$) (Figure 11). Though there were no significant changes in bloater chub average proportion of contribution to burbot diet ($P = 0.162$), there did seem to be a decreasing trend (Figure 12), which is consistent with recent biomass estimates of bloater in Lake Michigan (Madenjian et al. 2010). There was no change in crayfish average proportion of contribution to burbot diet ($P = 0.329$) from 1999 through 2012, though 86.4% of all crayfish present in burbot diet were from 1999 and 2000. There was no significant relationship between dreissenid mussel appearance and round goby appearance ($P = 0.105$)

The southeast region (MM7 and MM8) only had 26 burbot samples over the 11 years of sampling in this region. There were no trends in average proportion of contribution of

alewife ($P= 0.576$), cottid sculpin ($P= 0.141$) or round goby ($P=0.146$) to burbot diet overtime in this region (Figure 13). The northeast region (MM6 and MM7) had 300 burbot samples over 14 years of sampling in this region. There was no temporal trend detected in average proportion of alewife contribution to burbot diet ($P= 0.060$). Cottid sculpin average proportion of contribution to burbot diet decreased significantly in the northeast region ($P= 0.033$, $R^2= 0.350$, Average % Contribution= $53.428 - (0.0265 * \text{YEAR})$). Round goby average proportion of contribution to burbot diet increased significantly in the northeast region in this same time period ($P < 0.001$, $R^2= 0.704$, Average % Contribution= $-85.849 + (0.0429 * \text{YEAR})$). Both cottid sculpin and round goby average proportion of contribution stayed relatively stable until 2007, when the two shifted in opposite directions (Figure 14). The north region (MM2 and MM3) had 85 burbot samples; however most were in 1999 or 2012, with many years lacking samples. Trends in average proportion of contribution to burbot diet of round gobies and cottid sculpins respectively were consistent with other regional patterns (Figure 15), as well as overall results (Figure 16)

Average total length of cottid sculpins consumed, including back calculated lengths increased from 62.9mm ($\pm 0.2\text{mm}$) in 1999 to 72.6mm ($\pm 0.7\text{mm}$) in 2012 ($P= 0.026$, $R^2= 0.377$, Average Cottid Sculpin Total Length= $-1272.868 + (0.670 * \text{YEAR})$) (Figure 17). Average total length of alewives including back calculated values did not change from 1999 to 2012 ($P= 0.654$). Average total length of round goby consumed increased from 58.00mm ($N= 1$) in 2000 to 87.28mm ($\pm 6.17\text{mm}$) ($N=25$) in 2012 ($P= 0.011$, $R^2= 0.687$, Average Round Goby Total Length= $-6855.458 + (3.451 * \text{YEAR})$) (Figure 18). Sample size for round goby average total length per year were all under ten gobies, except 2012.

DISCUSSION: The decrease in CPUE of burbot over the 14 year time series is consistent with decreasing burbot populations found in Lake Superior (Gorman and Sitar 2013) and Lake Michigan (Madenjian et al. 2013; Stapanian et al. 2013). The current decrease in Lake Michigan is of great importance considering the lack of knowledge regarding burbot population dynamics in the lake. This is particularly troubling considering burbot are essentially the only native top level fish predator left in Lake Michigan, and their previous declines associated with alewife predation on burbot larvae and sea lamprey predation on adult burbot (Madenjian et al. 2010) are unlikely the cause of the current decline. Similarly, the cause of the current decline of burbot in Lake Superior (Gorman and Sitar 2013), predation by juvenile lake trout, is unlikely the cause in Lake Michigan because lake trout have yet to display a full population recovery.

In all regions of this study, burbot diet composition from 1999-2006 consisted almost exclusively of alewives and cottid sculpin with small contributions from other species. Diet composition for 1999-2006 was consistent among all fishing depths in this study, indicating that burbot had not yet made a depth-dependent switch from cottid sculpin and alewives to round gobies. It is likely that burbot maintained their mixed pelagic/benthic feeding strategy until round goby abundance reached a level of optimal foraging for burbot. From 2006-2008, round goby became a major constituents of burbot diet, which is consistent with the findings of Jacobs et al. (2010) for northern Lake Michigan burbot. However, Jacobs et al. (2010) found higher occurrences of both burbot and rainbow smelt in the burbot diet, whereas my findings revealed almost exclusive round goby composition of the diet with a small contribution from cottid sculpin in the northern region during this time period. From 2008 to 2012, round gobies became the dominant

prey item of burbot in all regions with a small contribution from cottid sculpin and alewives.

With continued decline of burbot populations in Lake Michigan, it is likely that burbot will cease to exert any sort of predatory control over round goby in the future, unlike in eastern Lake Erie (Madenjian et al. 2011). In eastern Lake Erie, burbot have been shown to consume 61% of the annual recruitment of round goby (Madenjian et al. 2011). This lack of control could result in continued expansion of these non-native fish in Lake Michigan. It is also likely that with or without burbot exerting a predatory control on round goby, other piscivorous fish may take advantage of the abundance of round goby, and switch from partially to entirely benthic feeding, which would have serious implications for the Lake Michigan food web.

Though fewer burbot were captured in deeper samples (N= 74) compared to shallow samples (N=336), there was a seven year gap between the two depth bins for the appearance of round goby in the diet of burbot. This suggests that either round goby were not widespread/abundant in deeper water until later or burbot in deeper water maintained their original prey utilization despite round goby presence. It is profound to see how rapidly a non-native fish can suddenly become a main diet item of a native predator, despite it being present in Lake Michigan for over a decade. Far too often in diet studies, the impacts of a non-native fish are only examined after non-native prey become dominant prey items. The secondary spread of an invasive species is not a simple matter of the physical processes of diffusion (Johnson et al. 2012). The concept of secondary spread of invasives may help explain the lag witnessed between round goby introduction to Lake Michigan and when round gobies became common in burbot diet. Once round

gobies appeared in burbot diet, their contribution to burbot diet increased exponentially. This rapid expansion of round goby as prey items may be indicative of their abundance increasing as a result of overcoming environmental and demographic constraints (Johnson et al. 2012).

Burbot in this study did not consume a lot of rainbow smelt (*Osmerus mordax*), deepwater sculpin (*Myoxocephalus thompsonii*), or burbot. These are surprising results considering both rainbow smelt and deepwater sculpin have historically constituted a significant portion of the burbot diet in Lake Michigan (Madenjian et al. 2005b; Madenjian et al. 2010), and burbot in the north diet region have been shown to be cannibalistic (Jacobs et al. 2010).

Relative to earlier reports of prey fish abundances in Lake Michigan, several prey-fish species, including alewife, bloater, rainbow smelt, and deepwater sculpin have shown a decline. A decrease in alewife abundance has been suggested to be due to high recruitment/natural reproduction of Chinook salmon and continued stocking, resulting in increased predation pressure (Bunnell 2012). This is consistent with lower contribution of alewife to burbot diet in recent years. However, the decrease in cottid sculpin contribution from 1999 through 2012 remains unexplained. Cottid sculpin biomass during 2005-2011 was 2.5 times greater than mean biomass estimates over the previous 32 years (Bunnell 2012). These data may provide support for a behavioral-based feeding strategy shift from native sculpin to non-native round goby in the benthic zone. This may be beneficial to burbot considering the recent overall increase in benthic biomass due to dreissenid mussels (Nalepa et al. 2009). This change in feeding behavior may aid in returning the benthic zone to a status of nutrient source to upper trophic levels rather than

a nutrient sink (currently), through burbot predation on round goby. This unexplained prey switch from abundant cottid sculpin to abundant round goby should be evaluated further to determine potential benefits of this switch.

