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## Round Goby, *Neogobius Melanostomus*, Abundance and Productivity in the Rocky Nearshore Zone of Lake Michigan

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ROUND GOBY, *NEOGOBIOUS MELANOSTOMUS*, ABUNDANCE AND PRODUCTIVITY IN  
THE ROCKY NEARSHORE ZONE OF LAKE MICHIGAN

by

Graceanne Tarsa

A Thesis Submitted in

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The University of Wisconsin-Milwaukee

August 2021

## ABSTRACT

### ROUND GOBY, *NEOGOBIOUS MELANOSTOMUS*, ABUNDANCE AND PRODUCTIVITY IN THE ROCKY NEARSHORE ZONE OF LAKE MICHIGAN

by

Graceanne Tarsa

The University of Wisconsin-Milwaukee, 2021  
Under the Supervision of Professor Harvey Bootsma

Few organisms are well adapted to efficiently feed on invasive dreissenid mussels, a dominant primary consumer in Lake Michigan and other lower Great Lakes. As a result, these mussels represent a potential trophic dead-end. However, round gobies (*Neogobius melanostomus*), an invasive species introduced to the Great Lakes region at the end of the 20<sup>th</sup> century, possess several adaptive advantages that allow them to make dreissenid mussels a significant portion of their diet. Since their invasion, round gobies have become the predominant shallow nearshore fish in Lake Michigan and their success, along with the success of dreissenid mussels, has caused major shifts in regional productivity, trophic structure, and energy flow pathways in the lake.

In the Great lakes, round gobies have been incorporated into the diets of numerous piscivorous species, and therefore may serve as a conduit of energy, nutrients, and contaminants to higher trophic levels. This potential has made round gobies a critical species to consider in management plans, especially in regions important for Great Lakes fisheries. For management to be successful, a deeper understanding of round gobies' effect on food web structure and energy flow is needed. This research aimed to quantify round goby abundance and productivity in the rocky nearshore zone of Lake Michigan, focusing on a rocky reef (10-11 m depth) in Good

Harbor Bay near Sleeping Bear Dunes National Lakeshore (SLBE) that has historically been used for spawning and feeding by native fish species such as lake trout and lake whitefish.

Productivity was estimated by quantifying several population and bioenergetic parameters in June-October 2020. Benthic sampling provided biomass estimates of nearshore primary producers and consumers as well as a stable isotope trophic baseline. Round goby population density and size-frequency were determined using visual and video transects. Age structure was estimated from sagittal otoliths and combined with length data to model growth. Round goby diet composition was determined based on gut content and stable isotope analysis and used to estimate the population's reliance on benthic algae production vs. dreissenid grazing of phytoplankton. The combination of these methods allowed for an estimate of total round goby productivity on the rocky reef. A comparison of round goby productivity with energy inputs in the rocky nearshore zone allowed for trophic transfer efficiency to be estimated.

Mean round goby density was  $2.6 \text{ individuals} \cdot \text{m}^{-2}$ . The population was found to have a right-skewed unimodal size distribution with a mean size of  $7.3 \pm 2.4 \text{ cm}$  ( $n = 1304$ ) and a maximum size of 15.9 cm. Males from Good Harbor Reef have a faster growth rate and obtain a greater maximum size and age than females. Diet analysis indicated an ontogenetic diet shift, with larger gobies being more reliant on invasive mussels than smaller gobies. However, at the population level, non-mussel benthic invertebrates accounted for over half of round goby prey. Round goby productivity was estimated to be  $0.009 \text{ g wet weight} \cdot \text{day}^{-1} \approx 0.041 \text{ kJ} \cdot \text{day}^{-1}$ . This resulted in an estimated reef transfer efficiency of 1.3 – 1.8% when accounting for both dreissenid and non-dreissenid benthic invertebrates. This low efficiency is due to only a small fraction of dreissenid production (3%) being consumed by round gobies. By contrast, round gobies appear to be consuming virtually all (81 – 122%) non-dreissenid benthic invertebrate

productivity. On a lake-wide scale, annual round goby productivity was estimated to be four times that of recent estimates of alewife production. These results suggest that round gobies represent a substantial portion of Lake Michigan prey fish biomass and have the potential to serve as an important energetic conduit from the benthic region and invasive mussels to upper trophic levels.

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## Chapter 1: Introduction

### 1.1 Background Information

Since the connection of the Great Lakes to the global shipping industry, numerous invasive species have entered the region. A particularly notorious set of invaders are zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis bugensis*) mussels, which both originated from eastern Europe and traveled to the Great Lakes via ballast water. Zebra mussels were first discovered in Lake St. Clair in 1988 but are thought to have invaded several years prior (Herbert et al., 1989). Isolated populations were quickly found in all five Laurentian Great Lakes (Griffiths et al., 1991), and zebra mussels soon dominated the benthic region in shallow nearshore areas. The congeneric quagga mussel soon followed, entering the Great Lakes region sometime between 1989 and 1991 (May and Marsden, 1992). In part due to their superior juvenile growth rates (Baldwin et al., 2002) and ability to survive under low food conditions (Nalepa et al., 2010), quagga mussels slowly began to displace zebra mussels (Mills et al., 1999). As quagga mussels colonized offshore regions as well as nearshore (Fahnenstiel et al., 2010a), they altered both the physical and chemical properties of the benthic region (Coleman and Williams, 2002; Hecky et al., 2004). In Lake Michigan, zebra mussel populations peaked in 2002/2004 before declining to nearly  $0 \cdot \text{m}^{-2}$  by 2008 (Nalepa et al., 2010).

Quagga mussels play a unique role in the food web as efficient filter feeders and ecosystem engineers. By drawing in the surrounding water and extracting phytoplankton, mussels strip the water column of particulate matter, including organic material, directly and indirectly influencing nutrient and energy dynamics. As mussels feed, some of the harvested energy is



Figure 1: Quagga mussels and *Cladophora* on lake bottom. Photo by Harvey Bootsma, 2020.

invested in the production of new mussel biomass while a large portion is egested as feces and pseudofeces, collectively referred to as biodeposits (Hecky et al., 2004), and an even larger portion is respired as CO<sub>2</sub> (DeVilbiss and Guo, 2017). The egested phosphorus-rich material concentrates in the benthic region where it can be readily used by

detritivores and benthic algae. Ultimately, the cycle redistributes phosphorus from pelagic to benthic communities in what is termed the “phosphorus shunt” (Hecky et al., 2004). Recent model simulations of Lake Michigan indicate that mussels could reduce the transport of particulate phosphorus to offshore regions, thereby increasing lake-wide ratios of dissolved phosphorus : particulate phosphorus and potentially harming pelagic fish abundance by limiting plankton productivity (Shen et al., 2020). This redistribution process is thought to apply to contaminants as well (Johannsson et al., 2000).

In addition to concentrating vital nutrients in the benthic region, filtering by mussels has also increased water clarity (Fahnenstiel et al., 1995; Howell et al., 1996) and thus the depth at which photosynthesis can occur (Francoeur et al., 2015). In conjunction with the rough substrate that mussel beds create, the larger illuminated area has increased the lake bottom area available for algal growth (Hecky et al., 2004; Auer et al., 2010). *Cladophora*, a nuisance filamentous green macroalga found commonly in marine and freshwater ecosystems (Dodds and Gudder, 1992), proliferates in environments with excess nutrients and increased light penetration such as atop mussel beds (Howell, 1998). The conditions created by dreissenids have facilitated a resurgence

of *Cladophora* production in the Great Lakes since phosphorus management strategies were implemented in the 1970s (Kuczynski et al., 2016). The complex mussel - *Cladophora* assemblage (Fig. 1) provides nutrients and refuge for benthic invertebrates such as chironomids, amphipods, oligochaetes, and isopods. In Lake Michigan, a positive relationship between the abundance of non-mussel invertebrates and dreissenid mussels has been observed (Kuhns and Berg, 1999).

The impact of dreissenid mussels has not been isolated to the nearshore benthic region. Over the last four decades, significant reductions in pelagic phytoplankton productivity have been observed, especially during the spring (Fahnenstiel et al., 2010b; Vanderploeg et al., 2010). Although causal mechanisms are difficult to determine conclusively, the reduction in phytoplankton biomass is suspected to have far-reaching consequences for the food web. For example, substantial reductions in the abundance of *Diporeia*, a formally abundant deepwater amphipod, have been observed across the Great Lakes (Nalepa et al., 2006, 2020). Additionally, between 2003 and 2007, an inverse trend in the biomass of dreissenid mussels (positive) and planktivorous fish (negative) was observed (Bunnell et al., 2009). While authors are unsure if



Figure 2: Round goby resting on large pectoral fins on the floor of Lake Michigan. Photo by Harvey Bootsma, 2020.

this was coincidental or causal, it is plausible that reduced phytoplankton biomass negatively impacts herbivorous zooplankton (i.e., *Diporeia*) and the organisms that depend on them.

The invasion of the Great Lakes region by dreissenid mussels was followed by the introduction of round gobies, *Neogobius melanostomus*, in 1990 (Fig. 2; Jude et al., 1992). Similar to zebra and quagga mussels, round gobies were presumably introduced through ballast water from transoceanic vessels traveling from the Ponto-Caspian region (Kornis et al., 2012). These aggressive benthic fish are known for their ability to adapt to varying environmental conditions (Marsden et al., 1996) including a broad thermal range (Lee and Johnson, 2005) and low dissolved oxygen levels (Marsden et al., 1996). Round gobies inhabit an assortment of temperate freshwater and brackish water ecosystems and have sizeable introduced populations in the Laurentian Great Lakes, the Baltic Sea, and several European rivers (Kornis et al., 2012). Large pectoral fins and lack of a swim bladder allow gobies to rest atop cobble and in crevices beneath rocks, providing them an advantage on rocky substrate (Jude et al., 1992, 1995). High-density populations have also been identified in areas with soft substrata and dense macrophyte growth (Johnson et al., 2005a; Taraborelli et al., 2009), and mussel beds (Yule et al., 2006).

After first being reported in the St. Clair River, round gobies quickly established themselves in all five Laurentian Great Lakes, with especially high concentrations in Lake Erie and southern Lake Michigan (Fig. 3; Marsden et al., 1997; Janssen and Jude, 2001). By 2001, round gobies had spread throughout Lake Michigan (Clapp et al., 2001) with populations in harbors and river mouths as well as in open water habitats (Janssen and Jude, 2001). Likely because of their tolerance of diverse conditions and extended spawning season, round gobies have been identified as having the fastest expansion rate of any previous fish invader in the Great Lakes (Charlebois et al., 2001). This rapid proliferation was probably aided by the comparatively few species of

parasites that infect round gobies in newly invaded areas versus their native territory (Corkum et al., 2004). As goby populations grew, they outcompeted native species such as mottled sculpin, darters, and sunfish (Ghedotti et al., 1995; Janssen and Jude, 2001; Lauer et al., 2004) and have now become the predominant shallow nearshore fish in several areas (Barton et al., 2005; Taraborelli et al., 2009). Over time, round gobies have also spread inland from the Great Lakes to tributary, marsh, and estuarial habitats, presumably via bait-bucket transfer (Kornis et al., 2012).

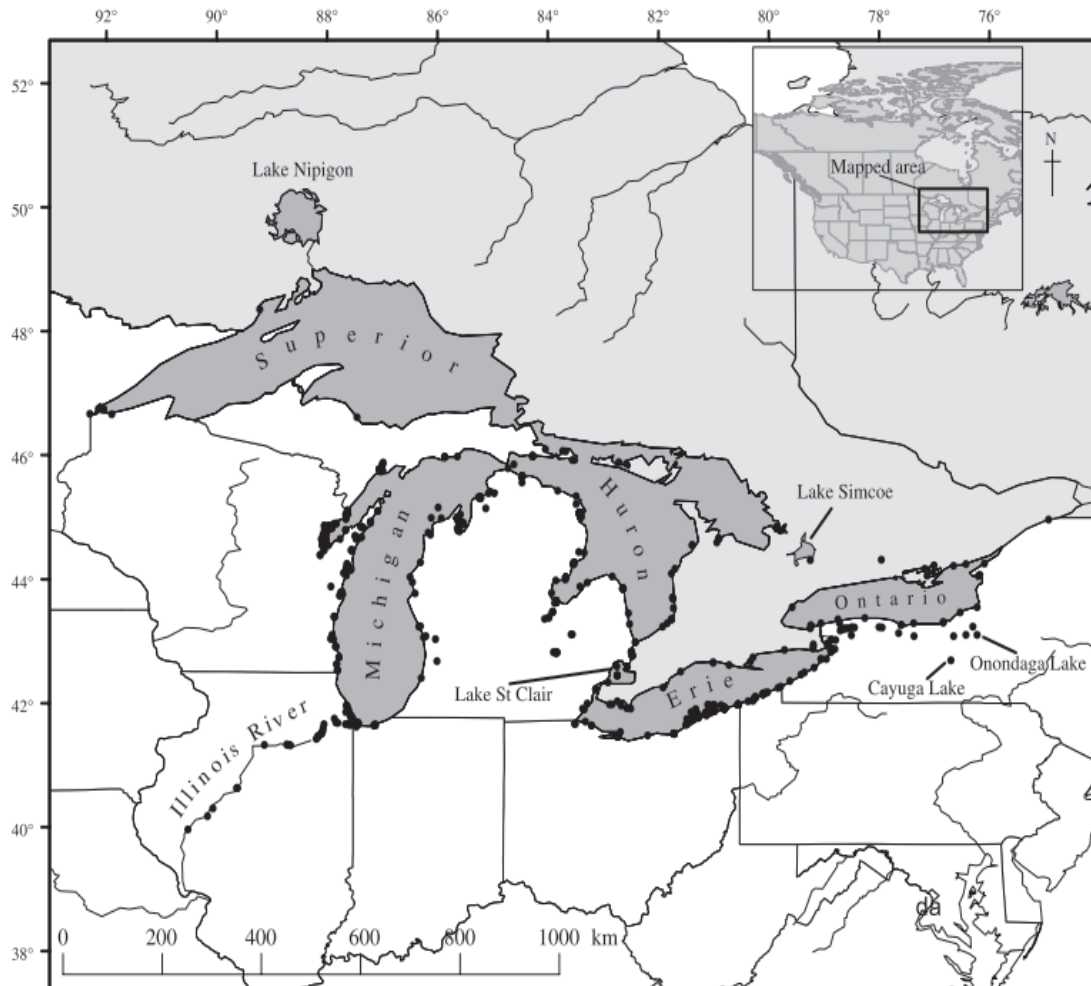


Figure 3: Distribution of *Neogobius melanostomus* in North America including (●) capture sites and reports confirmed by the U.S. Geological Survey. Figure originally published in Kornis et al. 2012.



## 1.2 Round goby diet composition

To crush the calcareous shell of dreissenid mussels and ingest them as a food source, a species must possess both upper and lower pharyngeal teeth or lower pharyngeal teeth and a chewing pad (French, 1993). Specialized pharyngeal teeth, like those found in round gobies, are typical of efficient molluscivores but uncommon in other fish (Ghedotti et al., 1995). As dreissenid mussels are also native to the Ponto-Caspian region, gobies are well adapted to feed on them and preferentially choose dreissenid mussels over native bivalves despite round gobies' inefficiency at harvesting clumped mussels or those with abundant byssal threads (Ghedotti et al., 1995). However, research indicates that this apparatus develops with age and therefore gobies less than 60mm in total length, do not possess the necessary structures to crush hard dreissenid shells (Andraso et al., 2011a). Within the *Dreissena* genus, however, gobies have not been found to differentiate between zebra and quagga mussels and readily consume both in feeding studies (Diggins et al., 2002). In addition to their specialized teeth, gobies possess no swim bladder, an important buoyancy control device in most fish. As a result, gobies are demersal their entire lives and are largely restricted to dreissenid and non-dreissenid benthic invertebrates, including an energy source (i.e., dreissenid mussels) that is both abundant and generally unused by native species (Janssen and Jude, 2001).

Round gobies' ability to prey on invasive dreissenid mussels likely aided their proliferation in the Great Lakes. Throughout their life, the most important food sources for round gobies are bivalves (primarily dreissenid mussels), chironomids, and amphipods although fish eggs and small fish, including round goby young of the year, are also consumed in smaller proportions (Jude et al., 1992). Gobies have been found to experience an ontogenetic diet shift (Jude et al., 1995; Lee and Johnson, 2005), feeding primarily on zooplankton and non-dreissenid benthic

invertebrates when small, but becoming increasingly reliant on mussels as total fish length increases (Jude et al., 1995; Barton et al., 2005). A study in Lake Ontario found dreissenids to compose 40-100% of the diet by volume for gobies age-2 and up, while gobies age-1 consumed similar volumes of dreissenids, chironomids, zooplankton, and amphipods (Taraborelli et al., 2010). In the late 1990s, the diet of round gobies in central Lake Erie was found to be dominated (40.8-57.2%) by dreissenid mussels with the second most abundant food source being chironomids, other mollusks, or zooplankton (Bunnell et al., 2005).