TABLES:

Table 1 Stomach contents from burbot diet analysis including major and minor prey items

| Stomach Contents | Count |
|---|--------------|
| Alewife (<i>Alosa pseudoharengus</i>) | 2340 |
| Cottid sculpin (<i>Cottus</i>) | 951 |
| Dreissenid mussels | 514 |
| Round goby (<i>Neogobius melanostomus</i>) | 358 |
| Ninespine stickleback (<i>Pungitius pungitius</i>) | 303 |
| Bloater chub (<i>Coregonus hoyi</i>) | 240 |
| Crayfish (Cambaridae) | 106 |
| Empty | 61 |
| Rock | 55 |
| Unidentified fish | 32 |
| Tapeworm (Platyhelminthes) | 27 |
| Johnny darter (<i>Etheostoma nigrum</i>) | 18 |
| Egg mass | 9 |
| Wood | 8 |
| Rainbow smelt (<i>Osmerus mordax</i>) | 7 |
| Snail (Gastropoda) | 4 |
| Burbot (<i>Lota lota</i>) | 2 |
| Coregoninae | 2 |
| Deepwater sculpin (<i>Myoxocephalus thompsonii</i>) | 2 |
| Asellidae | 1 |
| Mysis | 1 |
| Unidentified sculpin spp | 1 |
| Walleye (<i>Sander vitreus</i>) | 1 |

Table 2 The number of burbot samples from sites sampled more than one year, and the frequency of catch from 0-19.99m, 20-39.99m, and 40-59.99m.

| Site | 0- 19.99m | 20- 39.99m | 40- 59.99m | Total |
|-------------|------------------|-------------------|-------------------|--------------|
| Arcadia | 27 | 126 | 50 | 203 |
| Leland | 57 | 26 | 11 | 94 |
| Saugatuck | 10 | 4 | 4 | 18 |
| Charlevoix | 6 | 8 | 3 | 17 |
| Grand Haven | 4 | 6 | 2 | 12 |
| Irishmans | 3 | 9 | 0 | 12 |
| South Haven | 5 | 0 | 2 | 7 |

Table 3 Study-wide summary of burbot capture sites and the number of burbot caught per year per site. N (No netting performed), 0 (No burbot caught).

| Site | 1999 | 2000 | 2001 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | Total |
|-------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|-------|
| Arcadia | 20 | 29 | 9 | 21 | 21 | 24 | 25 | 11 | 13 | 13 | 4 | N | 21 | 211 |
| Big Reef | 12 | N | N | N | N | N | N | N | N | N | N | N | N | 12 |
| Cathead | N | N | 24 | N | N | N | N | N | N | N | N | N | N | 24 |
| Charlevoix | N | 1 | 4 | 9 | 3 | N | 15 | 0 | N | 0 | N | N | 3 | 35 |
| Fox Islands | N | 8 | N | N | N | N | N | N | N | N | N | N | N | 8 |
| Frankfort | N | N | N | N | N | N | N | N | N | N | N | 13 | N | 13 |
| Good Harbor | N | N | 5 | N | N | N | N | N | N | N | N | N | N | 5 |
| Grand Haven | 3 | 7 | N | N | 2 | 2 | N | N | 0 | 1 | 1 | N | 2 | 18 |
| Gull Island Shoal | 32 | N | N | N | N | N | N | N | N | N | N | N | N | 32 |
| Irishmans | 6 | 1 | N | N | N | N | N | N | N | N | N | N | 5 | 12 |
| Leland | N | N | N | 15 | 20 | 12 | 23 | 6 | 10 | 25 | N | N | 10 | 121 |
| Manistee | N | N | 2 | N | N | N | N | N | N | N | N | N | N | 2 |
| Manistique | 16 | N | N | N | N | N | N | N | N | N | N | N | N | 16 |
| Middle Ground | N | N | N | N | N | N | N | N | N | N | N | N | 7 | 7 |
| North Fox Island | 7 | N | N | N | N | N | N | N | N | N | N | N | N | 7 |
| Saugatuck | N | 2 | 1 | 0 | 2 | 3 | 3 | 0 | 1 | N | 4 | 2 | 0 | 18 |
| South Fox Island | 3 | N | N | N | N | N | N | N | N | N | N | N | N | 3 |
| South Haven | N | 1 | N | 0 | N | N | N | 0 | N | 2 | 0 | 2 | 2 | 7 |

FIGURES:



Figure 1 The diet regions that burbot in this study were collected from in accordance with the Lakewide Assessment Plan for Lake Michigan Fish Communities (LAPLMFC).

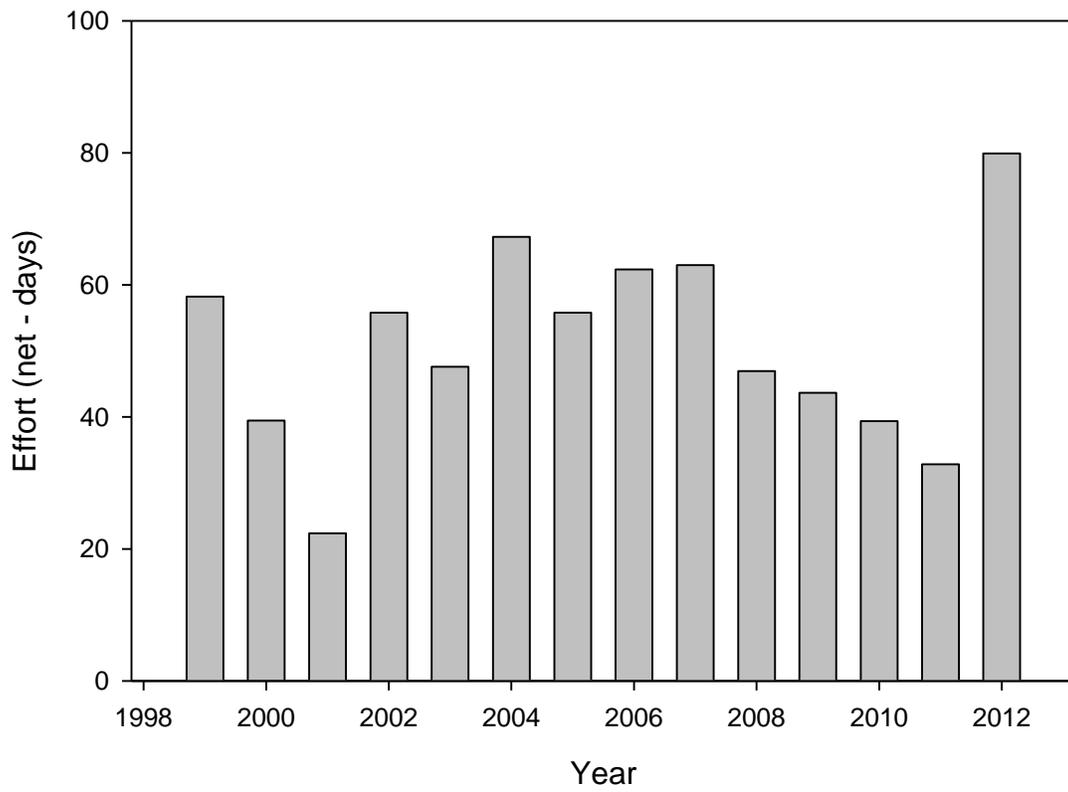


Figure 2 Gill net effort (net-days) from 1999 to 2012 in eastern Lake Michigan.

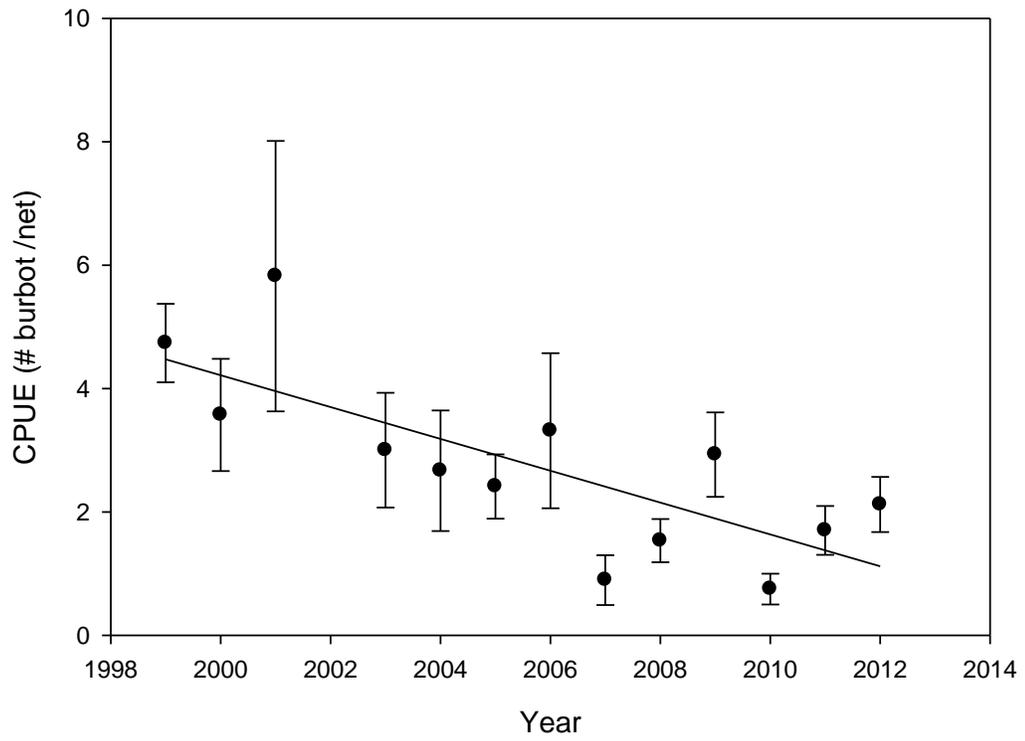


Figure 3 Catch Per Unit Effort (CPUE) as abundance of burbot per gill net from 1999-2012 Lake Michigan sampling. Points represent mean CPUE values with standard error bars. $P=0.003$, $R^2=0.571$, $CPUE=520.21 - (0.258 * year)$

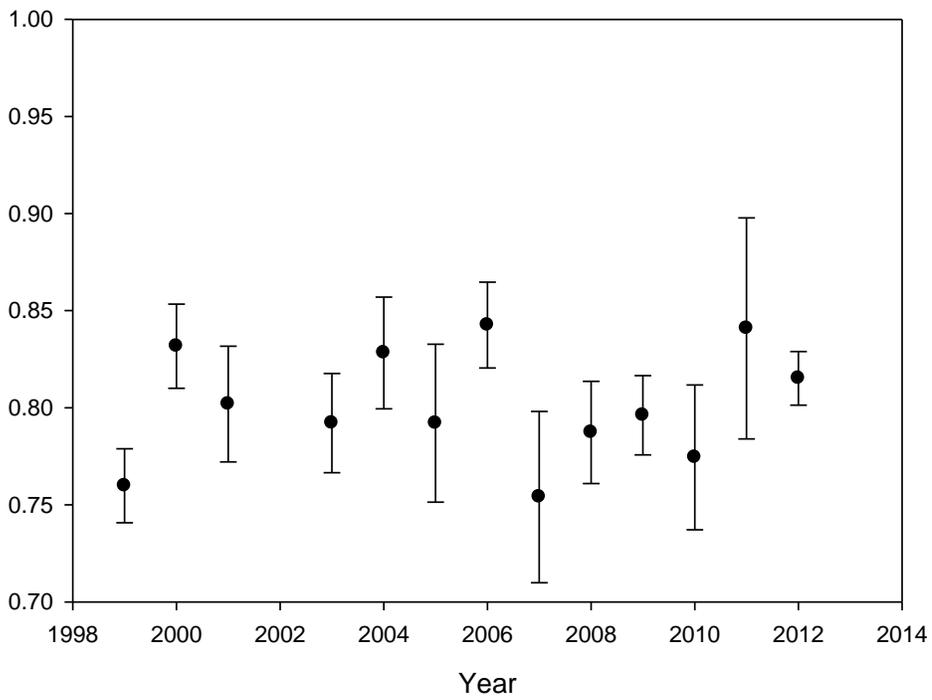
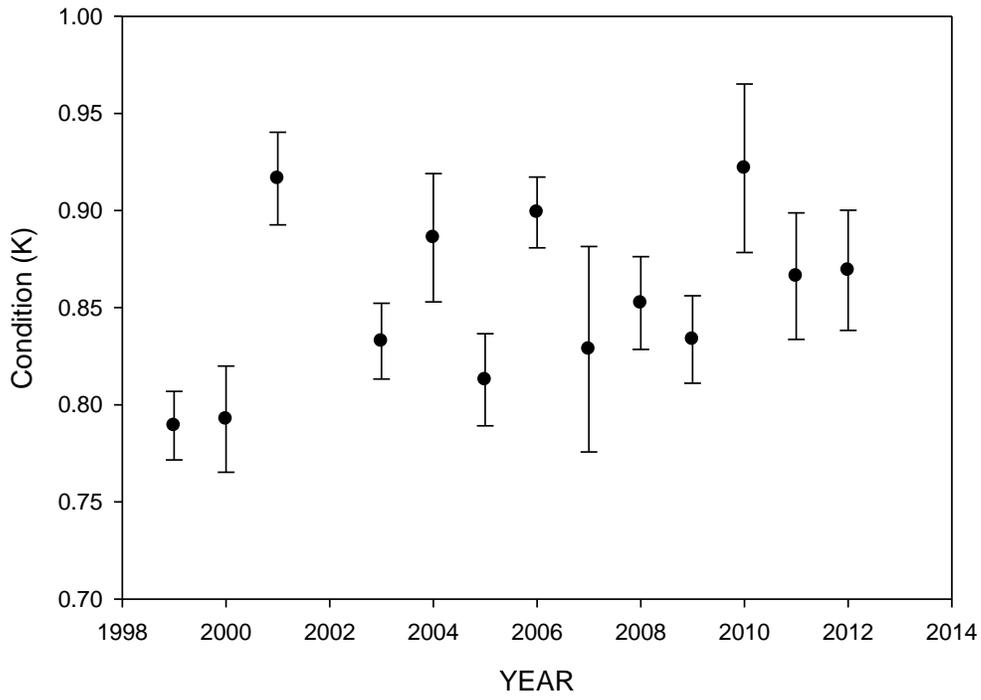


Figure 4 Average yearly condition factor for female (Top) and male (Bottom) burbot from 1999 to 2012 with standard error bars.

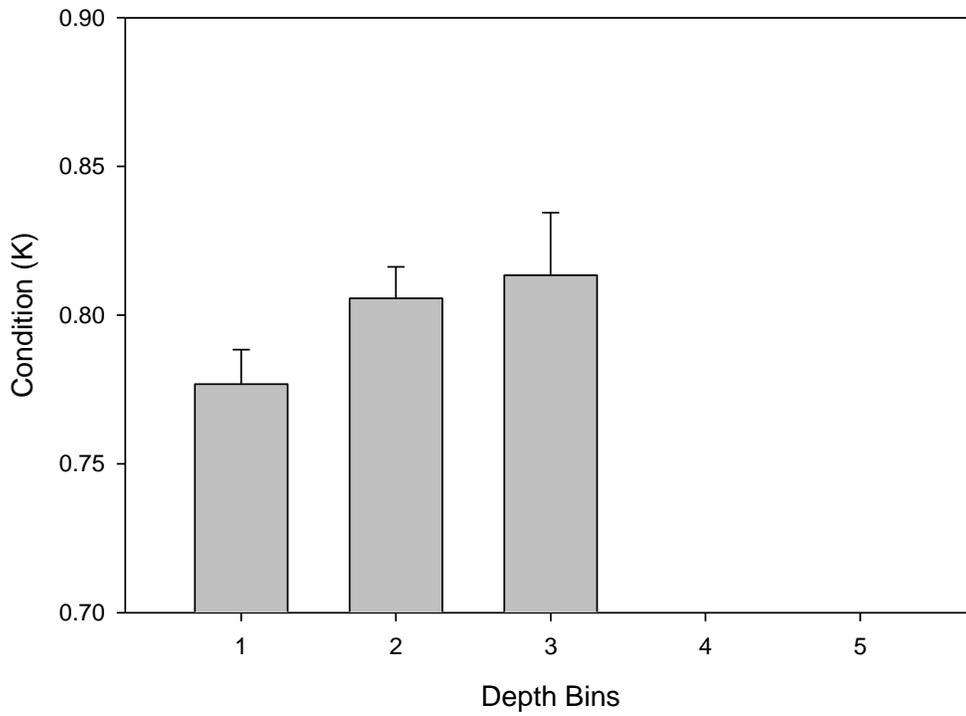
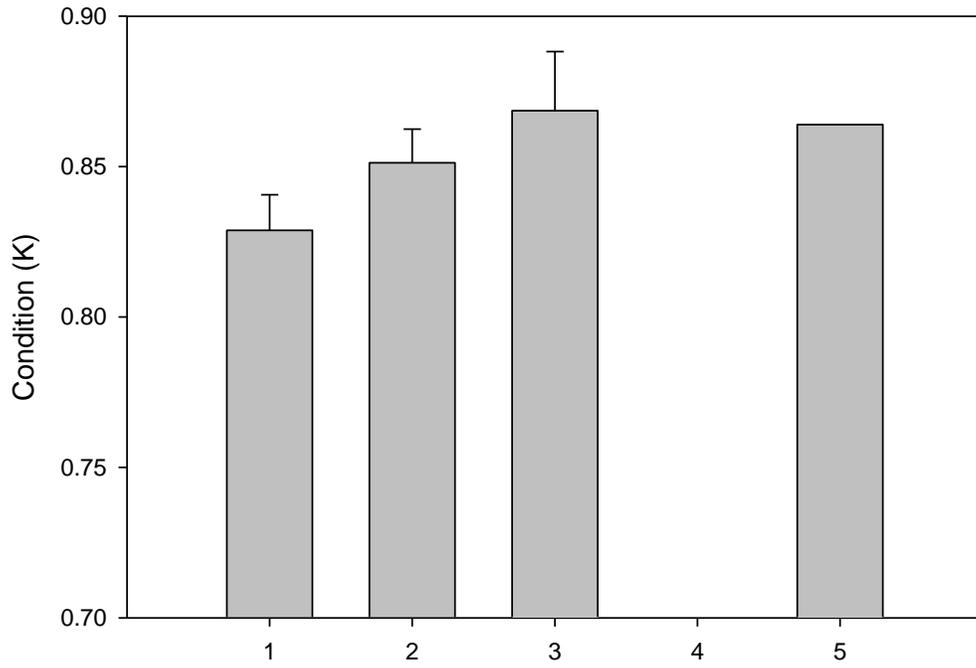


Figure 5 Average condition factor of female (Top) and male (Bottom) burbot across depth bins 1 (0-19.99m) 2 (20-39.99m) 3 (40-59.99m) 5 (80-99.9m).