It has been proposed that round gobies' ontogenetic diet shift could be explained by low encounter rates with motile prey such as invertebrates, rather than an inherent preference for mussels (Diggins et al., 2002). In dark or turbid conditions, dreissenid mussels comprise an increased proportion of the goby diet (Diggins et al., 2002), despite gobies superior lateral line system which allows them to feed at night and detect vibrations of otherwise undetectable prey (Jude et al., 1995). Complex and diverse substrates, such as mussel beds, can also impact diet proportions as non-dreissenid benthic invertebrates are better able to hide (Diggins et al., 2002). In areas with dense *Cladophora* growth such as atop rocks and mussel beds, algae can physically inhibit larger gobies and make mobile invertebrates less accessible (Barton et al., 2005). Even with a reduction in the proportion of invertebrates consumed, invertebrate populations have been found to decline in some environments in which round gobies are abundant (Kuhns and Berg, 1999; Lederer et al., 2008). It is unclear if this is a direct result of goby predation or an indirect result of changes to mussel colonies (Diggins et al., 2002). It is also possible that the identified shift in diet with fish length is a result of inaccurate consumption estimates based on gut content analysis (Ray and Corkum, 1997).

The diet composition of a fish can be analyzed using several methods, each with advantages and disadvantages. One common approach is gut content analysis, a method in which a fish's gut is either dissected or pumped, and the contents are identified and quantified. Although this approach does provide direct evidence of consumption, small prey items, especially those that are partly digested, can be difficult to distinguish. When identifiable, gut contents can be misleading due to differences in digestibility and assimilation rate of different prey types. Additionally, gut content analysis only provides evidence of what is currently in the gut and therefore only reflects feeding habits at the time of sampling. Despite these disadvantages, gut content analysis is a common approach to diet studies and is important for confirming and distinguishing specific prey types.

Another common approach to diet studies is the analysis of stable isotopes. Due to the preferential use of specific isotopes in some biochemical processes, the ratio of non-radioactive carbon ( $^{13}\text{C}:$  $^{12}\text{C}$ ) and nitrogen ( $^{15}\text{N}:$  $^{14}\text{N}$ ) isotopes follow predictable patterns through food webs, allowing for energy flow to be mapped through a system. Following each trophic transfer,  $\delta^{13}\text{C}$  values (the ratio of  $^{13}\text{C}:$  $^{12}\text{C}$  relative to the Pee Dee Belemnite carbonate international standard) experience only a 0-1‰ enrichment (Hecky and Hesslein, 1995; Vander Zanden and Rasmussen, 1999). As a result, the  $\delta^{13}\text{C}$  value of an aquatic consumer can indicate what primary energy source they are supported by if potential sources are isotopically distinct (Hecky and Hesslein, 1995; France 1995). Alternatively,  $\delta^{15}\text{N}$  (the ratio of  $^{15}\text{N}:$  $^{14}\text{N}$  relative to atmospheric N) is enriched by 3-4 ‰ during each trophic transfer (Minagawa and Wada, 1984), allowing it to serve as an indicator of an organisms' trophic level (Vander Zanden and Rasmussen, 1999). Unlike gut content analysis that provides direct evidence of consumption at a high resolution, stable isotope analysis can only provide an indirect estimate of diet components with a unique

isotopic signature. Therefore, this approach requires some previous knowledge of prey sources and the environment's isotopic baseline.

Stable isotope analysis also reflects a consumer's diet composition over an extended period, rather than exclusively at the time of sampling. While this can be beneficial, assumptions are typically necessary concerning the state of equilibrium between a predator's isotopic signature and the isotopic signature(s) of their prey at the time of sampling. The isotopic integration time in fast-growing fish is dependent upon growth rate as changes in isotope composition are determined primarily by the addition of new tissue (Hesslein et al., 1993). Therefore, if diet composition and/or the isotopic signature of prey sources changes more quickly than a consumer is growing, improperly accounting for integration time can lead to erroneous interpretation of results. The  $\delta^{15}N$  value of some Lake Michigan zooplankton species has been shown to vary substantially seasonally (Driscoll, 2014) provoking questions regarding the seasonal variation of other primary consumers. As round gobies are known to migrate seasonally, spatial and temporal variation of feeding is an important factor to consider when interpreting stable isotope results.

In the case of round gobies, a disconnect has been identified between gut content analysis, which suggests dreissenid are the dominant prey source, and stable isotope analysis, which indicates that other non-dreissenid benthic invertebrates are more important (Barton et al., 2005; Brush et al., 2012). Andraso et al. (2011) concluded that over 60% of dreissenids consumed by round gobies were crushed rather than swallowed whole, but on occasion, whole mussels have been found in the gut contents of gobies (Ghedotti et al., 1995; Jude et al., 1995). As hard exoskeletons take longer to evacuate than soft-bodied prey (the exoskeleton acts as a barrier, shielding the tissue from gastric juices) (Bromley, 1994), the inspection of gut contents can

overestimate the importance of mussels when shells are present (Ghedotti et al., 1995; Coulter et al., 2011). Alternatively, when gobies avoid or regurgitate the crushed shell, the importance of mussels as a food source can be underestimated based on gut content analysis (Ray and Corkum, 1997).

Because dreissenid mussels feed primarily on pelagic phytoplankton and non-dreissenid benthic invertebrates feed on nearshore benthic algae (Hecky and Hesslein, 1995), these prey sources have distinct isotopic signatures and can therefore be distinguished in stable isotope analysis. Generally, enriched (more positive)  $\delta^{13}C$  values in consumers reflect a reliance on a benthic algae-based food web while a depleted (more negative)  $\delta^{13}C$  value corresponds to a food web that relies on pelagic plankton as a primary energy source (France, 1995). As previously noted, gobies, especially large gobies, have been found to rely heavily on dreissenid mussels based on gut content analysis. This suggests that gobies would have a  $\delta^{13}C$  signature that is depleted, similar to that of their suspected dreissenid mussel food source. Interestingly, data on the isotopic signature of round gobies over the last 20 years indicates that this may not accurately represent their diet. Data collected in 2010/2012 in Lake Michigan indicated that round gobies had enriched  $\delta^{13}C$  values in comparison to a quagga mussel baseline (Turschak et al., 2014) suggesting a reliance on non-dreissenid benthic invertebrates such as chironomids and amphipods (Brush et al., 2012). This finding was corroborated by Huo et al. (2014) who found that chironomids represented a substantial portion of the diet of round gobies collected in Sleeping Bear Dunes National Lakeshore. Data collected in 2019 again supported this finding, although a slight depletion in  $\delta^{13}C$  signatures was observed in comparison to earlier findings (Hurst, 2020).

Due to intra-system variation in  $\delta^{15}N$  values, the  $\delta^{15}N$  of consumers must be interpreted in relation to the site-specific baseline  $\delta^{15}N$  values as determined from analysis of primary producers/consumers (Vander Zanden and Rasmussen, 1999). In Lake Michigan, temporal comparisons of round goby isotopic composition are possible when round goby  $\delta^{15}N$  values are normalized to a nearshore quagga mussel baseline. This has been done in multiple studies since the early 2000s (Turschak et al., 2014; Hurst, 2020). Even after accounting for some shift in baseline between 2002 and 2019, round gobies  $\delta^{15}N$  values have fluctuated significantly during this period with gobies collected in 2010/2012 having depleted  $\delta^{15}N$  signatures in comparison to round goby samples collected in 2002 (Turschak et al., 2014). Samples from 2019 indicated a rebound effect with comparatively enriched  $\delta^{15}N$  values (Hurst, 2020). These fluctuations indicate a shift in food web dynamics, with enriched  $\delta^{15}N$  values suggesting that round gobies are consuming higher trophic level food sources.

### **1.3 Nearshore Bioenergetics**

The consumption of dreissenid mussels is important not only for round goby population growth but also for energetics at the ecosystem level and possibly for the management of invasive mussel populations. Before the goby invasion, few organisms fed on dreissenid mussels, and as a result, energy, nutrients, and contaminants were sequestered by mussels in the benthic region (Johannsson et al., 2000). Post-invasion however, gobies created a channel for transferring energy, nutrients, and contaminants to higher trophic levels (Johnson et al., 2005b). In the Great Lakes region, round goby fish predators include, but are not limited to, yellow perch (Truemper and Lauer, 2005), lake whitefish (Lehrer-Brey and Kornis, 2014), lake trout (Dietrich et al., 2006; Happel et al., 2018), brown trout (Leonhardt et al., 2020), burbot (Jacobs et al., 2010), smallmouth bass (Crane and Einhouse, 2016), northern pike, largemouth bass, and

walleye (Taraborelli et al., 2010). Gobies are also a common food source for double-crested cormorants (Somers et al., 2003) and have been found in the gut content of an assemblage of birds killed by avian botulism (Leighton, 2000) including ring-billed gulls, red-necked grebes, and common loons (Essian et al., 2016). Since gobies are abundant and easy to capture, predators that rely on gobies as a food source have been found to experience high growth rates (Johnson et al., 2005b). One example is the Lake Erie water snake, which has recovered from near extinction by shifting to a diet primarily (more than 92%) composed of round gobies (King et al., 2006). Another example is smallmouth bass in Northern Lake Michigan, which were found to have greater length at age and improved condition (ages 5-7) after the round goby invasion (Kaemingk et al., 2012). A comprehensive list of species directly affected by interactions with round gobies was published by Kornis et al. (2012).

Although consuming gobies seems to offer an energetic advantage for piscivores, there is inconsistent evidence regarding the energy density of round gobies in comparison to other prey species. A recent study in Lake Michigan found round gobies to contain significantly more total energy than alewife of similar length (Bunnell et al., 2019b). This contrasts findings from a study on Lake Michigan tributaries which indicated that gobies are an energetically average food source (Ruetz et al., 2009). In Lake Erie, round gobies were found to have a low energy density, offering only 70% of the energy by weight of similarly sized prey species such as rainbow smelt and spottail shiners (Johnson et al., 2005b). The discrepancy in comparisons may reflect spatial and temporal variation. In one study, gobies were identified to be more energy-dense in the fall than in the summer and spring due to increased reserves for winter survival and spring reproduction (Ruetz et al., 2009). However, this contradicts a lack of seasonal energy density variability in round gobies from Lake Michigan and eastern Lake Erie (Johnson et al., 2005b;

Bunnell et al., 2019b). Other studies have found a positive correlation between energy density and size (Johnson et al., 2005b; Bunnell et al., 2019b). This conclusion is somewhat surprising as gobies likely increase their reliance on low-energy prey (i.e., dreissenid mussels) as they age and the energy density of predatory fish is often a product of prey quality (Ruetz et al., 2009). Spatial variation in prey quality and thus round goby energy density could be due to a variety of factors including the frequency of upwelling events, substrate type, the proximity to high-phosphorus loading tributaries (Bunnell et al., 2019b), and round gobies seasonal migration patterns (Johnson et al., 2005a).

In addition to the importance of accurate modeling for the management of upper trophic levels, modeling of round goby bioenergetics may provide insight into the viability of gobies as a management tool for mussel populations. Djuricich and Janssen (2001) concluded that gobies are unlikely to completely remove mussels from a given habitat due to several inefficiencies. First, gobies' lack of swim bladder means that elevated mussel colonies, such as those atop extra-large rocks or underwater structures, are inaccessible (Ghedotti et al., 1995). Second, research has found that although gobies try to feed on larger mussels, there is a significant size difference between mussels successfully removed by gobies and mussels unsuccessfully removed (Djuricich and Janssen, 2001). Larger mussels tend to have an increased abundance of strong byssal threads and a thicker shell which could explain why gobies preferentially consume mussels less than 13 mm in length (Djuricich and Janssen, 2001; Andraso et al., 2011b; Houghton and Janssen, 2014). Third, since gobies are inefficient at removing and consuming mussels located in tight crevasses, within large clumps, or hidden on the underside of rocks, small mussels can avoid predation by taking refuge in these locations (Djuricich and Janssen, 2001).



Even if complete mussel removal by gobies is unlikely, additional questions remain regarding the ability of round gobies to impact mussel abundance (Lederer et al., 2006). Round gobies' preference for small mussels has the potential to create a size bottleneck in which new mussels are unable to mature and thus the population is unable to grow (Djuricich and Janssen, 2001). In Green Bay, Lake Michigan, studies have found dramatically fewer mussels in areas where gobies have become established, and a statistically significant negative relationship between round goby density and mussel abundance (Lederer et al., 2006, 2008). Barton et al. (2005) concluded that round gobies reduced dreissenid populations in eastern Lake Erie by 94% from 2001 to 2004. In a recent study on Onondaga Lake in New York State, round goby abundance was inversely correlated with a quagga mussel biomass (Rudstam and Gandino, 2020) and in a controlled field experiment, round gobies caused a significant reduction in dreissenid abundance (Kuhns and Berg, 1999).

Some authors claim that gobies may cause declines in localized mussel populations, but that goby consumption rates are likely not high enough to reduce dreissenid populations on a system-wide scale (Patterson et al., 2005; Kornis et al., 2012). Although no causal relationship with



Figure 4: Underwater structure and monitoring equipment used in a mussel removal project on Good Harbor Bay reef, 2019 using the chemical molluscicide Zequanox (LimnoTech, 2020).

round gobies has been identified, mussel density in the nearshore zone of Lake Michigan has declined in recent years (Nalepa et al., 2020) and in Lake Ontario, round goby density at 11-26 m in depth was found to coincide with a relatively low percentage of edible size mussels (Karatayev et al., 2020). More research regarding gobies' impact on mussel populations is needed, as this may vary with the environmental conditions (Djuricich and Janssen, 2001). Further research is also needed regarding gobies' efficacy at maintaining low mussel populations in areas where mussel removal projects have occurred (Fig. 4), as well as the impact of these mussel removal projects on goby populations.

#### 1.4 Bioenergetic modeling

Determining the energetic impact of round gobies in the rocky nearshore food web requires a quantitative assessment of productivity, which can be facilitated through the application of bioenergetic models. In its basic form, a bioenergetic model balances the amount of energy gained by a system with the amount of energy lost (Fig. 5). For living organisms, energy is gained via consumption and is lost or used during growth, metabolism, reproduction, and waste production. Because of the mass balance requirement of the model, individual parameters can be estimated by difference if the others are known. Values for these parameters are species-specific and an array of studies have described them for numerous aquatic species. The Fish

$$\begin{aligned}
 \textbf{Consumption} &= \textit{metabolism} + \textit{waste} + \textit{growth} \\
 &= (\textit{respiration} + \textit{active metabolism} + \textit{specific dynamic action}) \\
 &\quad + (\textit{egestion} + \textit{excretion}) \\
 &\quad + (\textit{somatic growth} + \textit{gonad growth}) \\
 \textbf{C} &= (R + A + SDA) + (F + U) + (SG + GG)
 \end{aligned}$$

Figure 5: General bioenergetic model.

Bioenergetics 4.0 model (FB4; Deslauriers et al., 2017) has incorporated many of the published parameters into a user-friendly and adaptable application. Round goby-specific parameter values for respiration, specific dynamic action, egestion, excretion, gonad growth, and somatic growth have been described by Lee and Johnson (2005) and incorporated into FB4. The FB4 application and goby-specific parameters have been used to estimate prey consumption in several round goby studies (e.g. Johnson et al. 2005b, Taraborelli et al. 2010). A detailed analysis of the valuation of each parameter is described in Lee and Johnson's 2005 paper. Further description of the model can be found in section 2.4 and appendix A.

The validity of model output depends on the accuracy of model parameters and the sensitivity of output to each of these parameters. In the case of round gobies, sensitivity analysis was performed by Lee and Johnson (2005), who found model output to be heavily influenced by respiration, prey energy density (which affects somatic growth), and consumption. Consumption ( $C$ ) is expressed as a portion ( $p$ ) of the maximum daily food consumption ( $C_{max}$ ) of a fish of a particular wet mass ( $WW$ ) at a given temperature (Equation 1; Hanson et al. 1997):

$$C = C_{max} \cdot p \cdot f(T) \quad (1)$$

where  $f(T)$  is the functional temperature response,  $C_{max}$  is the theoretical maximum consumption rate, and  $p$  is a proportionality scaler that ranges from 0 to 1, representing consumption under field conditions as a fraction of  $C_{max}$ .  $C_{max}$  is an allometric function of fish mass:

$$C_{max} = i \cdot WW^j \quad (2)$$

where  $i$  and  $j$  are intercept and slope coefficients. In the round goby model developed by Lee and Johnson (2005),  $p = 0.350$ . Consumption estimates, and therefore growth estimates, are sensitive to this parameter. Previous studies have suggested  $p = 0.3$  is an appropriate average estimate when applying a bioenergetic model to field data (Hewett and Johnson, 1992) but variability is

expected based on food availability. Actively foraging fish such as round gobies are known to have increased levels of activity during periods of increased food consumption (Kerr, 1982). The costs associated with that activity have been found to vary between populations but have been estimated to account for as much as 40% of total energy in bioenergetic models (Boisclair and Leggett, 1989). As a result of the range of parameter values and sensitivity of the model to some parameters, further research is needed to determine the validity of the currently accepted constant multiple scalar  $p$  when estimating consumption by round goby populations. The temperature response function ( $f(T)$ ) can take a variety of forms but Lee and Johnson (2005) found round goby consumption to be well represented by a sigmoidal temperature function (Thornton and Lessem, 1978).