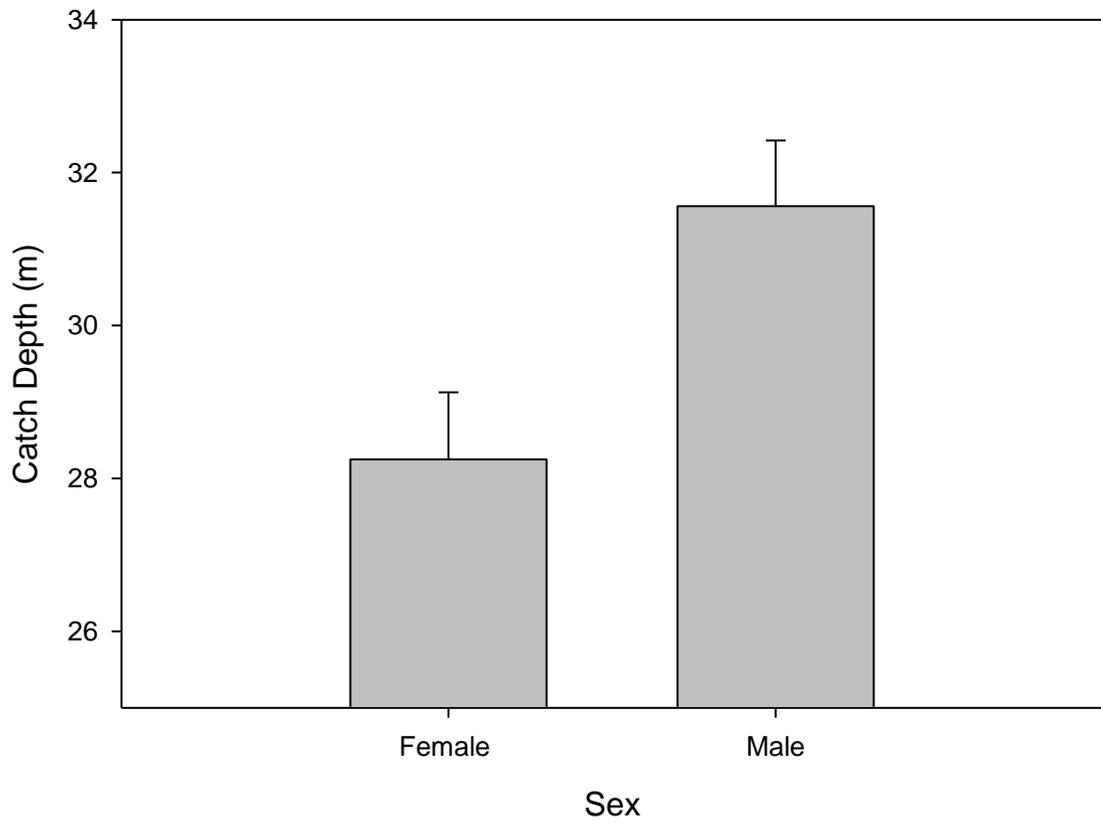


Figure 6 Average catch depth of male and female burbot with standard error bars.

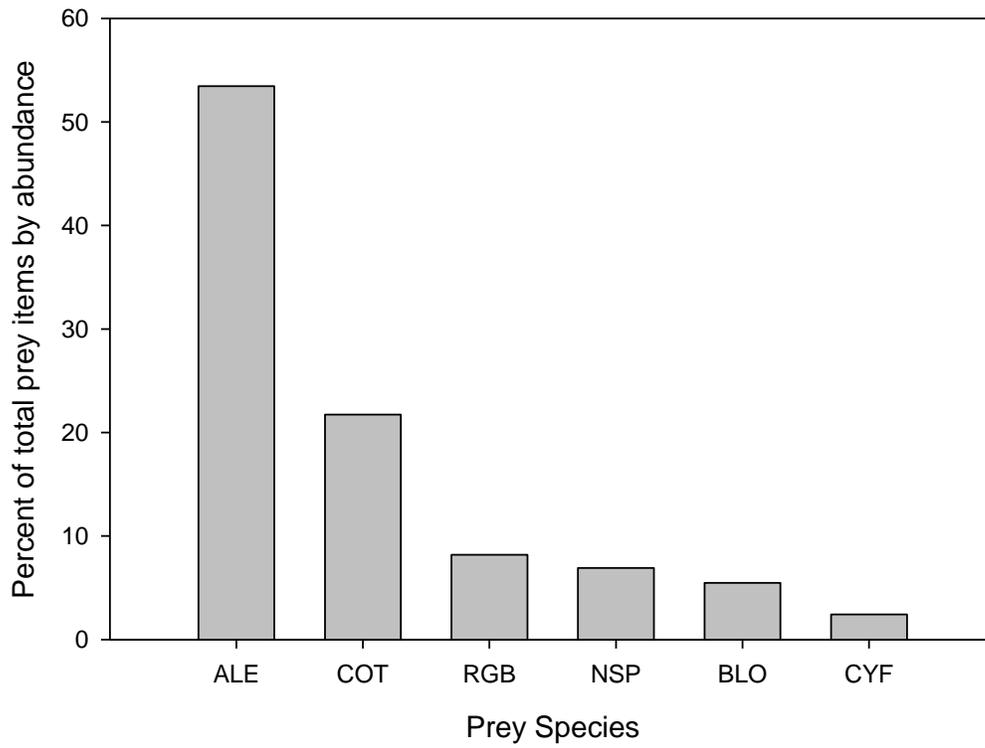


Figure 7 The six most common prey items and their percent contribution to overall prey total by abundance. ALE (Alewife), COT (Cottid sculpin), RGB (Round goby), NSP (Ninespine stickleback), BLO (Bloater), and CYF (Crayfish).

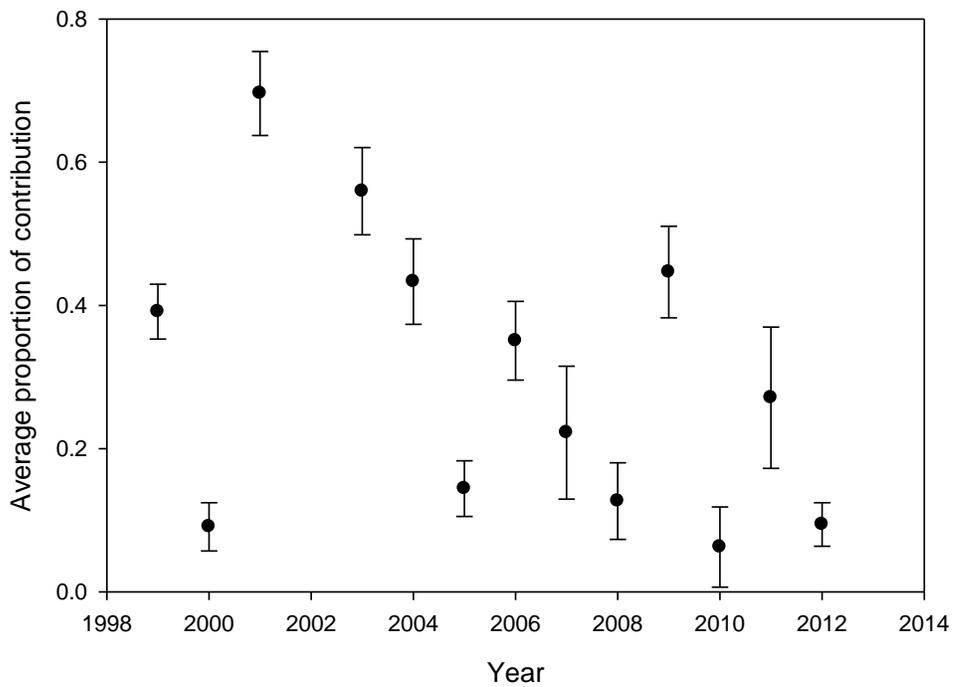
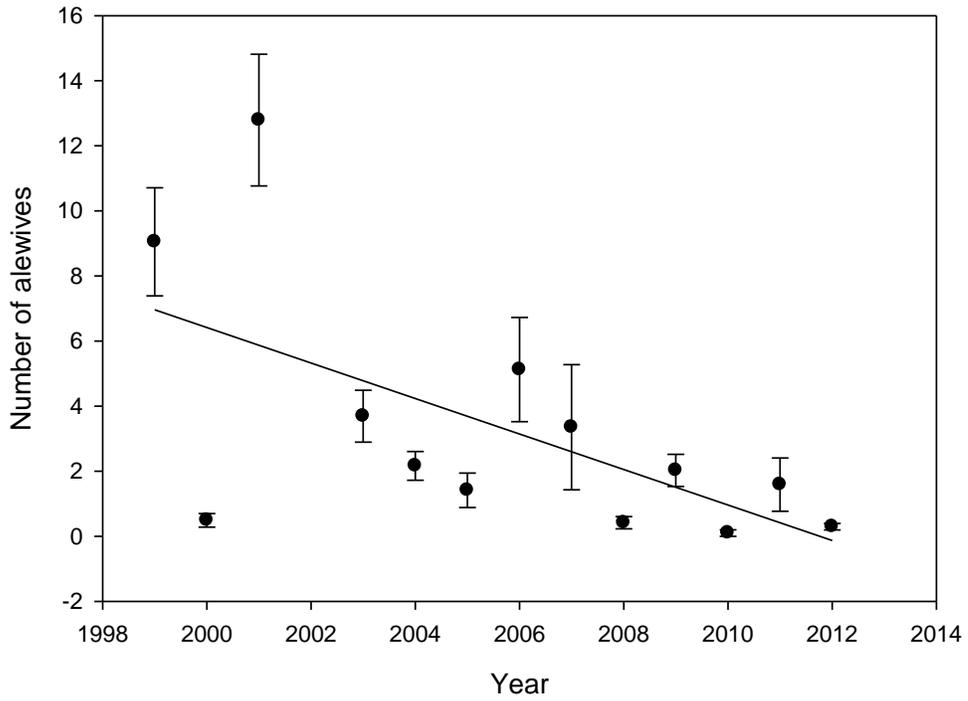


Figure 8 Average abundance of alewives per burbot stomach linear regression with standard error bars (Top) $P=0.0027$, $R^2=0.372$, $Abundance=1097.2-(0.545 * Year)$ and Average yearly proportion of contribution of alewives to burbot diet with standard error bars (bottom) $P=0.121$.

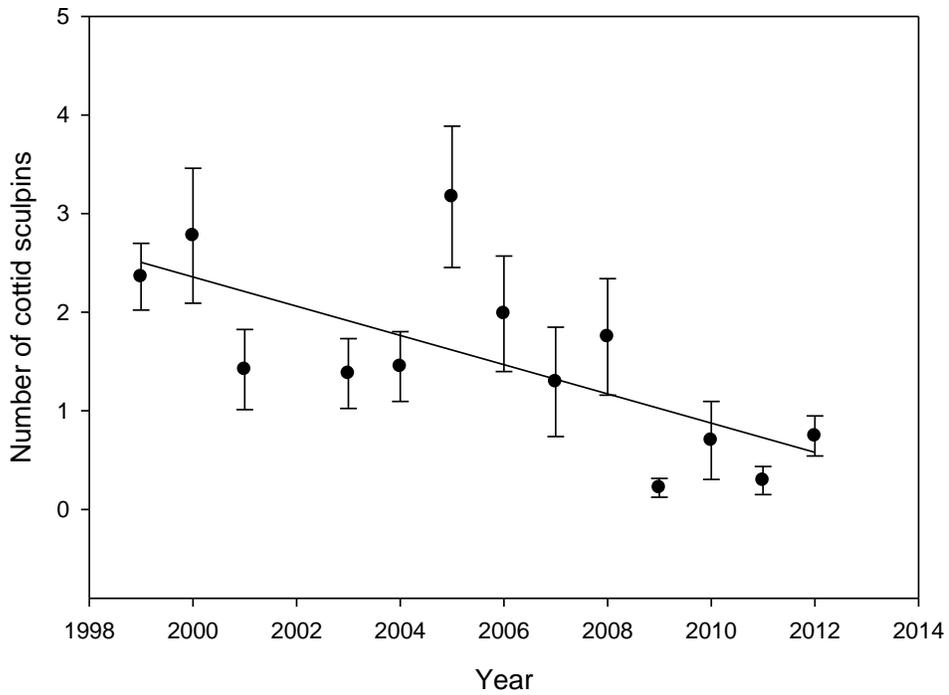
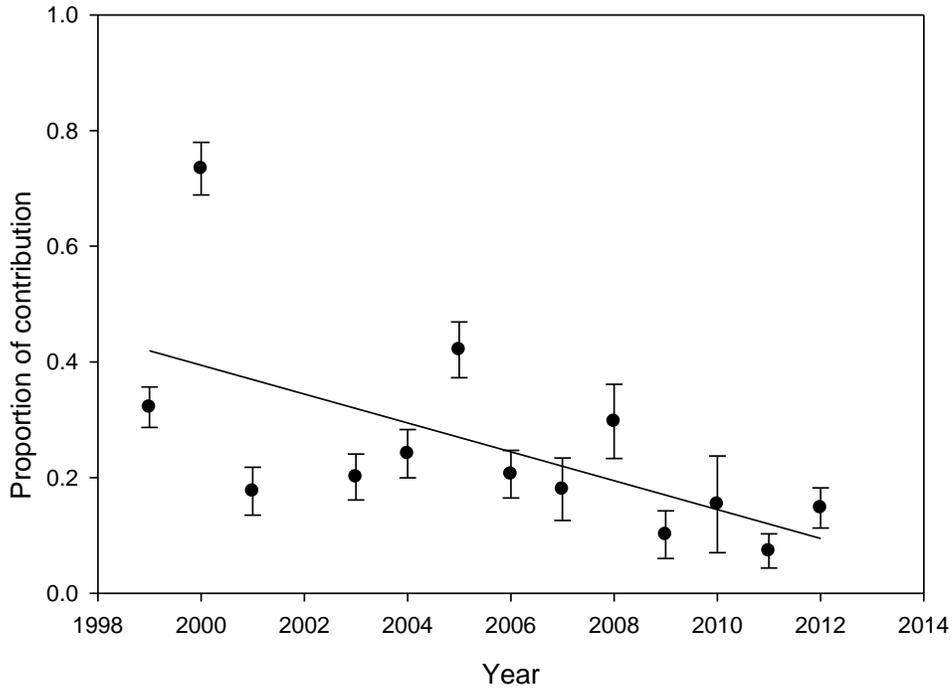


Figure 9 Average yearly proportion of contribution of cottid sculpin to burbot diet linear regression with standard error bars (Top) $P= 0.0027$, $R^2= 0.372$, proportion of contribution= $50.324 - (0.0250 * \text{Year})$ and average abundance of cottid sculpin per burbot stomach linear regression with standard error bars (Bottom) $P= 0.009$, $R^2= 0.479$, Abundance= $298.903 - (0.248 * \text{Year})$.

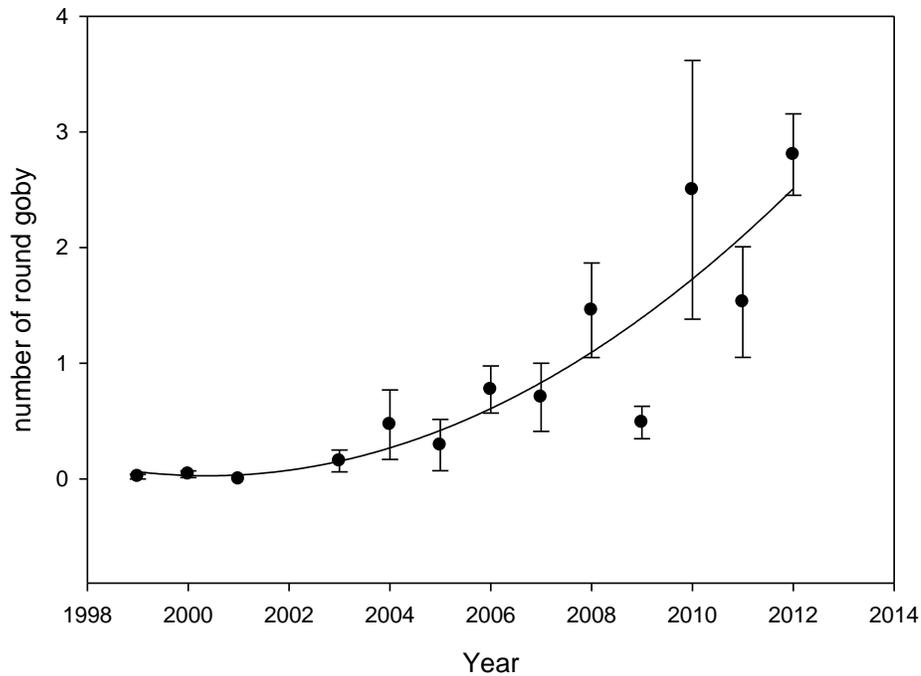
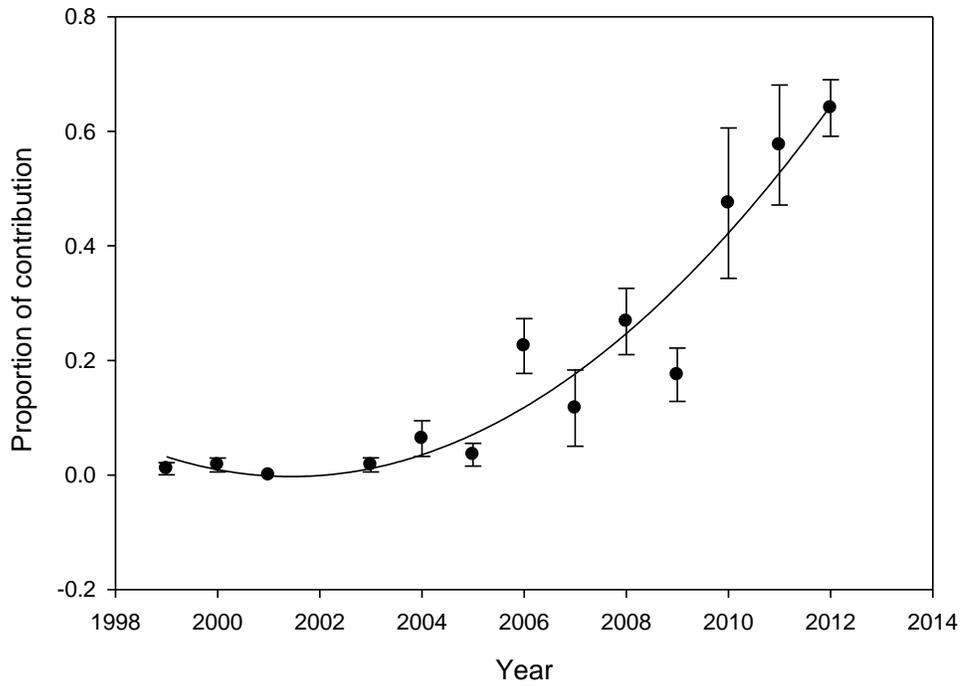