$C_{max}$  (Equation 2) is typically expressed as grams of prey consumed per gram of body mass per day and is estimated from *ab libitum* laboratory feeding experiments at optimal temperatures (Hartman and Hayward, 2007). Model parameterization for round gobies is based on a dreissenid exclusive diet (Lee and Johnson, 2005), which, as discussed previously, likely does not reflect the diet of round gobies in natural populations. It is possible that  $C_{max}$  is not dependent upon food type but more research is needed to support this conclusion.

When the values of respiration, specific dynamic action, egestion, excretion, and gonad growth parameters are known, somatic growth can be measured, and consumption can be estimated by balancing energy use with energy intake. Alternatively, if those same parameters are known but somatic growth cannot be measured, the consumption model described above can be applied (using a  $p$  value of 0.35), allowing for the determination of energy applied to somatic growth by difference. By comparing estimates of consumption and somatic growth using these

two separate approaches, the reliability of consumption and growth estimates for in-situ populations can be assessed.

### 1.5 Round goby growth

Round goby growth, which can vary spatially and temporally (Huo et al., 2014; Duan et al., 2016; Kornis et al., 2017), can be directly measured in individual fish or described by generalized size vs age curves. Age can be estimated by close examination of otoliths, scales, and other bony structures such as spines and vertebrae (Beamish and Harvey, 1969). Otoliths are calcium carbonate ear bones, located behind the brain, that help with hearing and balance. Although most fish possess three pairs of otoliths, sagittal otoliths are the largest and most commonly used for aging (e.g. Rice et al., 1985; French and Black, 2009; Gümüş and Kurt, 2009; Sokołowska and Fey, 2011; Duan et al., 2016; Kornis et al., 2017; Bose et al., 2018). The otolith of a newly hatched fish becomes the center of a growing fish's otolith and is called the focus (Fig. 6). As the fish grows, concentric circular growth rings/ridges called circuli (singular:

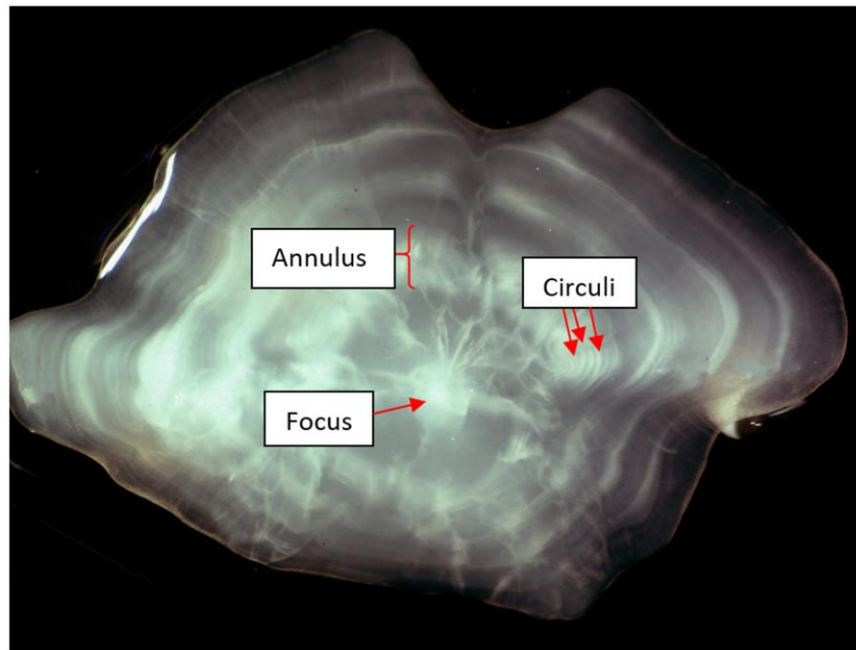


Figure 6: Image of a round goby whole sagittal otolith. Otolith was mounted on black slide and imaged under a dissecting microscope. Multiple annuli and circuli present besides those that are labeled.

circulus) develop around the focus on the outer edge of the otolith. During periods of rapid growth (i.e., during ideal summer conditions when feeding rate is high) circuli are spaced apart and create a translucent region. When growth slows (i.e., during the winter season), circuli grow tightly together and create a dense opaque region called an annulus (plural: annuli). Since true annuli only form once a year, the age of a fish can be determined by counting the number of annual rings present.

As the accuracy of enumerating annuli can depend on the species, the age of the specimen, and the structure being examined, Beamish and McFarlane (1983) emphasized the importance of validating age via several structures for each age class. This is especially important in old fish whose growth rate is slow even during the growing season, as distinguishing annuli on some structures (i.e scales) is difficult and can lead to underestimates in age (Schneider et al., 2000). Taraborelli (2010) compared age determination via scales and otoliths in round gobies and found comparable results in almost all cases.

Regardless of the structure, several factors can increase the difficulty of age estimates. First, because gobies are thought to spawn throughout the summer season (as seen in other Gobiidae species e.g., Kovačić, 2007; Iida et al., 2011; Mohammadi-Darestani et al., 2016), the date of capture does not necessarily provide informative details regarding a fish's age. Therefore, goby age cohorts may be indistinct and fish age within a cohort may vary by several months. Second, as round goby metabolic rate is impacted by temperature (Lee and Johnson, 2005), frequent oscillations between cool and warm water may cause sporadic growth and circuli formation resulting in false annuli.

## 1.6 Objectives and Hypotheses

The primary objective of this research was to quantify round goby abundance and productivity (i.e., the rate of production of new biomass and the quantity of potential energy supplied by round gobies) in the nearshore zone of Lake Michigan, focusing specifically on Good Harbor Reef near Sleeping Bear Dunes National Lakeshore. This was accomplished through field research aimed at measuring round goby population structure (i.e., density, size distribution) and several bioenergetic parameters (i.e., growth rate, diet composition). Ultimately, by combining these findings with productivity measurements of nearshore primary producers and consumers, this research aimed to estimate the carrying capacity of round gobies in the rocky littoral zone and the trophic transfer efficiency within that region.

As round goby population structure and bioenergetic parameterization is likely location and season-specific, it is challenging to predict how their productivity integrates into the nearshore food web. Nevertheless, past research provides some insight into this question. Field research conducted in 2010/2011, identified non-dreissenid benthic invertebrates as a significant prey source for round gobies on Good Harbor Reef (Turschak et al., 2019), and so similar results were expected in this study. If round gobies feed primarily on non-dreissenid invertebrates, then dreissenid production may represent a trophic dead end. However, larger round gobies feed on dreissenids (Lee and Johnson, 2005), and if these dreissenids support a substantial portion of round goby productivity, then round gobies may mobilize otherwise unused energy from the benthic nearshore zone and make it available to higher trophic levels. Based on this information, it was hypothesized that round gobies would be found to have a mixed diet of dreissenid and non-dreissenid benthic invertebrates, but, because of the abundance of dreissenid mussels in the rocky nearshore zone, trophic transfer was hypothesized to be relatively inefficient.

Previous research has also found round gobies near Good Harbor Reef to experience faster growth rates than individuals from other regions in Lake Michigan (Huo et al., 2014). Therefore, it was hypothesized that high individual growth rates would be reflected in high population productivity measurements at Good Harbor Reef (in comparison to Atwater), assuming round goby density is high (e.g., Chotkowski and Marsden, 1999; Karatayev et al., 2020). Additionally, because non-dreissenid benthic invertebrates have a higher energy density than dreissenid mussels (Cumminns and Wuycheck, 1971; Schneider, 1992), it was hypothesized that measured productivity from growth curves would be greater than predicted productivity using literature defined consumption estimates. If upper trophic level piscivores incorporate round gobies into their diets (e.g. Taraborelli et al., 2010; Leonhardt et al., 2020), round goby productivity (high or low) may support upper trophic level species. Fully answering questions regarding the significance of round gobies as a conduit of energy transfer from the nearshore benthic region to upper trophic levels would require comprehensive diet analysis for an array of predatory species and was beyond the scope of this study.



## Chapter 2: Methodology

Prior to beginning field sampling, an animal care protocol for the humane capture, housing, and euthanasia of fish samples was submitted to the UWM Institutional Animal Care and Use Committee (IACUC). Formal approval of the protocol (19-20 #29) was granted by the IACUC on June 5, 2020. Additional measures to maintain approval (i.e., trainings, certifications, and continued education) were completed as necessary. The base of all operations was the



Figure 7: Location of sampling sites. GS10 is a long-term monitoring site off Sleeping Bear Dunes National Lakeshore. ATW is near Milwaukee, WI.

University of Wisconsin Milwaukee – School of Freshwater Sciences (UWM-SFS) in Milwaukee, WI. Sample collection occurred at two Lake Michigan field locations (Fig. 7)): a long-term monitoring site (GS10) in Good Harbor Bay off the shore of Sleeping Bear Dunes National Lakeshore in Leland, MI, and a nearshore site offshore of Atwater Beach in Milwaukee, WI (ATW). Both sites were 10 m deep, had rocky/cobble substrate, were easy to access via boat, and have been studied for the past decade as part of a research program to understand causes of nuisance benthic algal growth and the effects of dreissenids on nutrient cycling. Samples were collected on four dates (June, July, August, and October) at the GS10 location. Sample collection at ATW was carried out in conjunction with other research projects and occurred twice (July, September).

All statistical analyses were completed in R (R Core Team, 2020). Comparisons were deemed not statistically significant at  $p \geq 0.05$ . In most instances, the mean value of a measurement and the variation around that measurement were important. Therefore, unless otherwise noted, all variability measures are standard deviations. To compare mean measurements between two populations, two-tailed unpaired t-tests were performed if the data met the necessary assumptions (variable was continuous, samples were randomly selected, population was normally distributed, sample size was reasonably large, and samples had homogenous variance). Unless otherwise noted, measurements were taken from distinct samples (i.e., duplicate measurements were not collected from a single individual).

Because of Good Harbor Reef's location off the shore of Sleeping Bear Dunes National Lakeshore, the field site is not only an environmentally relevant area but also a popular tourist destination. Working from a nearby harbor, Leland's Historic Fishtown, provided an opportunity for education and outreach to community members, visitors, and fishermen regarding the work we were doing and the impacts it may have on the management of Great Lakes aquatic resources.

## **2.1 Sample Collection**

### **2.1.1 Round goby sampling**

Past research has examined different methods of round goby collection (Johnson et al., 2005a; Diana et al., 2006). For this work, a method that fairly sampled a range of size classes, did not alter gut content (such as baited capture), and did not cause undue stress to the fish was needed. Fish were collected using a 6m long micromesh gillnet deployed by scuba divers. Divers deployed the net parallel to water current and corralled gobies towards the net for collection. Due to the size of the mesh ( $0.6 \text{ cm}^2$ ), small gobies (i.e., those less than  $\sim 6 \text{ cm}$  total length) were able

to swim through the net. Fish caught in the gill net were gently extracted by hand. Larger gobies that were not entangled in the net were collected using a hand net. All collected gobies were placed in underwater holding chambers that allowed for ample water flow through until being brought to the surface and transferred to an aerated chamber filled with lake water.

Fish not being used for feeding experiments were euthanatized with an overdose of tricaine methanesulfonate (MS-222) following the American Veterinary Medical Association (AVMA) 2020 guidelines. Following euthanasia, fish were rinsed of anesthetic and initial measurements including length, wet weight, and sex were recorded. Fish were then frozen until further analysis. All fish length measurements throughout the entirety of the research refer to total length (length from the tip of the snout to the tip of the caudal fin lobe), measured to the nearest 1 mm. Wet weight was measured to the nearest 0.01 g. Sex was determined by examination of the genital papilla which is long and triangular-shaped in males but short and rectangular-shaped in females (Macinnis and Corkum, 2000). For additional analyses (i.e., age determination, gut content analysis, and stable isotope analysis), a subset of fish from six size classes (<6, 6-9, 9-12, 12-15, and >15 cm) was haphazardly selected. Size classes were determined based on the size-frequency distribution of collected gobies.

### **2.1.2 Benthic sampling**

The collection of benthic algae (primarily *Cladophora*), dreissenid mussels, and non-mussel invertebrates (hereafter referred to as benthic invertebrates) followed procedures that have been used at both sites for the past decade (Bootsma, personal communication). Although the explicit purpose of this research was not to determine long-term trends, following the established methodology allowed data from this study to contribute to the long-running time-series databases for both sites. A total of 6 benthic samples were collected on each sampling day: triplicate

samples from the top of rocks and side of rocks. Due to the rocky/cobble substrate and an abundance of dead mussel shells, soft sediment was not prevalent at either site. Initial sampling of small sediment patches was conducted but dreissenid mussel and benthic invertebrate densities were found to be very low and further sediment sampling was not conducted.

To collect benthic samples, a scuba diver placed a quadrat on the top or side of a rock that appeared to be representative of the site's *Cladophora* and mussel populations. The contents of the designated area were carefully scraped into a Whirl-Pak®, ensuring that no loose *Cladophora* floated away. When the quadrat was unable to be secured, such as on rock sides, the diver held the quadrat in place and prescribed the area by scraping away the surrounding benthic material. Once prescribed, the diver set the quadrat aside and collected the sample into a Whirl-Pak®. A 20 x 20 cm and 10 x 10 cm quadrat were used for top and side samples respectively.

Scraped samples were separated into *Cladophora*, benthic invertebrate, and dreissenid mussel portions within 24 hours of sampling. *Cladophora* samples were freeze-dried and weighed. Benthic invertebrates were identified and counted. All invertebrates of the same taxon were freeze-dried and weighed together. Dreissenid mussels were counted and the length of each was measured to the nearest 1 mm. Tissue from a subset of mussels on each sampling day and each scrape location (i.e., top or side) were removed, freeze-dried, and weighed. For each set of mussels, a power regression was fit to length and weight data and then applied to length-frequency data to estimate the total biomass of collected samples.

To determine total areal densities of algae, invertebrates, and mussels, repeated rugosity measurements were collected to determine the profile surface area within a 1 m<sup>2</sup> areal area of lake bottom. Rugosity was determined by the ratio of profile distance, the vertical and horizontal distance between two points, to geometric distance, the straight horizontal distance between the

same two points. A tape measure was suspended above the substrate in a straight 10m line parallel to the lake bottom, this represented a 10m geometric transect. The starting end of the measuring tape was secured to the substrate while a diver marked the other end of the 10m transect and held the measuring tape reel. A second diver moved along the designated transect, starting at the secured end, and folded the line to follow the contours of the substrate and lake bottom. When needed, the diver holding the reel, allowed extra tape to be unspooled. When the second diver reached the end of the original 10m transect (as marked by the first diver), the total length of tape unspooled was recorded. This represented profile distance. Rugosity measurements were repeated 6 times in different locations at the study site and an average rugosity value was determined. Benthic data from top and side scrapes were scaled appropriately using rugosity values and were combined into total per area measurements. Hereafter, all per area measurements refer to areal area (i.e., account for rugosity).

## **2.2 Round goby population structure**

### **2.2.1 Density and size distribution**

Round goby density and size distribution were surveyed using visual and video recorded transects. Despite potential sources of error, transect counts are considered to be an effective method for assessing round goby density (Johnson et al., 2005a) and visual transect counts have been used on the two study sites for the past decade. Triplicate video transects were performed on each sampling day and triplicate visual transect counts were performed during June and August sampling at GS10.

A subset of time-lapse images collected at GS10 was also analyzed to estimate round goby density. A time-lapse camera used for long-term monitoring at the GS10 site was deployed and left undisturbed for 30 days. Images were captured once every hour. Upon retrieval of the

camera, 86 images collected over 6 days were analyzed (night images were not analyzed) and the number of gobies in each was recorded. The areal area within the field of view was estimated using natural points of reference. Density measurements from time-lapse images were compared to video and visual transect counts to determine if such methods were biased due to the presence of a diver.

Visual and video transects were performed simultaneously to produce the most comparable results. A tape measure was secured to the lake bottom and a 22 m transect was designated. To perform visual transect counts, a diver swam 2-3m above the bottom and counted gobies within 1m on either side of the transect line. A second diver followed with a camcorder in an underwater housing unit to video record the same transect. Securing the end of the transect line often attracted round gobies due to their natural curiosity and the food sources made available by the disturbance. To ensure that this did not lead to overestimations in round goby abundance, the first and last meter of the transect line were not included in video or visual counts.

During visual counts, gobies were grouped into two size classes, less than and greater than 6 cm, as has been done during long-term monitoring at this site in previous years (Bootsma, personal communication). The diver approximated size using natural points of reference such as the expected size range of dreissenid mussels (Johnson et al., 2005a). Data from 2019 and 2020 at GS10 indicate a bimodal distribution in mussel length-frequency with the second mode at 2.3-2.5 cm (Bootsma, unpublished). Therefore, the diver performing counts was confident that an average mussel in the larger size class was approximately this size.

A more thorough assessment of round goby size distribution was possible from video transects which were analyzed in stop-motion. In frames in which a goby(s) was present, a still image was collected and the length of individuals was measured using ImageJ (Schneider et al.,

2012). Parallel lasers mounted 35 cm apart on the underwater housing unit of the camcorder provided a scale for recorded videos. When lasers were not visible in the recording due to dense *Cladophora* growth or the lasers provided scale at the incorrect depth of field (i.e., lasers provided scale on the bottom but the goby was atop a rock), dreissenid mussels were used as an approximate scale reference (Johnson et al., 2005a) as above. Total round goby density and size-specific density measurements were averaged for video and visual transects separately. Results from the 2020 sampling were compiled with past density estimates to analyze seasonal and annual trends.

### 2.2.2 Length-weight relationship

Length-weight regressions and Fulton's condition factor were used to assess the robustness of individuals and thus the population. The measured wet mass of each fish was transformed into an estimated dry mass using a conversion factor developed from a subset of fish from each size class and was applied to fish collected on all sampling days. Samples analyzed for dry mass were cut into ~20 mm pieces, placed in a freeze-drier, and weighed after 4 days and then every 24 hrs. thereafter until a constant dry weight was achieved (Bunnell et al., 2019b). Wet (*WW*) and dry weight (*DW*) measurements of fish collected on each sampling day were plotted against total length (*L*) and fit with a power regression (Equation 3; Taraborelli et al., 2010). Wet and dry mass regressions were log-log transformed to produce linear models (Equation 4). Fulton's condition factor (*K*; Equation 5) was used to assess possible differences in goby robustness due to site, sex, and season (Ricker, 1975).

$$DW \text{ or } WW = a(L)^b \quad (3)$$

$$\log(DW \text{ or } WW) = b * \log(L) + \log(a) \quad (4)$$

$$K = \frac{WW(g)}{L(cm)^3} \times 100 \quad (5)$$

Three-factor ANCOVA's were used to compare regressions and condition factors seasonally. Weight and condition factor were dependent variables. In both ANCOVA's, length was a covariate and site, date, and sex were fixed factors. In Accounting for length as a continuous variable to explain Fulton's condition factor is critical as round gobies are suspected to display allometric growth patterns.

Length-weight regressions, length-frequency distributions, and density estimates were combined to estimate round goby biomass (g wet weight · m<sup>-2</sup>) on each sampling day (Equation 6). Length (L) was assumed to be the integer value of each size class (e.g. an initial length of 2 was assigned to all gobies of length x when 2 ≤ x < 3) and was converted to a wet weight using date-specific length-weight regressions (Equation 3). The relative frequencies of goby lengths 1 -16 cm (*f(L)*) were determined on each sampling day using video transects. Density on each sampling day was estimated to be the mean density observed during visual transects.

$$Biomass = \sum(density * f(L)) * a(L)^b \quad (6)$$

### 2.2.3 Growth

A subsample of 0 – 5 individuals from each size class on each sampling day was haphazardly selected to be aged using whole sagittal otoliths. When possible, a subsample of 5 was chosen, however, smaller sample sizes were used when few or no fish from a specific size class were collected. After noting the length and sex of the individual, the braincase was accessed ventrally and carefully cracked open. Sagittal otoliths, which are free-floating and therefore easy to remove, were extracted from either side of the braincase. Otoliths were processed and mounted using the methodology described by Kornis et al. (2014). Mounted



otoliths were imaged using a Motic SMZ 168 series dissecting scope with a mounted MotiCam 5.0 MP digital camera using reflected light.

Otolith images were analyzed by two independent readers without reference to fish size, sex, or date of capture. The transition from a translucent to opaque region was interpreted as the annual growth mark. If no annuli were visible, the fish were assigned an age of 0 (Macinnis and Corkum, 2000). Each reader assigned an age as well as a confidence level to their interpretation. If readers did not agree on an estimated age and both readers indicated low confidence in their estimate, the otolith was discarded and not included in further analysis. If either reader expressed confidence in their estimates but no agreement was reached, the otolith was reexamined by one reader at least 30 days after the first reading, without reference to fish information or prior age estimates. If an agreement was still not reached after reexamination, the otolith was not included in further analysis.

Age data for each site and sex was fitted to a von Bertalanffy growth model:

$$L(t) = L_{\infty} - (L_{\infty} - L_0) e^{-kt} \quad (7)$$

where  $L(t)$  represents total length (cm) or wet weight (g) at age  $t$  (years),  $L_{\infty}$  represents asymptotic size (either length or weight), the maximum theoretical size that a species will tend toward (Pardo *et al.*, 2013),  $L_0$  represents size at age zero, and  $k$  represents the growth coefficient ( $\text{year}^{-1}$ ) - the rate at which growth approaches the asymptote (Pardo *et al.*, 2013). Due to the method of collection, small gobies (less than 6 cm) were rarely collected. The literature suggests that at age 0 there is no significant difference between the size of males and females (Kornis *et al.*, 2012), and so  $L_0$  was set at 0.73 cm (Leslie and Timmins, 2004) in all models. Other parameters in the model were estimated using a Newton-Gaussian nonlinear regression

algorithm (Huo et al., 2014) with the ‘nls2’ package in R (Grothendieck, 2013). This accounts for size variation within age groups which can be high (Macinnis and Corkum, 2000; Huo et al., 2014).

Length and age were log-transformed and growth was compared between populations using likelihood ratio tests in which log(age), site, and sex were considered as possible explanatory factors for observed differences in log(length). This approach evaluates if the observed data were significantly more likely to have come from a more complex model (one containing site or sex as a factor) relative to a simple model. Likelihood ratio tests are preferred over Wald tests when working with a small sample size such as those in this study.

### **2.3 Round goby diet composition**

Analysis of round goby diet composition was completed 1-2 months after collection. A subset of 0 – 5 gobies from each size class was randomly selected for gut content and stable isotope analysis. After recording the length and sex of the individual, a thin incision was made from the anus to operculum. Because round gobies have no distinction between their stomach and intestine, the entire digestive tract (hereafter referred to as their gut) was removed and dissected. Contents were emptied into a Petri dish, spread to a uniform depth, identified to the lowest possible taxonomic classification, and grouped as non-dreissenid benthic invertebrate, dreissenid mussel, or other. The percent volume (to the nearest 5%) of each prey type in the diet was determined visually (Taraborelli et al., 2010). Gut contents were freeze-dried and weighed.

After removal of the gut and other organs, dorsal muscle tissue was scraped away from the skin and freeze-dried for stable isotope analysis following the methodology used by Hurst 2020. Turschak et al. (2013, 2014) found no significant difference in the  $\delta^{13}\text{C}$  value of dorsal muscle and whole fish homogenate; however, they did find that round goby dorsal muscle had slightly

elevated  $\delta^{15}N$  values in comparison to samples of whole fish homogenate. To reduce variability between samples and allow for a comparison of findings with past research, dorsal muscle tissue was used for all stable isotope analyses. Dried tissue samples were homogenized and a small portion of each sample (0.75-1.25 mg) was weighed ( $\pm 0.001$  mg) and folded into a tin capsule. Five acetanilide standards (0.2 – 1.0 mg), along with several blank and control capsules, were prepared in the same manner. Stable isotope analysis was conducted using an isotope ratio mass spectrometer (IRMS; Delta V Plus, Thermo Fisher, Bremen) equipped with a front-end elemental analyzer (ECS 4010, Costech Instruments, Valencia), and an autosampler. Acetanilide control and blank capsules were analyzed every 12<sup>th</sup> sample to verify instrument calibration and avoid drift in the baseline. Instrument precision was 0.10‰ and 0.22‰ for  $\delta^{13}C$  and  $\delta^{15}N$  respectively. An instrument-specific correction was applied to raw isotope values to express results as the per mil difference (‰) between the sample and reference material:

$$\delta^{13}C = \left( \frac{^{13}C_{Sample}/^{12}C_{Sample}}{^{13}C_{PDB}/^{12}C_{PDB}} - 1 \right) * 1000 \text{ ‰} \quad (9)$$

$$\delta^{15}N = \left( \frac{^{15}N_{Sample}/^{14}N_{Sample}}{^{15}N_{air}/^{14}N_{air}} - 1 \right) * 1000 \text{ ‰} \quad (10)$$

Site and season-specific  $\delta^{13}C$  baselines were developed by repeating this process with a subsample of benthic invertebrates, benthic algae, and dreissenid mussel tissue samples collected on coincident sampling days.

Since lipids are depleted in  $^{13}C$  relative to carbohydrates and proteins,  $\delta^{13}C$  values for benthic invertebrates, round gobies, and dreissenid mussels were corrected before statistical analysis (Post et al., 2007; Table 1). The relative dependence on a phytoplankton-based vs benthic algae-based food web was estimated with a single tracer (lipid corrected  $\delta^{13}C$ ) linear

Table 1: Species specific lipid correction equations for  $\delta^{13}C$  values. See Post et al. (2007) for more information about the aquatic animals used derive the listed lipid correction equation.

Species	Lipid correction equation	Source
Round goby	$\delta^{13}C_{Lipid\ Corrected}$ $= \delta^{13}C + [0.3992 (C:N - 3.0324)$ $+ 0.3133]$	Turschak, personal communication
Dreissenid mussel	$\delta^{13}C_{Lipid\ Corrected}$ $= \delta^{13}C + [0.8842 (C:N - 4.0755)$ $+ 0.2284]$	Turschak, personal communication
Benthic invertebrate	$\delta^{13}C_{Lipid\ Corrected} = \delta^{13}C + [0.99 (C:N) - 3.32]$	Post et al. (2007) – Aquatic animals

mixing model using the ‘MixSAIR’ package (Stock and Semmens, 2016) developed in R (R Core Team, 2020) which accounted for collection site and round goby total length as a random effect factor and covariate respectively. Dreissenid mussels and benthic invertebrates, and their associated mean site-specific  $\delta^{13}C$  values, were input as potential prey sources. All taxa of non-dreissenid invertebrates were grouped as a single source. A  $^{13}C$  discrimination factor (mean  $\pm$ SD) of  $0.4 \pm 1.3\text{‰}$  was also input into the model (Post, 2002). Convergence of triplicate Markov chain Monte Carlo simulations (length = 300,000, burn-in = 200,000, thinning factor = 100) was determined using Gelman-Ruben and Geweke diagnostics.

## 2.4 Bioenergetic modeling

All bioenergetic modeling was done using round goby specific values of respiration, specific dynamic action, egestion, excretion, gonad growth, and consumption parameters (Lee and Johnson, 2005) incorporated into the FB4 application (Deslauriers et al., 2017b). Site-specific data for water temperature, diet composition, the proportion of prey that is indigestible, prey energy density, and predator energy density were input into the model. Water temperature at GS10 was obtained from a YSI sonde deployed on the lake bottom October 2019- October 2020. As round gobies are demersal, temperatures on the bottom of the lake more accurately reflect

their in-situ habitat than surface temperatures. Water temperature at ATW was obtained from a thermistor string suspended at 10m from a nearby buoy. The temperature observed throughout the season at both sites was within the thermal range for which the sigmoidal functional temperature response has been previously used to describe round goby metabolism and consumption (Lee and Johnson, 2005). Respiration and consumption estimates are temperature dependent (Appendix A) which allows model simulations to account for seasonal differences in these parameters.

Diet composition was estimated separately for each model simulation based on the initial size of the goby and the corresponding diet composition as estimated from the linear isotope mixing model described previously. Because all calculations within the model are done in units of energy, output values for prey consumption (g) were converted to units of energy using prey energy density values obtained from the literature (Cumminns and Wuycheck, 1971; Schneider, 1992). The energy of benthic invertebrates ( $3.327 \frac{kJ}{g WW}$ ) was estimated as the average energy density of chironomids and amphipods as these have been identified as prominent prey species in past studies (Taraborelli et al., 2010). Energy density and diet proportions were based on non-dreissenid invertebrates and shell-free mussel tissue and therefore, the proportion of prey that was indigestible was assumed to be zero. Input values of goby initial and final size also needed to be converted from units of mass to units of energy. Round goby energy density ( $ED; \frac{kJ}{g WW}$ ) was estimated to be  $4.6 \frac{kJ}{g WW}$  by Lee and Johnson (2005). However, ED has been found to depend on goby size and was therefore determined based on the regression developed for Lake Michigan round gobies (Bunnell et al., 2019b):

$$ED = 3.646WW^{0.0736} \quad (11)$$

The FB4 application can fit the bioenergetic model to a user-defined value for final wet weight, total wet weight of prey consumed, percent of daily wet weight that is consumed, set amount of daily wet weight consumed, or the p-value of consumption. For this study, the model was fit to final wet weight. Therefore, consumption was calculated by difference, i.e., the energy needed to support respiration, specific dynamic action, egestion, excretion, gonad growth, and somatic growth. Estimates for respiration, specific dynamic action, egestion, excretion, gonad growth came from Lee and Johnson (2005). Gonad growth was assumed to be proportional to body weight and energy losses due to spawning were assumed to occur twice a year (June and July; Taraborelli et al., 2010). Estimates for somatic growth came from growth models derived from otoliths as part of this study. All model parameter values can be found in appendix A.

The model was run fifteen times, once for each size class with an input starting size of 1 to 15 cm. Each model run spanned 365 days (6/24 – 6/23) and was fit to a final weight ( $aL_f^b$ ) as derived from the growth model and length-weight regressions. The model ran on daily time steps, solving for consumption based on the input values for all other parameters. Daily consumption and productivity were assumed to be  $\frac{1}{365}th$  of yearly production with the understanding that summer values are probably higher and winter values are probably lower.

Round goby population productivity (Equation 12 and 13) was estimated by combining average daily somatic growth estimates with length-frequency distributions, energy density models (Equation 11), and mortality estimates.

$$Productivity \left( \frac{g\ WW}{year} \right) = \sum [density * f(L_i)] * a(L_f^b - L_i^b) \quad (12)$$

$$Productivity \left( \frac{kJ}{year} \right) = \sum [density * f(L_i)] * a(L_f^b - L_i^b) * 3.64 (aL_i^b)^{0.0736} \quad (13)$$

Productivity to biomass ( $P : B$ ) and consumption to biomass ( $Q : B$ ) ratios were determined. For modeling purposes, the relative frequencies of goby lengths 1-16 cm ( $f(L)$ ) were determined to be the mean relative frequency of each size class observed in video transects collected throughout the sampling season. Total density was determined from visual transects at GS10 during June and August 2020. Initial length ( $L_i$ ) was assumed to be the integer value of each size class (e.g. an initial length of 2 was assigned to all gobies of length  $x$  when  $2 \leq x < 3$ ). Since sex determination was not possible during transect counts, final length ( $L_f$ ) was determined by solving a mean site-specific growth model (Equation 7) for  $t + 1$  where  $t$  was the age of the goby at the initial length. Initial and final weights were estimated using a site-specific length-weight regression (Equation 3). Due to the limited number of gobies collected at ATW, productivity was only estimated at GS10.

Round gobies in non-harbor waters of Lake Michigan have been found to experience annual mortality rates between 79% and 84% (Huo et al., 2014). Specifically, at SLBE, Huo et al (2014) found gobies to experience an annual mortality rate of 81%. Similarly high mortality rates have been found in the Bay of Quinte, Lake Ontario (Taraborelli et al., 2010), and central Lake Erie (Bunnell et al., 2005). In comparison, round goby mortality rate in harbors is substantially lower, 33% in Duluth Harbor, Lake Superior (Lynch and Mensinger, 2013) and between 26-44% in Hamilton Harbour, Lake Ontario (Ve'lez-Espino et al., 2010). Data suggests that this difference is due to predation pressure (Taraborelli et al., 2010; Huo et al., 2014). The objective of this study was to quantify the potential of round gobies to support higher trophic levels, therefore it is important to consider all energy production, including that which is consumed by higher trophic levels. For this reason, the assumed annual mortality rate for this study (33% for all size classes)

accounted only for natural mortality and was set as the reported annual mortality rate in harbor populations. Hence population productivity was estimated based on a 67% annual survival rate.

To provide a comparison between somatic growth estimates from this study with modeled somatic growth using the bioenergetic parameters described by Lee and Johnson (2005), goby productivity was modeled in the FB4 application using their defined consumption parameter and a set  $p$  value of 0.35. In this scenario, the model was provided an initial weight and calculated a final weight (i.e., somatic growth) by difference. The value of all other parameters and inputs remained the same.