Figure 10 Non-linear quadratic regression of average proportion round goby contribution to burbot diet by abundance with regression line and standard error bars (Top) $P < 0.001$, $R^2 = 0.923$, proportion of contribution = $23255 + (-23.239 * \text{Year}) + (0.0058 * (\text{Year}^2))$ and non-linear quadratic regression of average number of round goby per burbot with regression line and standard error bars (Bottom) $P < 0.001$, $R^2 = 0.804$, abundance = $73534 + (-73.521 * \text{Year}) + (0.0184 * (\text{Year}^2))$.

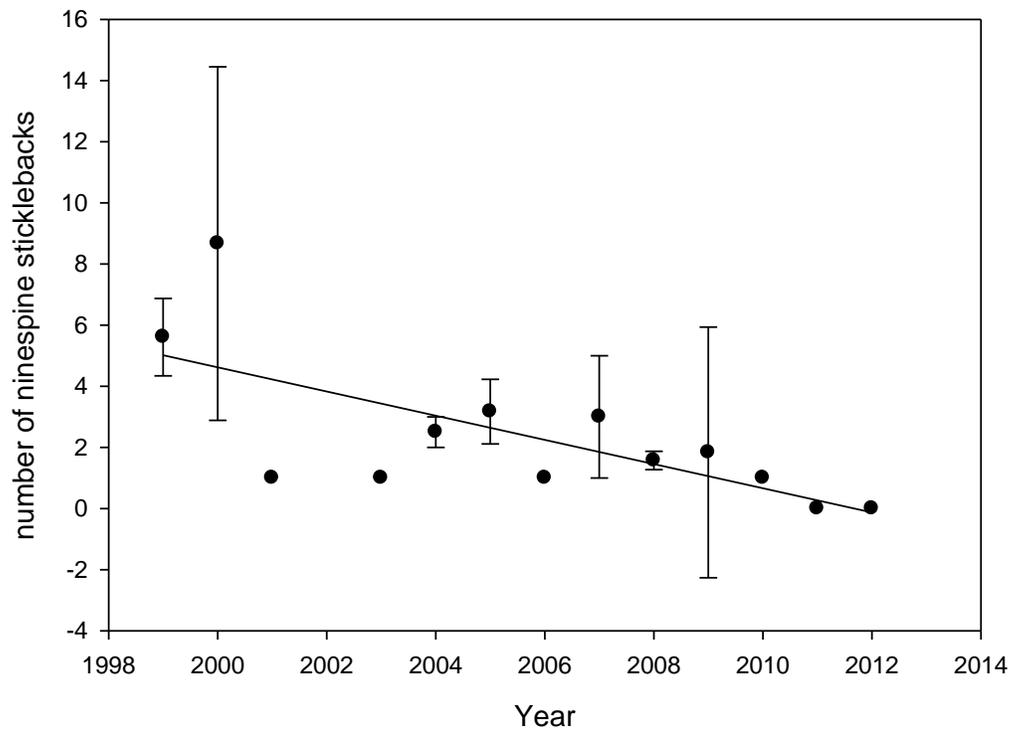
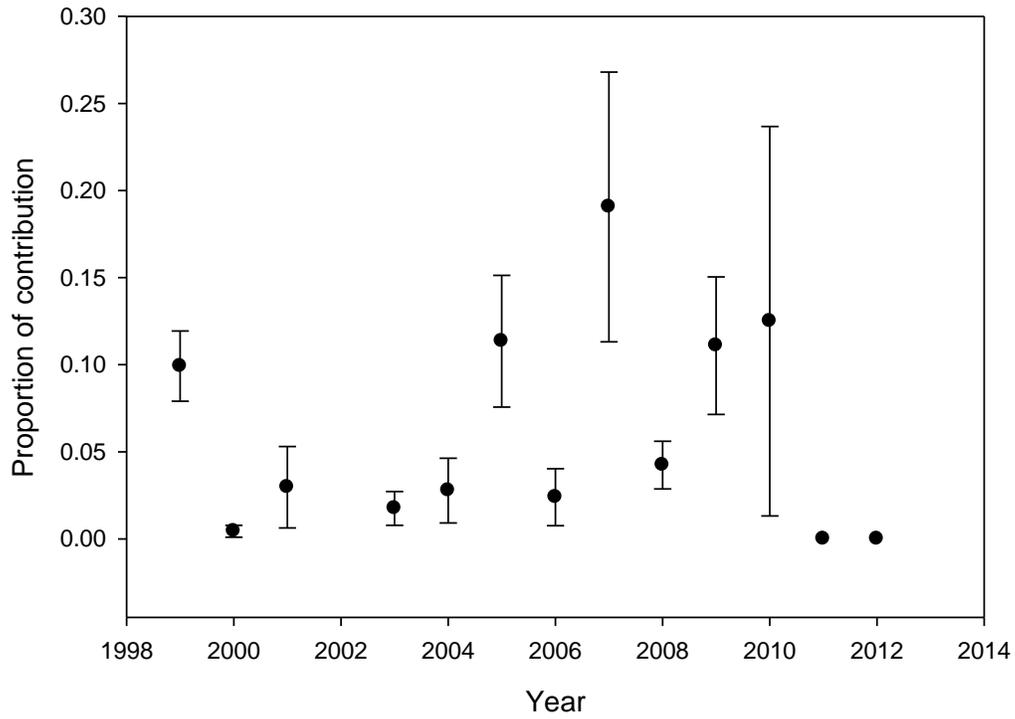


Figure 11 Average proportion of contribution of ninespine stickleback to burbot diet by abundance with standard error bars (Top) $P= 0.833$ and average abundance of ninespine sticklebacks in burbot stomachs containing at least one ninespine stickleback from 1999 to 2012 with regression line and standard error bars (Bottom) $P= 0.009$, $R^2= 0.473$, $Abundance= 795.7 - (0.396 * Year)$.

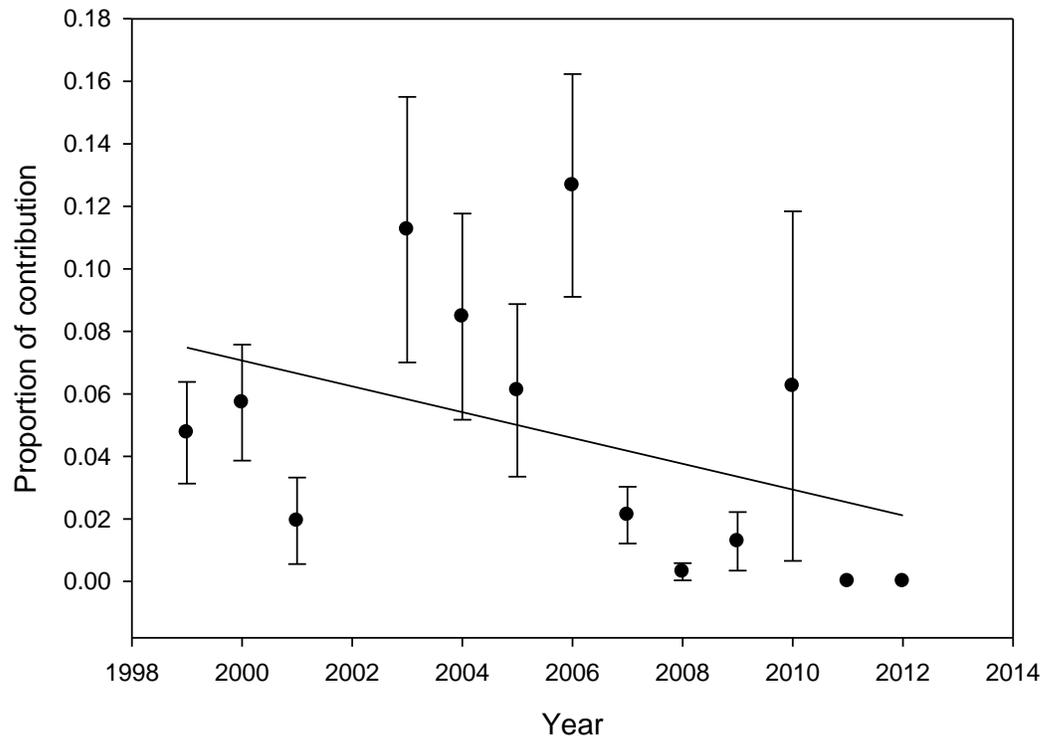


Figure 12 Average proportion of contribution of bloater to burbot diet by abundance with regression line and standard error bars $P=0.162$.