## 2.5 Efficiency of reef transfer

The trophic levels of *Cladophora*, benthic invertebrates, dreissenid mussels, and round gobies were estimated with Equation (14) (Turschak et al., 2014 modified from Post et al., 2000). This approach assumes a universal trophic enrichment factor of 3.4‰ and a trophic level of 2 for profundal dreissenids. The fraction of a taxon's carbon derived from pelagic sources ( $\alpha$ ) was calculated with Equation (15). No profundal mussels were collected in this study and therefore alpha calculations were conducted based on the isotopic signature of nearshore mussels which are assumed to be feeding on pelagic phytoplankton and have the same  $\delta^{13}\text{C}$  as phytoplankton. The mean  $\delta^{13}\text{C}$  of benthic invertebrates across taxa and season was designated as the benthic carbon value. In the few cases where a sample's  $\delta^{13}\text{C}$  signature was greater than  $\delta^{13}\text{C}_{\text{benthic invert.}}$ ,  $\alpha$  was assumed to be 0.

$$\text{Trophic Level} = 2 + \frac{\delta^{15}\text{N}_{\text{taxa}} - [(\delta^{15}\text{N}_{\text{nearshore dreissenid}} * \alpha) + (\delta^{15}\text{N}_{\text{benthic invert.}} * (1 - \alpha))]}{3.4} \quad (14)$$

$$\alpha = \frac{\delta^{13}\text{C}_{\text{taxa}} - \delta^{13}\text{C}_{\text{benthic invert.}}}{\delta^{13}\text{C}_{\text{nearshore dreissenid}} - \delta^{13}\text{C}_{\text{benthic invert.}}} \quad (15)$$



The concept of progressive trophic transfer efficiency (TE; Equation 16) was first described by Lindeman (1942) and represents the net energy production at one trophic level ( $\lambda_n$ ) relative to that of the next lowest level ( $\lambda_{n-1}$ ). This process is generally inefficient and is colloquially referred to as the “ten percent law”. Despite this name, TE is not a strict proportion and it has been found to vary depending on the system and organisms involved (Lindeman, 1942). Following the standard convention, productivity levels in this study refer to net productivity (energy associated with somatic growth) rather than gross productivity (energy associated with somatic and gametic growth, metabolism, and respiration). As round goby productivity was only estimated at GS10, TEs were also only determined for GS10.

$$TE = \frac{\lambda_n}{\lambda_{n-1}} * 100 \quad (16)$$

Before TE calculations, the productivity of separate components of the nearshore food web needed to be estimated. Rather than estimating phytoplankton productivity, the rate of energy input into the benthic nearshore zone from phytoplankton was estimated based on the organic carbon grazing rate of dreissenid mussels, which can exceed local phytoplankton production if offshore phytoplankton are advected through the nearshore zone (e.g. Waples et al. 2017). Mussel grazing rate is regulated by multiple factors (Tyner et al., 2015; Xia et al., 2021). For this application, grazing rate was estimated from modeled respiration rates following the methodology of Tyner et al. (2015). Values for the parameters in this model were derived from experiments conducted at organic carbon concentrations of  $138 \mu\text{g} \pm 22 \mu\text{g C}\cdot\text{L}^{-1}$  which are similar to the organic carbon concentrations at GS10. Daily grazing rate was estimated over a 365-day period, using bottom temperature at GS10, and then averaged.

Mussel productivity estimates were calculated using zebra mussel bioenergetic parameters (Schneider et al. 1992) incorporated into the FB4 application (Deslauriers et al., 2017a). Seven iterations of the model were run based on the mean mussel size in seven size classes (<4, 4-7, 8-12, 13-17, 18-22, 23-27, 28-34 mm). Defined consumption parameters are based on the consumption of prey wet mass rather than carbon; therefore, a conversion factor of 1 g phytoplankton WW = 0.2 g phytoplankton DW = 0.1 g C (Hecky and Kling, 1981) was used to convert dreissenid mussels grazing rate of organic carbon to a grazing rate of phytoplankton wet weight. Defined consumption parameters for dreissenids were also developed based on the amount of material ingested (i.e., the amount of material grazed that was not rejected as pseudofeces). However, at low seston concentrations such as those in Lake Michigan, the mass of pseudofeces produced by mussels is negligible (Baldwin et al., 2002) and therefore grazing rate was assumed to be equivalent to ingestion rate. It should be noted that although the mass of pseudofeces may be negligible, due to the high quality of pseudofeces that are produced (Baldwin et al., 2002), its impact on nutrient dynamics may be significant.

Because parameters only accounted for food that was ingested, the mussel diet was assumed to be entirely phytoplankton and the proportion of indigestible prey was assumed to be 0. Predator and prey energy density values were obtained from the literature (Schneider, 1992). The average density of mussels in each size class throughout the sampling season was determined and applied to the appropriate model simulation. Class-specific measures of productivity were summed to determine population productivity.

Benthic invertebrate productivity was estimated from published production : biomass ratios (P:B). Published benthic invertebrate annual P:B values are highly variable, ranging from <1 to >100, with a mean of 5 (Benke and Huryn, 2010). Chironomids can have exceptionally high

growth rates under some conditions (Jackson and Fisher, 1986). However in a cool north temperate stream, annual chironomid P:B values were estimated to be relatively low, ranging from 4.7-21.9 (Berg and Hellenthal, 1991). Based on long-term monitoring conducted at GS10 and more recent monitoring at ATW, it was expected that amphipods would account for the majority of benthic invertebrate biomass in the rocky nearshore zone. As such, total benthic invertebrate production was estimated by applying a P:B ratio of 3.13, the mean annual P:B ratio of a shallow amphipod species in Lake Michigan (Winnell and White, 1984), to total benthic invertebrate biomass.

Transfer efficiency from benthic nearshore primary consumers to round gobies was estimated using equation 16 in which  $\lambda_{n-1}$  represented the summed productivity of dreissenid mussels and non-dreissenid benthic invertebrates and  $\lambda_n$  represented round goby productivity. The transfer efficiency from each prey source to round gobies was then estimated using equation 16 in which  $\lambda_{n-1}$  represented the productivity of dreissenid mussels or non-dreissenid benthic invertebrates and  $\lambda_n$  represented round goby productivity attributed to that food source based on diet proportion estimates.

## Chapter 3: Results

### 3.1 Round goby population structure

#### 3.1.1 Density and size distribution

At GS10, video transect counts ( $n = 3$  on each sampling day) revealed an increase in round goby density (mean  $\pm$  standard deviation) from  $3.7 \pm 1.3$  to  $9.1 \pm 1.1$  individuals  $m^{-2}$  between June and August, followed by a slight decline in October ( $8.1 \pm 1.5$  individuals  $m^{-2}$ ). Substantially lower density estimates were obtained from visual transects ( $n = 3$  on each sampling day) with a slight decrease from June ( $3.0 \pm 0.7$  individuals  $m^{-2}$ ) to August ( $2.2 \pm 0.4$  individuals  $m^{-2}$ ). A density of  $2.4 \pm 2.6$  individuals  $m^{-2}$  was estimated from the analysis of 86 time-lapse images collected at a fixed site in August. Because transects were only performed at ATW in July, no seasonal trends in density or size distribution could be determined for that site. The mean density at ATW in July was  $1.4 \pm 1.2$  individuals  $m^{-2}$  ( $n=3$ ).

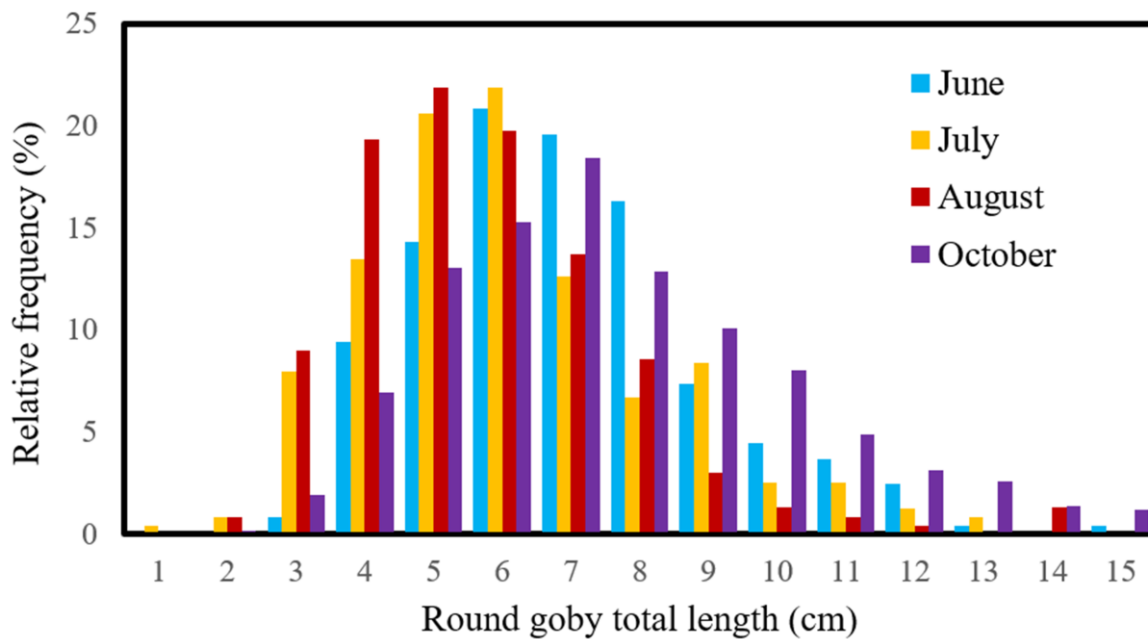


Figure 8: Relative frequency of gobies from video transects collected during June, July, August, and October at Good Harbor Reef.

At both sampling locations and throughout the 2020 season, length-frequency measurements from video transects resulted in a right-skewed unimodal distribution. Round gobies at GS10 ranged from 1.9 to 15.9 cm, with the majority being between 4 and 8 cm (Fig. 8). Mean goby length at GS10 ( $7.3 \pm 2.4$ ,  $n = 1271$ ) was significantly larger than the mean length at ATW ( $6.4 \pm 1.3$ ,  $n = 64$ );  $t = 3.08$ ,  $df = 104$ ,  $p < 0.01$ ). Numerous small gobies, less than 4 cm, were observed while diving but few were visible during video transects or physically collected.

### 3.1.2 Length-weight relationship

In total, 279 round gobies (216 from GS10, 63 from ATW) were included in length-weight regressions and condition factor calculations. Fish ranged from 2.7 to 11.7 cm at ATW and 6.2 to 15.5 cm at GS10. Round goby dry mass (DW) was linearly correlated to wet mass ( $r^2=0.99$ ,  $n = 30$ ; Equation 17):

$$DW = 0.2424 WW \quad (17)$$

Sex was not a significant factor to explain variation in either the weight ( $F_{1,237} = 0.12$ ,  $p = 0.73$ ) or condition factor ( $F_{1,237} = 0.04$ ,  $p = 0.84$ ) of individual fish; therefore, males and females were combined in the analysis. After correcting for variance due to a fish's length, region was a significant factor in explaining a fish's weight ( $F_{1,237} = 59$ ,  $p < 0.01$ ) and condition factor ( $F_{1,237} = 54$ ,  $p < 0.01$ ). The mean condition factor of gobies <8 cm and 8 – 12 cm collected from GS10 ( $1.3 \pm 0.1$ ,  $1.4 \pm 0.1$ ) were higher than that of fish in the same size class from ATW ( $1.1 \pm 0.1$ ,  $1.2 \pm 0.1$ ; Fig. 9). When fish collected throughout the season were analyzed collectively, the length-weight regressions for GS10 and ATW were  $WW = 0.009(L)^{3.198}$  ( $r^2 = 0.990$ ,  $n = 216$ ) and  $WW = 0.012(L)^{2.970}$  ( $r^2 = 0.975$ ,  $n = 63$ ) respectively (Fig. 10). Insufficient data was collected at ATW to determine if the weight or condition factor of an individual was dependent upon the date of collection. At GS10 there was a significant difference in the weight ( $F_{1,194} = 13$ ,

$p < 0.01$ ) and condition factor ( $F_{1,194}=13$ ,  $p < 0.01$ ) of individuals collected during different months.

Weight at length was highest in June and lowest in August (Fig. 10). The mean condition factor followed a similar trend (Fig. 9)

Mean round goby biomass on Good Harbor Reef June – October was  $13.6 \pm 5.5$  g wet weight  $m^{-2}$ . Round goby biomass was estimated to be  $4.6 \pm 2.8$  g wet weight  $m^{-2}$  at ATW during July but was not estimated again during the 2020 season.

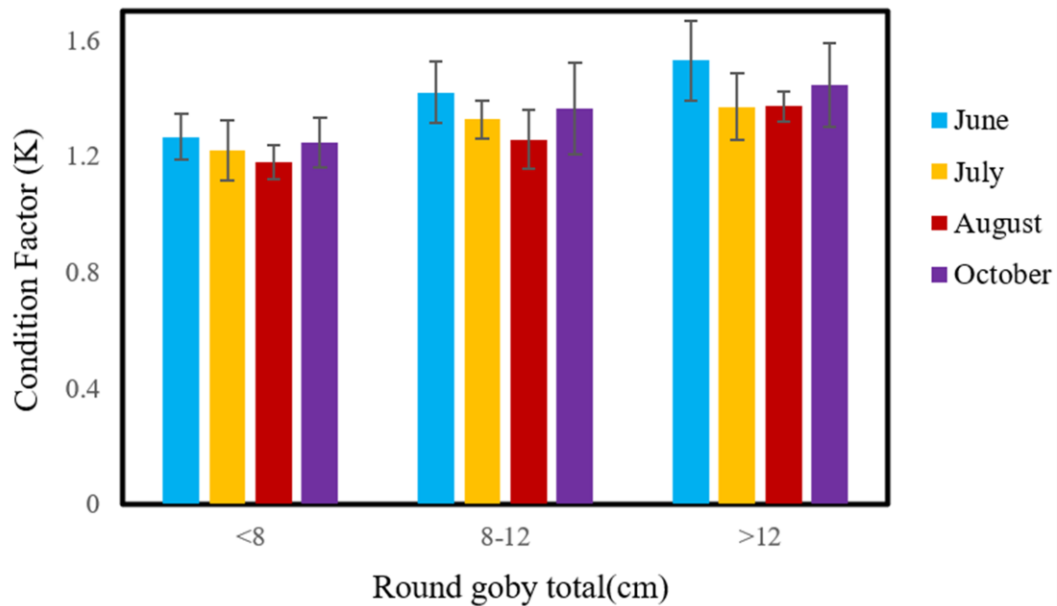


Figure 9: Condition factor of fish in three size classes throughout the sampling season. Whisker bars represent standard deviations.

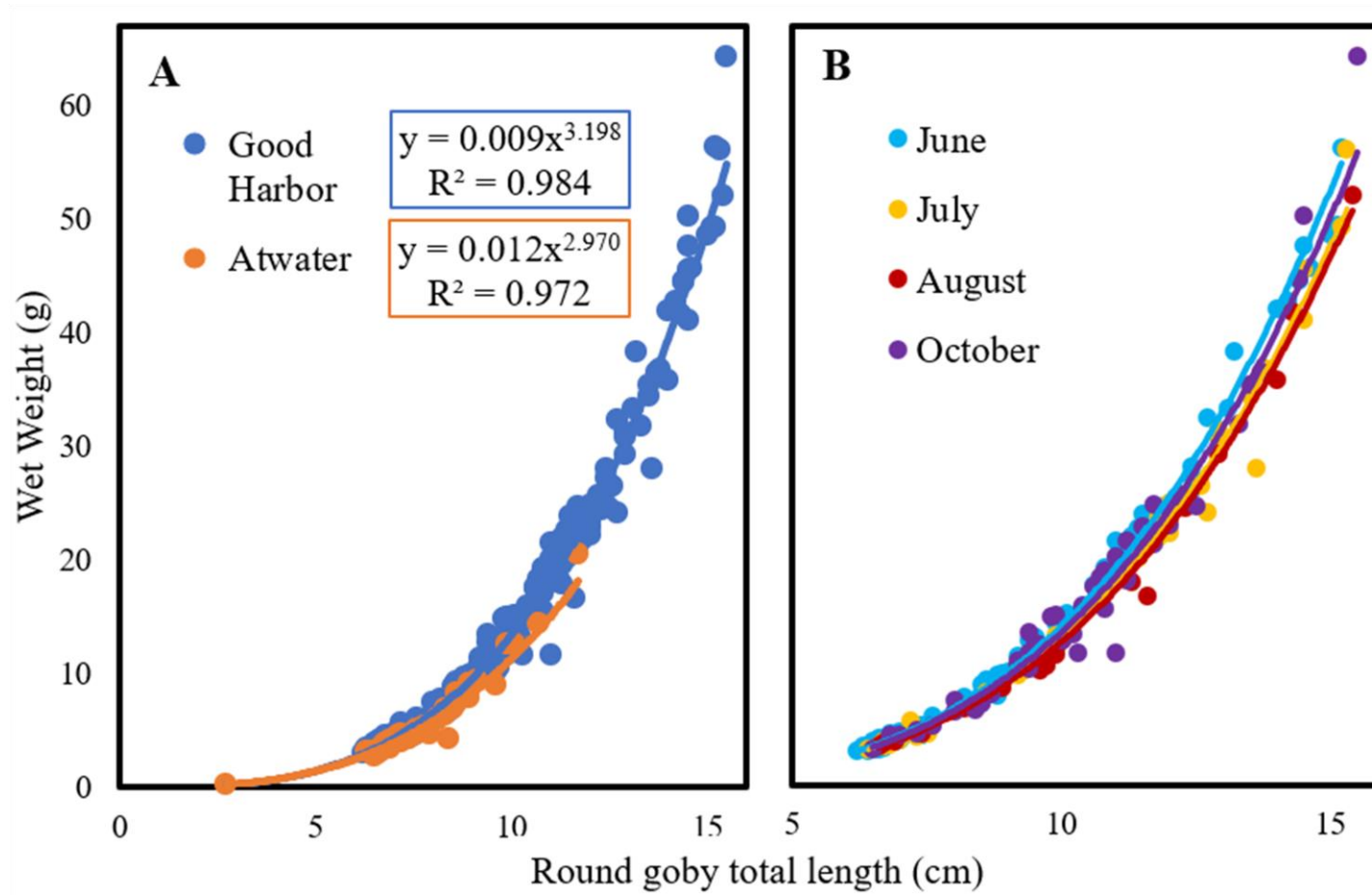


Figure 10: Round goby total length (cm) – wet weight (g) relationships. A. Round goby length-weight data grouped by collection site and fit with site specific power regressions. B. Length-weight relationship for fish collected at GS10, grouped by month of collection and fit with date specific length-weight regressions.