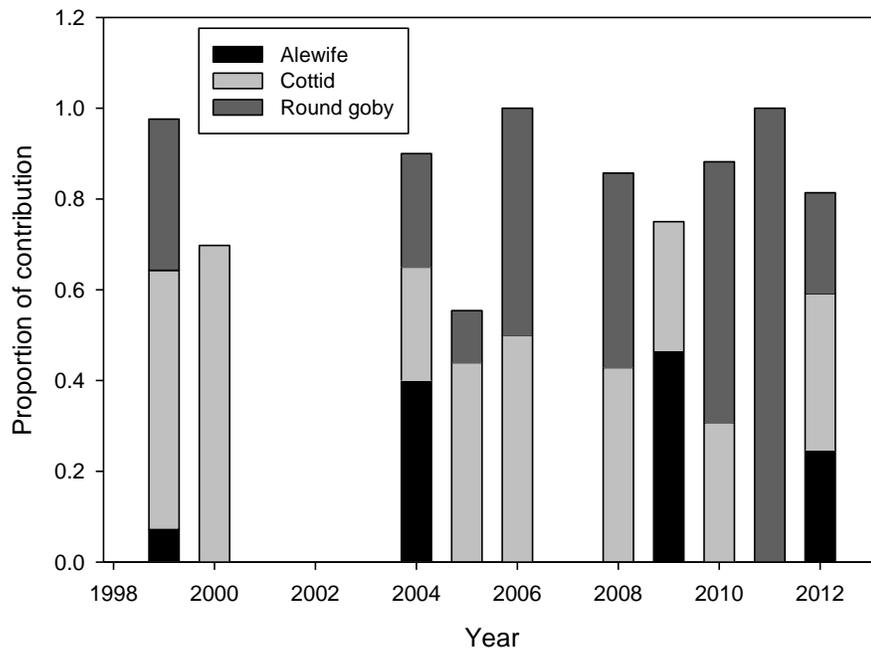


Figure 13 Proportion of contribution of alewife, cottid sculpin, and round goby to burbot diet by abundance in southeast region (MM7 and MM8) from 1999 to 2012.

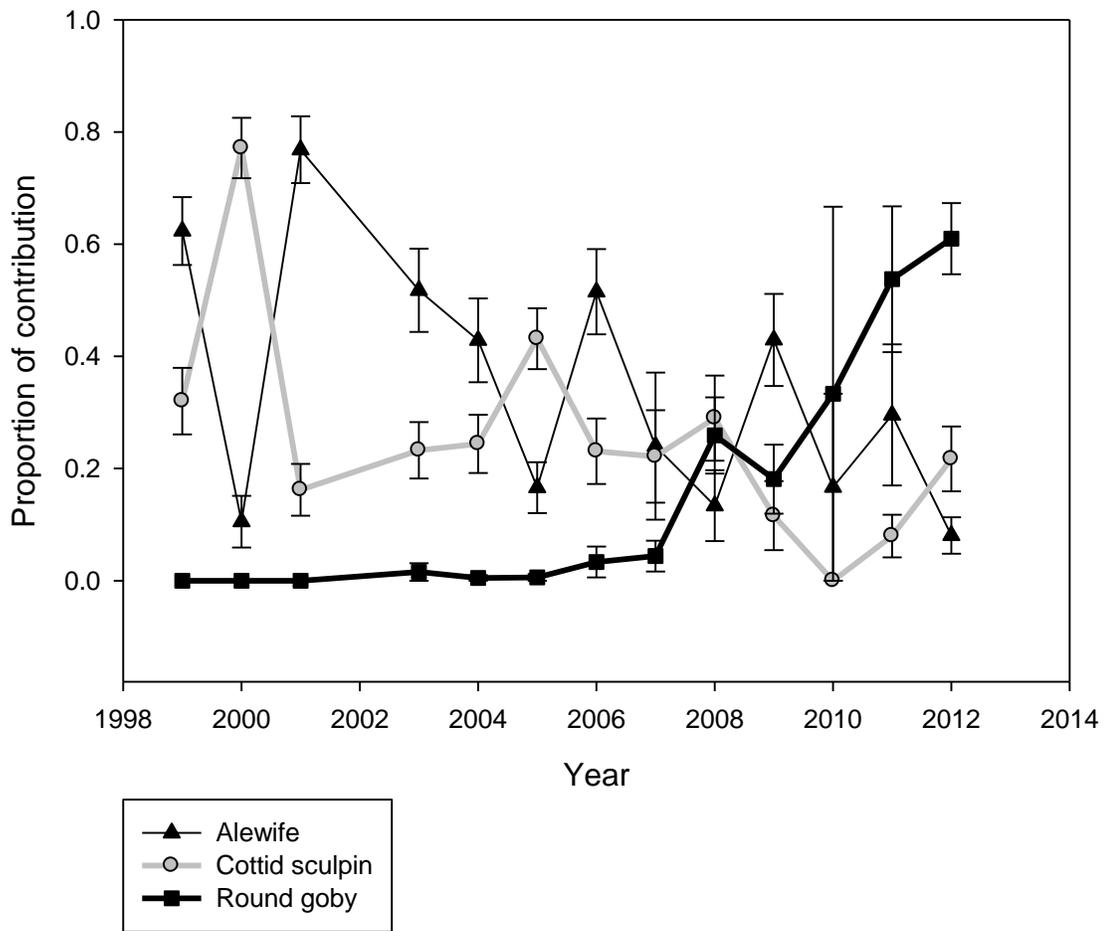


Figure 14 Average proportion of contribution of alewife, cottid sculpin, and round goby to burbot diet by abundance in the northeast region (MM5 and MM6) from 1999 to 2012 with standard error bars.

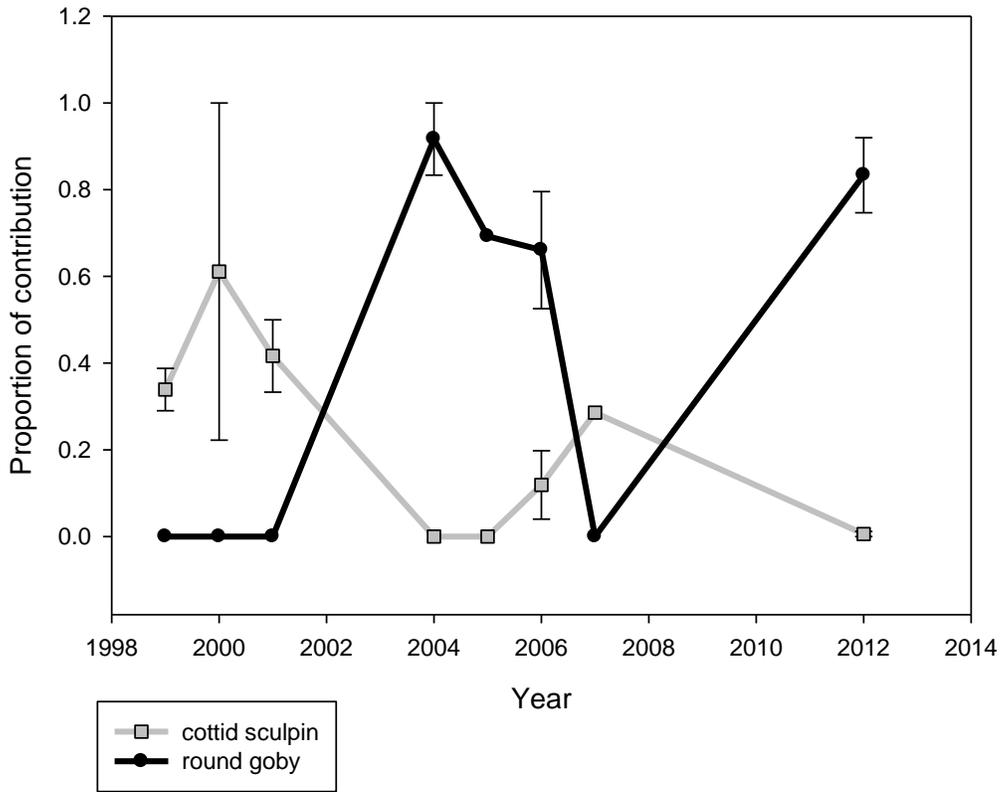


Figure 15 Average proportion of contribution of round goby and cottid sculpin to burbot diet by abundance in north region (MM2 and MM3) 1999 through 2012 with standard error bars.