### 3.1.3 Growth

Otoliths were extracted and examined from 91 round gobies throughout the season, 24 from ATW and 67 from GS10. Of these, a total of 16 (8 from ATW and 8 from GS10) were discarded due to disagreement between readers or low confidence in age estimates, resulting in an age estimate acceptance rate of 88% and 66% for GS10 and ATW respectively. At GS10, gobies ranged from 1-6 years old. At ATW, gobies ranged from 0-5 years old (with no age 4 gobies collected).

A likelihood ratio test indicated that, within the GS10 population, a model including sex as an explanatory variable for length at age had a significantly higher likelihood than the constrained model (i.e., without sex;  $\chi^2 = 26.97$ ,  $df = 1$ ,  $p < 0.01$ ). This suggests that length at age data is significantly different between sexes within the GS10 population, with males being larger than females at a given age. Because of this, no pooled comparison (males and females) between ATW and GS10 was conducted. Additionally, due to the small sample size of ATW females, no comparison was made between females and males at ATW or between females at ATW and GS10. However, the likelihood ratio test indicated that amongst males, a model including site as an explanatory variable for length at age had a significantly higher likelihood than the constrained model (i.e., without site;  $\chi^2 = 8.80$ ,  $df = 1$ ,  $p < 0.01$ ). This suggests that length at age data is significantly different for males at GS10 than it is for males at ATW, with GS10 males being larger at a given age.

In each iteration of the model, mass normalized round goby growth was greatest from age 0 to age 2 (Fig. 11), although very few age-0 and age-1 fish were analyzed. Length increased by 5.5 to 7.5 times a fish's starting length in the first year and 0.3 to 0.7 times their starting length in



the second year. Similarly, goby weight increased by 425 to 550 times a fish's starting weight in the first year and 1.3 to 3.8 times their starting weight in the second year.

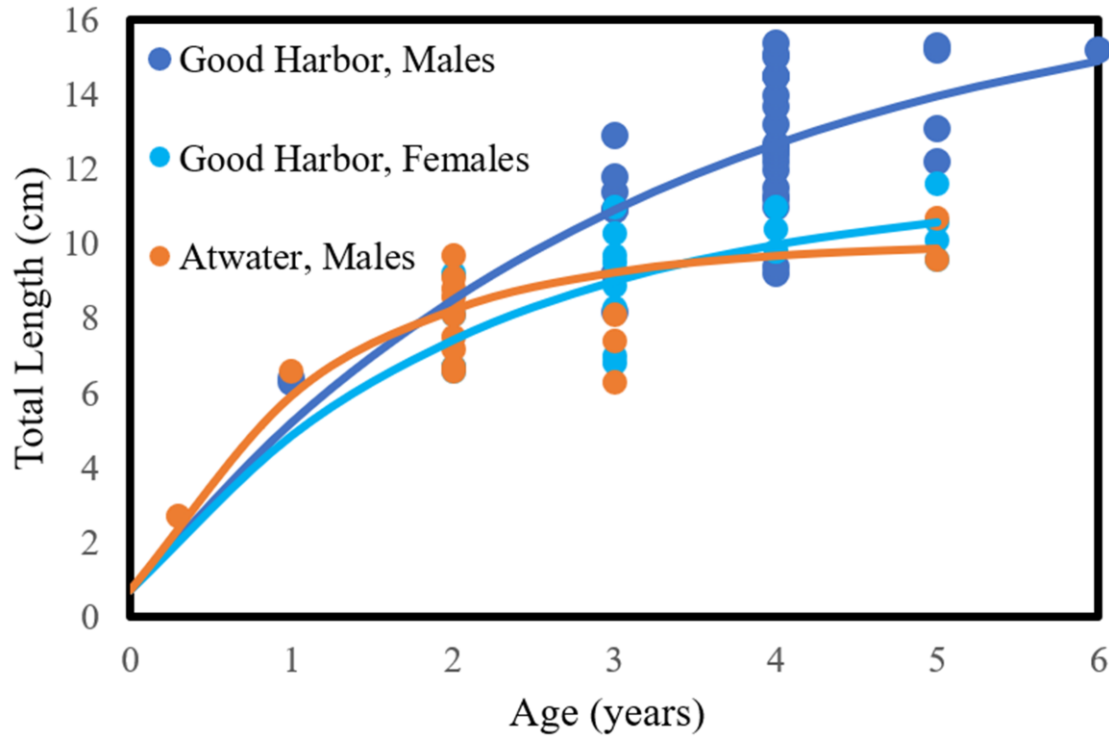


Figure 11: Length (L; cm) at age of round gobies collected during the 2020 season. Age was determined from whole sagittal otoliths. Data for each group of fish was fitted with the von Bertalanffy growth model curve.

Table 2: von Bertalanffy growth parameters. Parameters were estimated using a nonlinear least squares approach with brute force. Reported standard error values refer to the variance in the distribution of parameters values in iterative attempts to minimize the residual sum of squares.

		Estimate	Std. Error	Number of Fish
Atwater, Males	$L_{\infty}$	10.03	0.720	12
	$k$	0.821	0.208	
Good Harbor, Males	$L_{\infty}$	17.49	2.841	35
	$k$	0.31	0.104	
Good Harbor, Females	$L_{\infty}$	11.57	1.080	21
	$k$	0.48	0.119	

### 3.2 Round goby diet composition

Gut content analysis revealed a large amount of variation in both diet composition and gut fullness within the round goby populations at both sites. In total, gut content was analyzed from 63 round goby individuals (13 from ATW, 50 from GS10) ranging from 6.5 to 15.4 cm in length. There was no statistical difference in diet composition (ANCOVA  $F_{1,59} = 2.66$ ,  $p = 0.108$ ) or gut fullness (ANCOVA  $F_{1,59} = 1.36$ ,  $p = 0.248$ ) between the two sites when accounting for length as a covariate. Therefore, samples were combined for analysis. Dreissenid mussels, as evident from whole and fragmented shells, were found in the gut content of 89% of samples, including fish of all size classes analyzed. Non-dreissenid benthic invertebrates comprised 0 to 100% of the diet by volume of gobies less than 12 cm, while they comprised 0 to 33% of the diet by volume of gobies larger than 12 cm (Fig. 12).

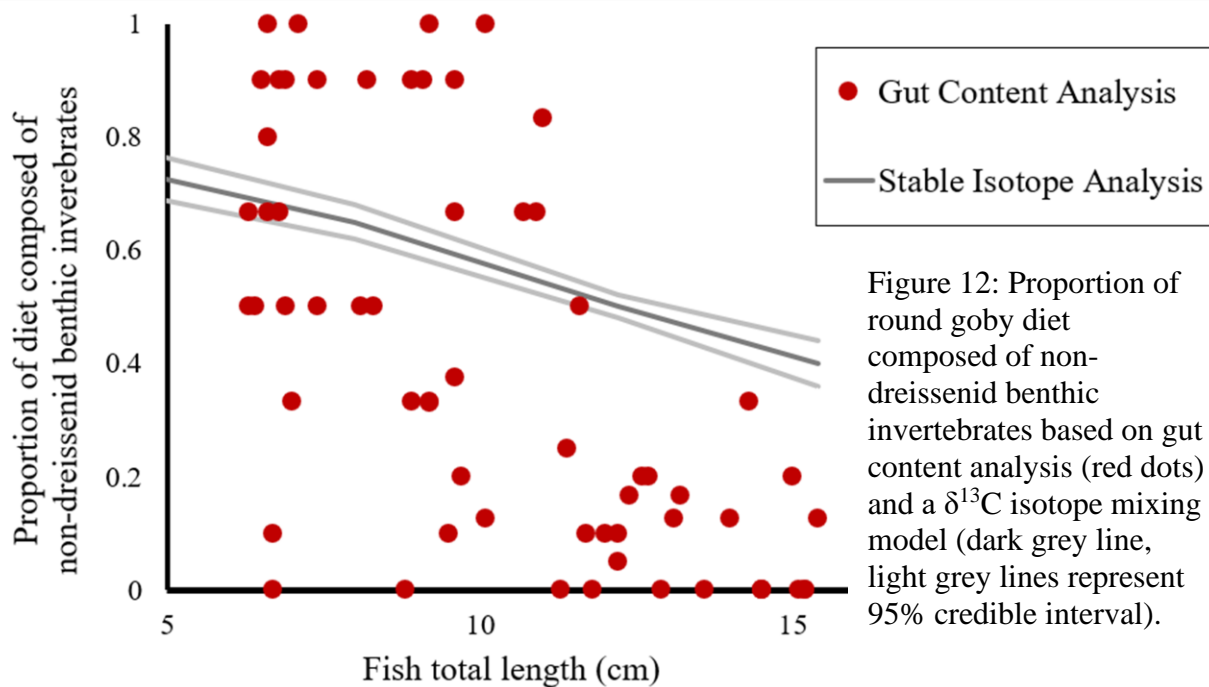


Figure 12: Proportion of round goby diet composed of non-dreissenid benthic invertebrates based on gut content analysis (red dots) and a  $\delta^{13}\text{C}$  isotope mixing model (dark grey line, light grey lines represent 95% credible interval).

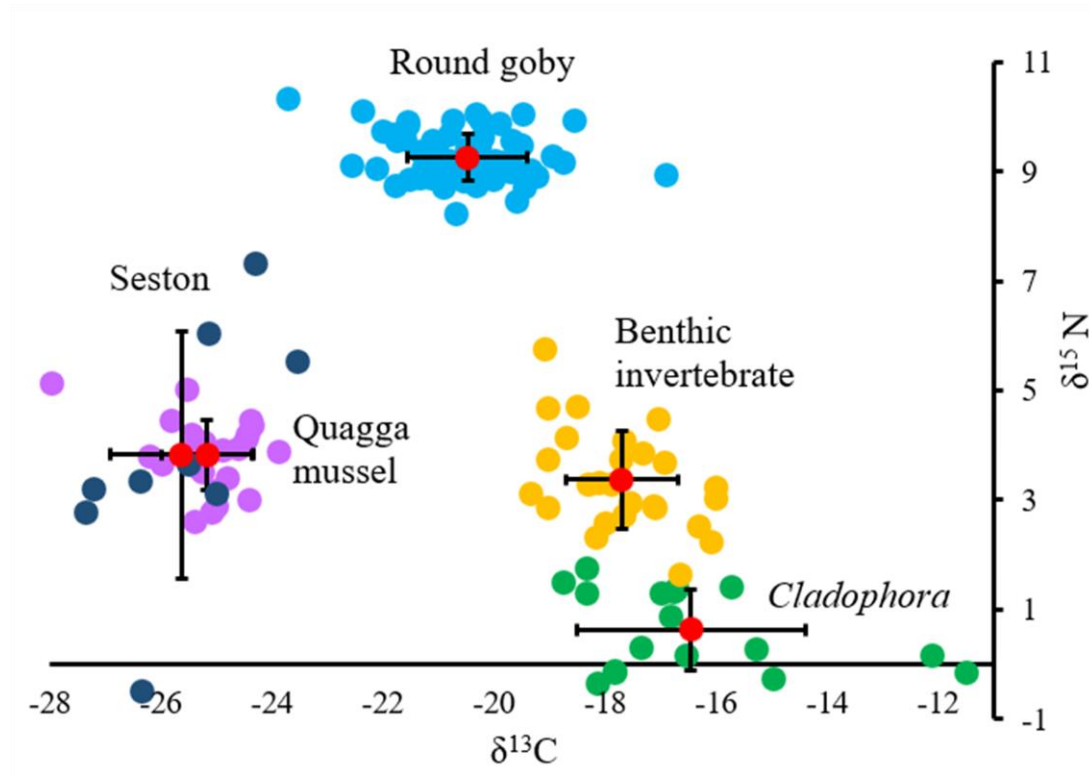


Figure 13: Isotopic signature of round gobies (light blue), nearshore quagga mussels (pink), benthic invertebrates (yellow), *Cladophora* (green), and seston (dark blue). Red dots and the associated error bars represent the mean and standard deviation isotopic signature of each group.

In total, 71 round goby stable isotope samples were analyzed from 65 fish ranging from 2.7 – 15.4 cm. The isotopic signature *Cladophora* was only analyzed at GS10. The isotopic signature of dreissenid ( $t = 0.132$ ,  $df = 24$ ,  $p = 0.902$ ) and non-dreissenid invertebrates ( $t = 0.922$ ,  $df = 26$ ,  $p = 0.372$ ) and round gobies (when compared to other individuals within their size class) were not significantly different between GS10 and ATW (ANCOVA  $F_{1,61} = 3.458$   $p = 0.067$ ). Therefore, sites were analyzed collectively. Reflecting a pelagic primary energy source, the mean lipid-corrected  $\delta^{13}C$  signature (hereafter referred to as  $\delta^{13}C$ ) of quagga mussels was found to be depleted in  $\delta^{13}C$  relative to benthic invertebrates which had a  $\delta^{13}C$  similar to that of nearshore *Cladophora*. Round gobies'  $\delta^{13}C$  signature during the 2020 season ( $-20.48 \pm$

1.07 ‰) was positioned between that of benthic invertebrates and dreissenid mussels (Fig. 13). This finding was consistent with the results of Hurst (2020) who observed a relative depletion of round goby  $\delta^{13}C$  values between 2010/2012 and 2019. After normalization to a nearshore quagga mussel baseline, the round goby  $\delta^{15}N$  signature from 2020 sampling ( $5.44 \pm 0.43$ ) was similar to that of 2019 samples and enriched from 2010/2012 samples.

Round goby  $\delta^{13}C$  values were negatively correlated with total body length ( $F_{1,63} = 57.4$ ,  $p < 0.01$ ), with smaller gobies having a more  $^{13}C$  enriched signature. Correspondingly, the  $\delta^{13}C$  linear mixing model indicated a negative relationship between total length and the proportion of diet composed of benthic invertebrates (Fig. 12). At the minimum (2.7 cm), mean (9.7), and maximum (15.4) length analyzed, non-dreissenid benthic invertebrates represented 78, 60, and 40% of the diet respectively. At a length of 12 cm, benthic invertebrates and quagga mussels made up equal proportions of the diet.

### 3.3 Bioenergetic modeling

Using growth rates derived from length at age curves (as determined with otoliths) of gobies collected at GS10, consumption was modeled using the FB4 application (Deslauriers et al., 2017a). When accounting for natural mortality, net round goby productivity was estimated to be  $25.4 - 38.2 \frac{mg\ WW}{m^2\ day}$ . This range, and the range presented for subsequent estimates, results from the 95% confidence interval around round goby biomass density. Using the determined wet to dry mass conversion (Equation 17) and the mean carbon content of round goby muscle tissue (Table 3), biomass productivity was estimated to be  $2.8 - 4.2 \frac{mg\ C}{m^2\ day}$  and consumption was estimated to be  $9.8 - 14.7 \frac{mg\ C}{m^2\ day}$ . Consumption consisted of an estimated 53% and 47% of benthic invertebrates and dreissenid mussels respectively. These estimates resulted in an annual

production to biomass ratio (P:B) of 0.70 – 1.03 and an annual consumption to biomass ratio (Q:B) of 5.21 – 7.81.

When modeling goby productivity using Lee and Johnson's (2005) estimated values for consumption and a  $p$  value of 0.35, net round goby productivity was estimated to be  $1.9 - 2.9 \frac{mg\ C}{areal\ m^2*day}$ . To support this growth, consumption was estimated to be  $8.0 - 10.0 \frac{mg\ C}{m^2\ day}$ . The value of all other parameters including mortality, diet composition, and population density remained unchanged.

Gross conversion efficiency (GCE) is a useful parameter when determining an organism's ability to convert food energy into biomass and is defined as the ratio of growth per unit of feed intake in terms of energy (Brett and Groves, 1979). Round goby consumption and production estimates equated to a conversion efficiency of 20% based on measured growth at GS10. By comparison, when using literature defined consumption parameters, GCE was estimated to be 18%. A strong negative relationship existed between length and GCE, with gobies less than 4 cm having a GCE of 25% and those larger than 13 cm having a GCE below 10%.

Table 3: Mean  $\pm$  standard deviation of trophic level and percent carbon by mass for each group of organisms. All taxa of non-dreissenid benthic invertebrates are grouped.

	n	Trophic level	% Carbon by dry weight
<i>Cladophora</i>	17	$1.19 \pm 0.21$	$22.03 \pm 0.72$
Benthic invertebrate	26	$1.98 \pm .26$	$28.45 \pm 1.76$
Quagga mussel	23	$1.92 \pm 0.18$	$42.31 \pm 1.24$
Round goby	65	$3.66 \pm 0.12$	$45.5 \pm 0.28$

### 3.4 Reef trophic transfer efficiency

At GS10, lake bottom rugosity was found to be  $1.18 \pm 0.02$ . Therefore, 1 areal  $\text{m}^2$  is equal to 1.39  $\text{m}^2$  of lake bottom (1  $\text{m}^2$  from the top of rocks and 0.39  $\text{m}^2$  from the sides of rocks). No rugosity measurements were collected at ATW, but the substrate composition is similar and therefore rugosity values from GS10 were applied to ATW. Measurements of abundance and total carbon biomass from top and side benthic scrapes were scaled appropriately and combined (Fig. 14). All per area measurements hereafter are areal, accounting for bottom rugosity.

Benthic samples were collected at ATW only in July and August and therefore seasonal trends in the biomass of *Cladophora*, benthic invertebrates, and dreissenid mussels were not

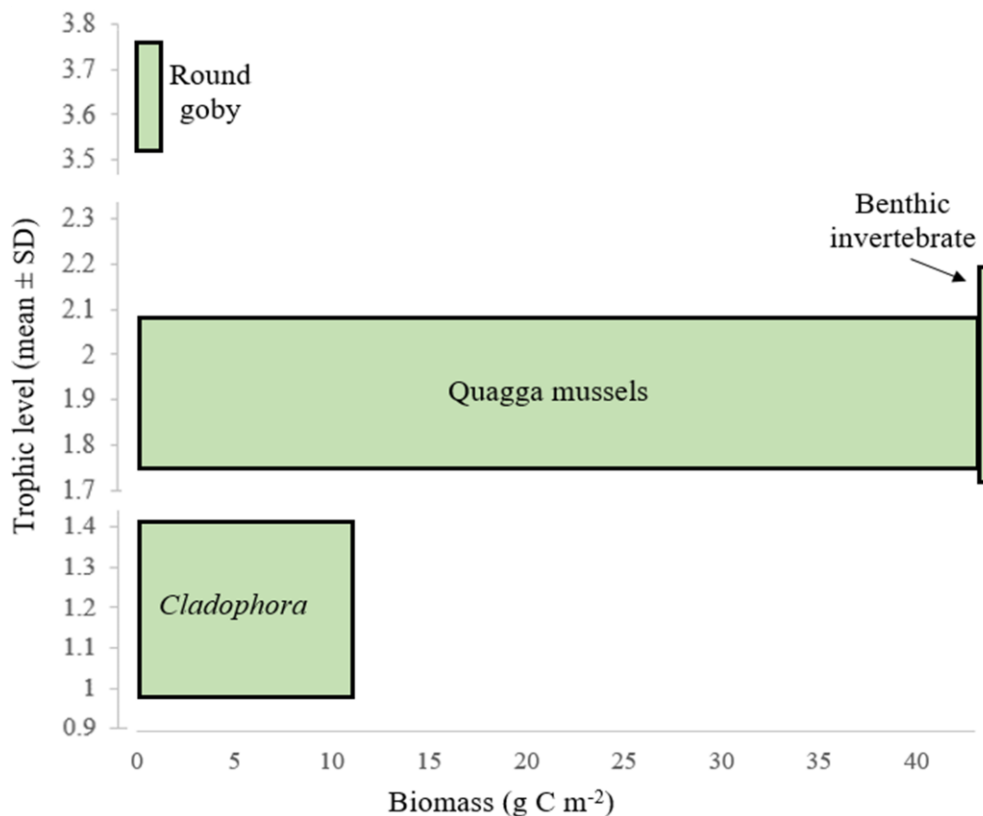


Figure 14: Mean biomass by trophic level at GS10. Trophic level ~2 divided into quagga mussels (shell free) and benthic invertebrate portions. The height of each rectangle represents that mean  $\pm$  SD trophic level of each taxon.

analyzed. At GS10, seasonal changes in *Cladophora* biomass were evident (Fig. 15) increasing from  $3.36 \pm 1.69$  g DW  $\text{m}^{-2}$  in June to  $85.60 \pm 12.88$  and  $91.83 \pm 30.46$  g DW  $\text{m}^{-2}$  in July and August respectively, and then decreasing to  $18.00 \pm 8.03$  g DW  $\text{m}^{-2}$  in October. During July and August, *Cladophora* biomass was significantly lower at ATW ( $9.96 \pm 3.98$  g DW  $\text{m}^{-2}$ ) than at GS10 ( $t = 4.44$ ,  $df = 5$ ,  $g_{\text{Hedges}} = 8.03$ ,  $p < 0.01$ ).

Quagga mussel biomass at GS10 did not follow a significant seasonal trend (Fig 15; ANOVA  $F_{2,23} = 0.151$ ,  $p = 0.928$ ) and had a mean biomass of  $102.39 \pm 41.5$  g shell-free DW  $\cdot \text{m}^{-2}$  throughout the season. Between the two sites, mussel biomass was not significantly different ( $t = 0.189$ ,  $df = 5$ ,  $p = 0.88$ ), however, at GS10, quagga mussel biomass fluctuated by less than 10% throughout the season while it varied by nearly 55% between sampling days at ATW ( $119.39 \pm 36.84$  g shell-free DW  $\cdot \text{m}^{-2}$  in July and  $77.44 \pm 25.41$  g shell-free DW  $\cdot \text{m}^{-2}$  in August). This temporal variation with ATW was not statistically significant ( $t = 1.62$ ,  $df = 5$ ,  $p = 0.18$ ) due to

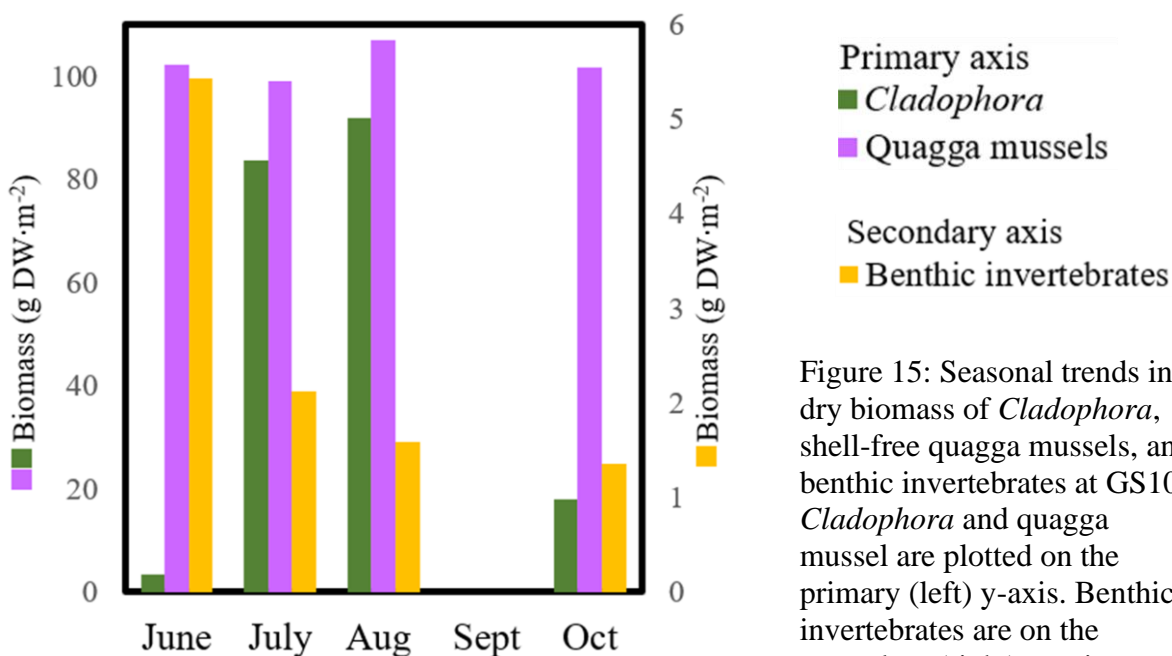


Figure 15: Seasonal trends in dry biomass of *Cladophora*, shell-free quagga mussels, and benthic invertebrates at GS10. *Cladophora* and quagga mussel are plotted on the primary (left) y-axis. Benthic invertebrates are on the secondary (right) y-axis.

the large variance among replicate samples. Throughout the season, the length-frequency distribution of mussels was bimodal with peaks at 2-4 mm and 23-25 mm (Fig. 16). Benthic invertebrate biomass was variable between replicate samples and was estimated to be  $2.62 \pm 0.44$  and  $1.14 \pm 0.38$  g DW m<sup>-2</sup> at GS10 and ATW respectively. This difference was statistically significant ( $t = 7.38$ ,  $df = 11$ ,  $g_{\text{Hedges}} = 3.51$ ,  $p < 0.01$ ). No seasonal trend was identified at GS10 (ANOVA  $F_{3,8} = 0.554$ ,  $p = 0.660$ ).

The trophic level of *Cladophora*, non-dreissenid benthic invertebrates, and dreissenid mussels were near the expected value of primary producers (Table 3). Round goby trophic position was weakly but significantly negatively correlated with length (linear regression  $F_{1,63} = 7.284$ ,  $r^2 = 0.089$ ,  $p < 0.01$ ; Fig. 17). No seasonal trends were observed in an individual taxon's percent carbon by weight (Table 3) or wet to dry weight conversions. At GS10, the total mussel

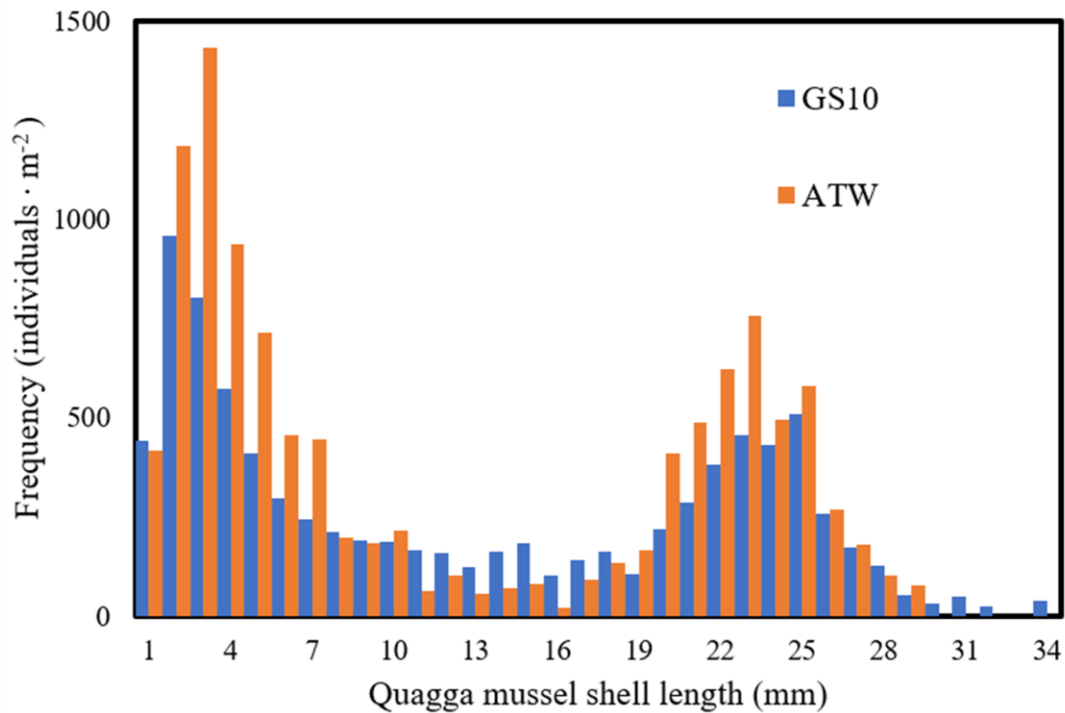


Figure 16: Average length-frequency distribution of quagga mussels collected throughout the sampling season at both sites.



carbon grazing rate was estimated to be  $467 \frac{mg\ C}{m^2\ day}$ . Mussel populations on the tops and sides of rocks accounted for 53% and 47% of the grazing rate respectively and total mussel productivity was estimated as  $223 \frac{mg\ C}{m^2\ day}$  (Fig. 18). Although sides of rocks only contributed to 28% of rocky habitat, they represented 50% of total mussel density. Benthic invertebrate productivity was estimated as  $6.4 \frac{mg\ C}{m^2\ day}$  (Fig. 18).

Consumption by round gobies was equivalent to 2.0 – 2.9% of mussel productivity and 81.3 – 122% of benthic invertebrate productivity. The TE of energy from benthic invertebrates and dreissenid mussels to round gobies was estimated to be 1.2 – 1.8%. When separated, the TE from benthic invertebrates to round gobies was 28 – 42% while the TE from mussels to gobies was 0.4 – 0.6 %, reflecting the fact that, while both of these food sources are important for round gobies, they consume a much larger fraction of non-dreissenid benthic invertebrate production than dreissenid production.

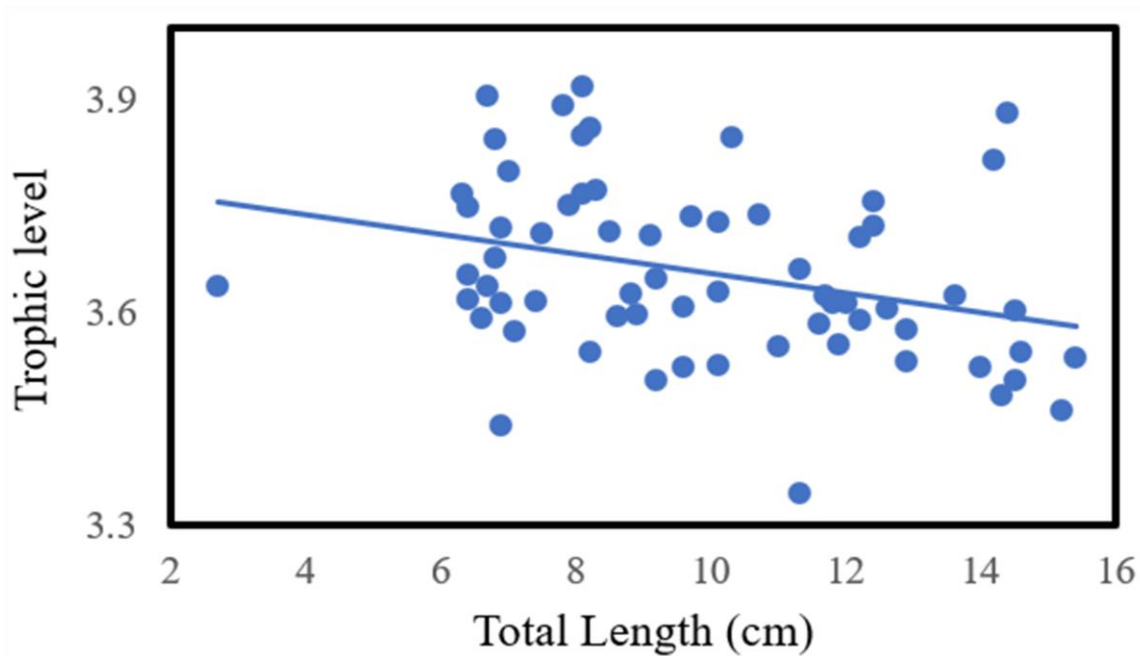


Figure 17: Trophic level of round goby based on total length. Data fits with linear regression ( $r^2 = 0.089$ ,  $p < 0.01$ ).