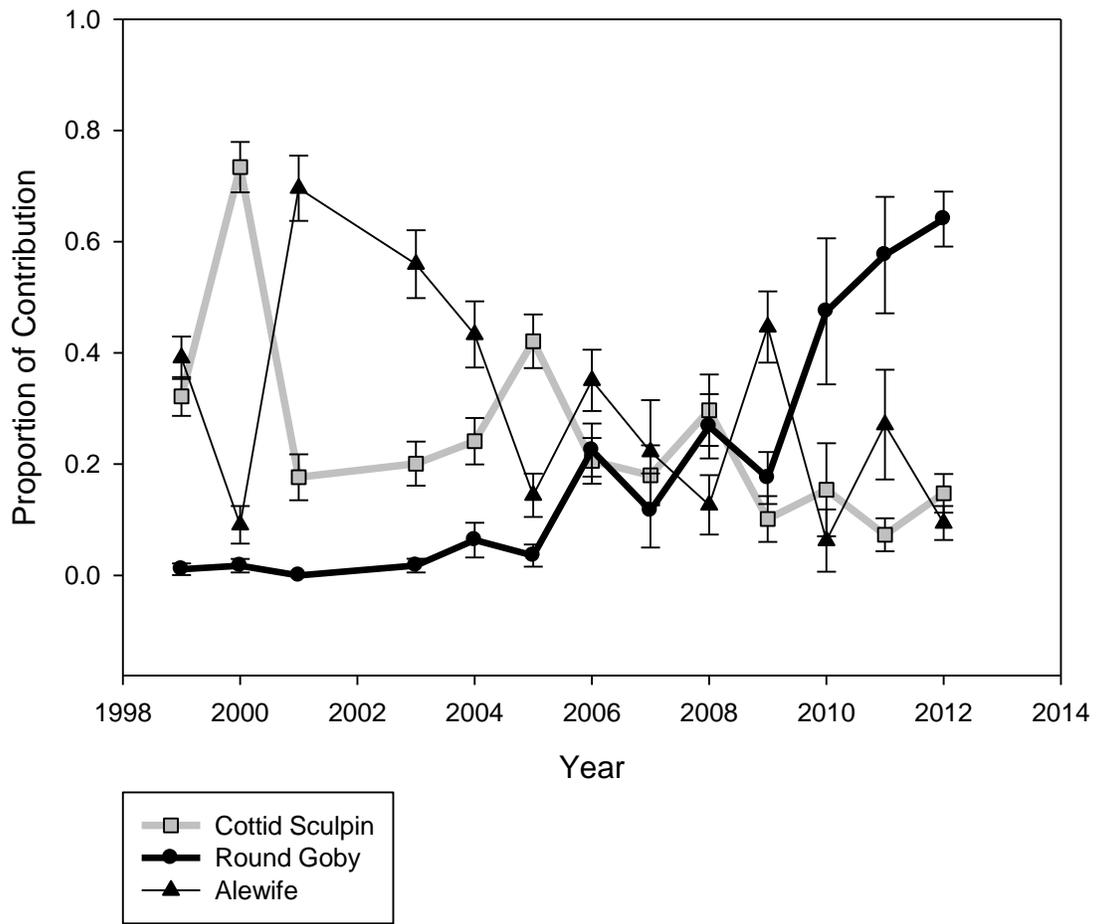


Figure 16 Average proportion of contribution of round goby, cottid sculpin, and alewife to burbot diet by abundance overall from 1999 through 2012 with standard error bars.

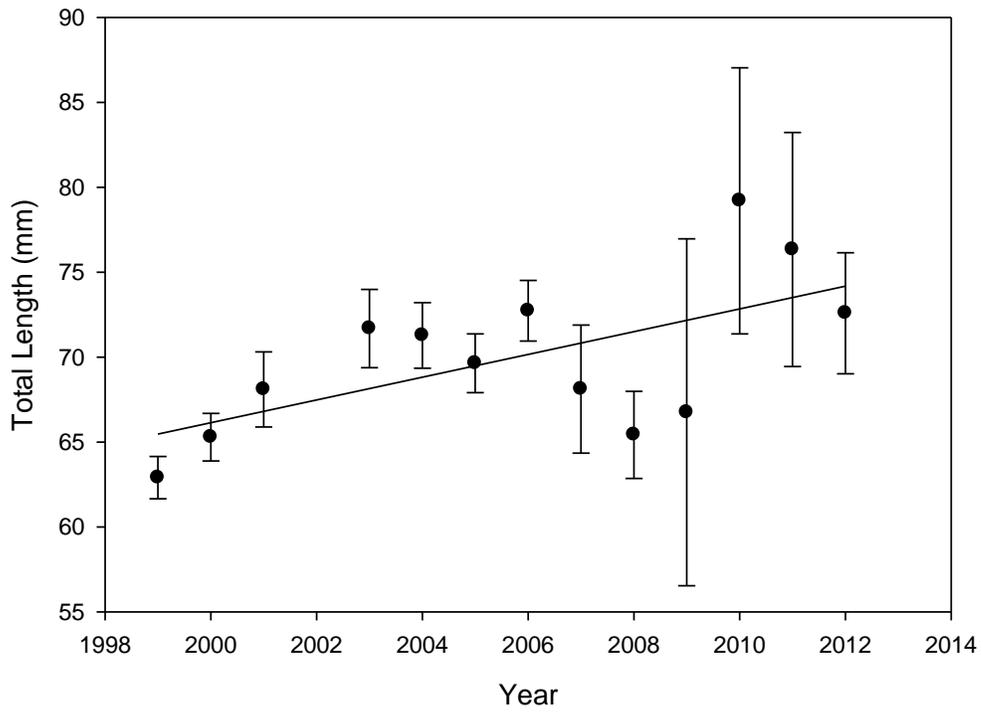


Figure 17 Average total length of cottid sculpin consumed from 1999 to 2012 including back calculated lengths regression line and standard error bars $P= 0.026$, $R^2= 0.377$, total length= $-1272 + (0.670 * \text{Year})$.

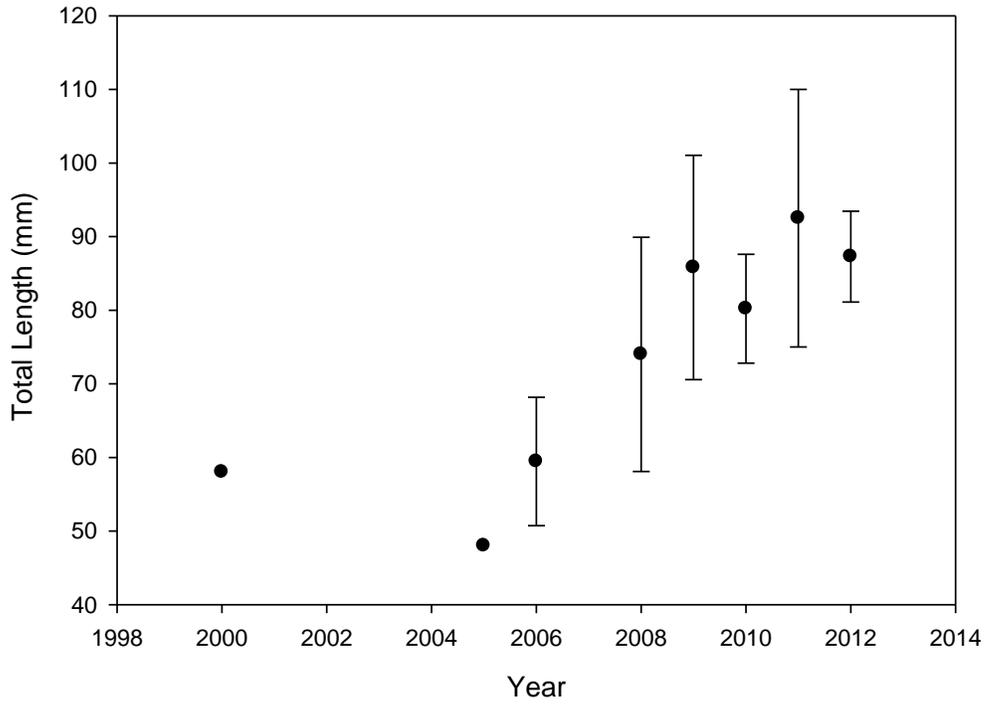


Figure 18 Average total length of round gobies consumed from 1999 to 2012 with standard error bars. $P=0.011$, $R^2=0.687$, total length = $-6855 + (3.451 * \text{Year})$.

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