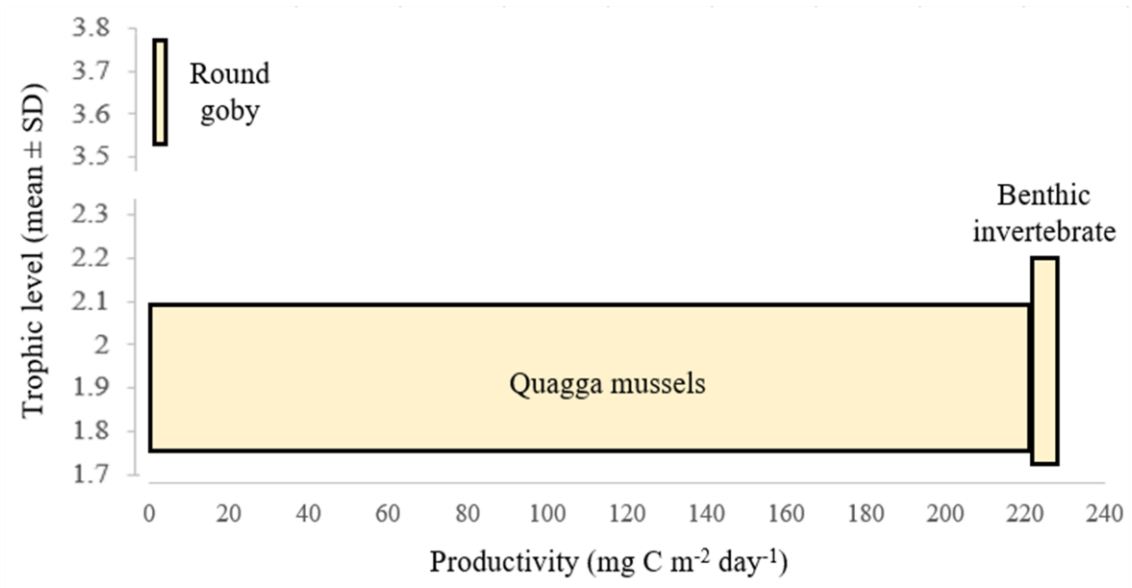


Figure 18: Productivity by trophic level. Trophic level ~2 divided into quagga mussels and benthic invertebrate sections. The height of each rectangle represents that mean  $\pm$  SD trophic level of each taxon.

## Chapter 4: Discussion

### 4.1 Round goby population structure

Diver visual and video transects produced substantially different density estimates. Gobies' sudden and fast swimming behavior can make accurate counting difficult, especially in real-time visual counts. While this is less of a problem in video transects that are slowed down and analyzed repeatedly, video analysis is more sensitive to the double-counting of individuals if they repeatedly leave and re-enter the frame of view. Regardless of the methodology used, round goby density may be underestimated due to round gobies' tendency to hide under rocks and burrow in soft sediment (Ray and Corkum, 2001). On the other hand, both methods are also susceptible to overestimation as curious gobies may be attracted to diver-created disturbances (Johnson et al., 2005a), or even just the divers themselves. This potential bias is avoided when using time-lapse imagery, however, this method only gathers data from a small ( $2 \text{ m}^2$ ) area and therefore does not account for heterogeneity at the site.

The density of round gobies, as reported in the literature, is highly variable in the Great Lakes. Reported densities in the nearshore zone (individuals  $\text{m}^{-2}$ ) include 0.003 - 0.058 in central Lake Erie (Bunnell et al., 2005), 0.8-7.76 in western Lake Erie (Johnson et al., 2005a), 4.2 in Lake Ontario (Karatayev et al., 2020) and up to 19 on cobble substrate in Calumet Harbor, Lake Michigan (Chotkowski and Marsden, 1999). On Good Harbor Reef, round goby density has been periodically estimated via diver visual transects since 2010 and has been found to range from 1 to 9.3 individuals  $\text{m}^{-2}$ . Although video transect density estimates during the 2020 season were within this range, they fall on the higher end and contradict the observed negative trend in annual mean goby density at GS10 since 2010. Visual transect density estimates from the 2020 season are consistent with data collected in years past and agree with density estimates from time-lapse

imagery. For these reasons, it was concluded that video transects likely overestimated round goby density, and so they were not used in biomass or productivity estimates.

While they were not used for density estimates, video transects allowed for more precise size estimates and were therefore used to calculate the relative frequency of each size class, with the assumption that any multiple counting of individuals was not size selective. The relative frequency of gobies less than 6 cm in video and visual transects was 35% and 57% respectively. During visual transects, a diver ran their hands through algae and under rocks to flush out small fish that were hiding. Therefore, visual counts may more accurately account for small round gobies that remain unseen in video transects. It is also possible that the higher frequency of small gobies in visual counts was due to the unintentional inclusion of some slightly larger gobies (~7cm) in the smaller size class as all sizes were quickly estimated using natural points of reference. The relative frequency of gobies <7cm in video transects was 55% suggesting the presence of many 6-7 cm gobies that could have been included in the smaller size class during visual counts. Additional research is needed to determine which method most accurately accounts for small round gobies in density estimates.

Size-frequency distributions, as based on video transects, were similar throughout the season. No trend in the median or mean size of gobies, that would be indicative of cohort growth, was observed. This is potentially due to the varied growth rate between individuals, gobies multiple spawning events per season, and the inability to distinguish males and females during transects. Additionally, the population structure may have naturally varied between sampling days as different size and sex gobies likely shift their habitat throughout the year (Ray and Corkum, 2001; Johnson et al., 2005a). Based on the high frequency of 4-7cm long individuals at GS10, gobies of age-1 are suspected to be the most abundant age class at this site, although age-

frequency data is uncertain because of the variability in size at age. Age-0 gobies were likely underestimated at both sites due to their small size and tendency to hide.

The minimum size observed in this study was 1.9 cm, although it is expected that smaller gobies were present but not visible during transects and were therefore not measured. The maximum size observed in this study was 15.9 cm. This is within the observed size range observed by Kornis et al. (2017) for Lake Michigan round gobies but exceeds many previous maximum length measurements in the Great Lakes and other invaded territories (Duan et al., 2021). The maximum estimated age in this study was 6 years old (total length 15.4 cm), determined in a male collected from GS10. In 2014, Huo et al. found the maximum age at Sleeping Bear Dunes to be 7, the oldest age recorded for round gobies. Other estimates of maximum age using scales, whole otoliths, and/or sectioned otoliths range from 3-6 years (Macinnis and Corkum, 2000; Taraborelli et al., 2010; Sokołowska and Fey, 2011; Grul'a et al., 2012). Spatial variation in maximum length and age is unsurprising as some habitats are likely more supportive of greater growth and longevity (e.g. increased food abundance, decreased predation, etc). Additional variation may be due to the collection and aging technique used. For example, sectioned otoliths generally result in greater maximum age estimates than other structures (Huo et al., 2014).

Males and females represented 53% and 36% of collected fish respectively. Past studies have suggested that males could represent a larger portion of catch due to their more exploratory behavior and increased residency time in shallow areas after spawning (Kornis et al., 2012). Some fish were not confidently identified as males or females (11%) and were therefore assigned no sex and were not included in sex-specific analysis. In Lake Michigan, Kornis et al. (2017) reported the average age at which 50% of round goby females reach maturity to be 2.4 years. As

most unsexed gobies were below this age, based on total length and growth models, immaturity likely increased uncertainty in sexing. A limited presence of intersex round gobies has been reported in the Baltic Sea (Guellard et al., 2015) and a contaminated site in Hamilton Harbor, Lake Ontario (Marentette et al., 2010), but no additional gonad analysis was completed on the unsexed fish collected for this study.

As all biomass, productivity, and efficiency calculations are built upon density and size distribution estimates, small inaccuracies in these values could potentially have a significant impact on the interpretation of results. While there remains a need to more accurately quantify round goby biomass and its spatial and temporal variability in Lake Michigan, the methods used in this study likely result in estimates that are more accurate than those derived from more conventional approaches such as traps and netting, and as a result, the estimates of productivity and trophic efficiency are considered accurate within the range of uncertainty reported here. Multiple approaches of estimating round goby density should also be used at ATW in the future as a single video transect was the only density estimate collected during the 2020 season.

#### **4.1.1 Growth**

On average, round gobies collected from ATW had a lower weight at length and condition factor than round gobies collected at GS10. ATW male gobies also grew at a slower rate than male GS10 gobies. Although too few females were collected to make a comparison between sites, it is suspected that the same pattern exists. Within a population, summer seasonal trends in goby weight at length and condition factor were observed on Good Harbor Reef and agree with seasonal trends that have been identified in southwestern Lake Michigan (Stacy-Duffy et al., 2021) and western Lake Ontario (Young et al., 2010).

Past research has identified less desirable substrate, reduced availability of high-quality food, increased competition for those food sources, and differences in water temperature as potential causes of spatial variation in growth rate and condition (Young et al., 2010; Huo et al., 2014; Duan et al., 2016). Both sites and their surrounding area have similarly desirable substrates, but ATW supports a lower biomass of benthic invertebrates and a more spatially variable dreissenid mussel population than GS10. This suggests that bottom-up control and intraspecific competition for food resources may be limiting goby growth. Interspecific competition was not analyzed during this study but fish species other than round gobies were rarely observed by divers or photographed by deployed cameras and it [interspecific competition] was therefore assumed to be negligible at both sites throughout the season. This is likely in part due to round gobies' competition with and eventual extirpation of species such as mottled sculpin, darters, and sunfish.

At GS10, benthic invertebrate biomass decreased after June while the abundance of mussels within the desired size range for gobies (3-12 mm) (Ghedotti et al., 1995; Ray and Corkum, 1997) increased throughout the season. Round goby access to benthic invertebrates may also have been restricted during the middle of the sampling season due to the increased *Cladophora* growth observed in July and August. As benthic invertebrates are a higher energy food source, seasonal shifts in diet could explain seasonal differences in fish condition. These differences in fish condition may also be a result of the summer spawning season (Young et al., 2010). Monitoring the condition factor of fish earlier in the season may provide more insight into the cause of changes in condition.

Water temperature could be an additional contributor to the observed spatial differences in growth rate and robustness (Huo et al., 2014; Stacy-Duffy et al., 2021). The bottom

temperature July-October 2020 at GS10 was 5.8°C warmer on average than the bottom temperature at ATW (Fig. 19). Although both sites reached maximum temperatures of 21°C during this period, frequent upwelling events at ATW resulted in bottom water temperatures below 10.1°C (the minimum temperature observed at GS10) over 50% of the time. As round goby metabolic rate has been found to increase exponentially from 0-26°C (Lee and Johnson, 2005), cooler temperatures at ATW could reduce the rate and consistency of growth and result in lower condition factors and smaller maximum size. For example, a 35g round goby exposed to the average temperature at GS10 during July-October (17.6°C) is modeled to consume 190% more food resulting in nearly 300% more net productivity during this period than a 35g goby exposed to the average temperature at ATW (11.8°C). Additionally, at temperatures less than 7°C round goby net productivity is negligible or negative and GCE is  $\leq 0\%$ .

Within a region, past studies have found variation in growth and condition between sexes, with males growing faster (Macinnis and Corkum, 2000; Sokołowska and Fey, 2011; Huo

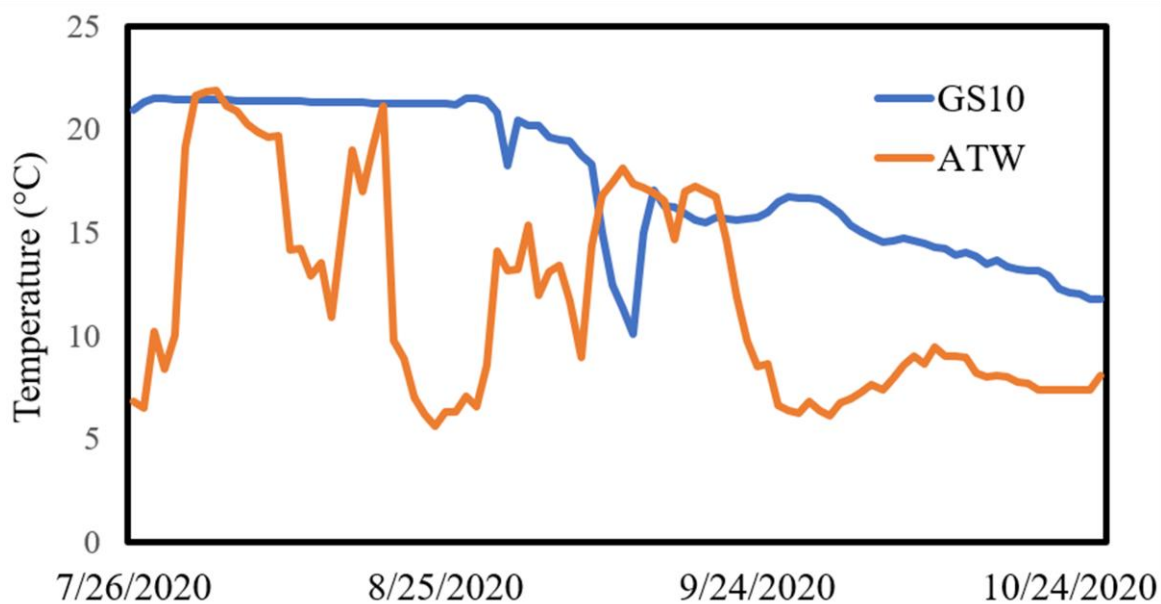


Figure 19: Bottom temperature at GS10 and ATW July – October 2020.



et al., 2014), living longer (Tomczak and Sapota, 2006), and reaching larger asymptotic lengths (Macinnis and Corkum, 2000; Schneider et al., 2000). Our results corroborated this conclusion as female gobies collected at GS10 were found to reach a smaller maximum size and experience slower growth rates than their male counterparts. Due to the small number of age-0 and age-1 gobies collected, no comparison statements can be made between growth models for gobies under 2 years of age. However, the rapid growth rates predicted by our models between age 0 and 2 agree with past findings (Sokołowska and Fey, 2011; Grul'a et al., 2012).

The high variability of length at age observed in this study is similar to observations made by others (Macinnis and Corkum, 2000; French and Black, 2009; Gümüş and Kurt, 2009; Sokołowska and Fey, 2011; Huo et al., 2014; Duan et al., 2016). Because round gobies spawn throughout an extended period and otoliths were used to age gobies to the year, gobies of a specific assigned age may in reality differ in age by several months. In Lake Superior, maximum goby growth has been found to occur in July and August, with almost no growth observed from October to March (Lynch and Mensinger, 2013). In central Lake Erie, the growing season was found to be extended with simulated round gobies losing weight December- April (Bunnell et al., 2005). Similarly, based on bioenergetic modeling of Good Harbor Reef gobies, growth appears to slow or cease as water temperatures cool November-May. The summer growing season may exaggerate a small age difference as a goby several months younger does not have as much time to grow. This may be compounded at ATW where extreme temperature fluctuations due to upwelling may alter the feeding and growing period. Other factors could also result in natural variation of length at age. For example, male reproductive morphs have been found to differ in their length at age, with guarder males having larger body sizes and faster somatic growth rates than sneaker males (Bose et al., 2018). Finally, growth is partly dependent on feeding rate;

therefore individual variability in maximum consumption rate as observed in lab experiments (Lee and Johnson, 2005) may explain individual variability in growth rates.

The results presented here suggest that understanding how food availability and physical conditions influence goby growth and condition will be important for the incorporation of gobies in predator-prey models (Stacy-Duffy et al., 2021). For example, if goby productivity is sensitive to both temperature and food (benthic invertebrate) availability, then the rate of potential energy available to goby predators can be expected to be greatest in parts of the lake where temperatures are warm and where there is substrate that supports high invertebrate biomass. Ironically, the west side of the lake, such as our ATW site, has more rocky substrate to support benthic invertebrates than the east side of the lake (especially south of SLBE), but it also has colder temperatures. The more isolated rocky areas on the east side of the lake, such as the GS10 site in this study, may be round goby hotspots, due to their combination of favorable substrate and warmer temperatures.

It should also be noted that understanding the causes of variation in somatic growth may increase the confidence of age estimates as differences in somatic growth patterns are likely reflected in otolith growth as false or tightly packed annuli that are difficult to interpret. It is suspected that slow and/or sporadic somatic growth patterns at ATW reduced the readability, and thus the acceptance rate, of otoliths from ATW gobies.

## **4.2 Round goby diet composition**

While gut content analysis provides direct evidence of consumption at the time of collection, stable isotope analysis provides indirect evidence of the assimilation of isotopically distinct food types over an extended period. Stable isotope field studies often assume that the isotopic composition of an animal's tissue is in equilibrium with the diet, but this is not always

the case (Vander Zanden et al., 2015). Using a regression developed for ectotherm vertebrate muscle tissue (Vander Zanden et al., 2015), the half-life of  $\delta^{13}\text{C}$  in a 10 g round goby is approximately 41 days. This translates to an integration period of more than 200 days before a goby's isotopic composition is near equilibrium with its food sources (such as a goby switching from a purely dreissenid mussel diet to a purely non-dreissenid benthic invertebrate diet). Therefore, it is not surprising that stable isotope values did not reflect a purely non-dreissenid invertebrate or dreissenid mussel diet as sometimes seen in gut content analysis. Rather,  $\delta^{13}\text{C}$  signatures reflected a mixed diet of these food sources for all sizes analyzed, although the relative amount of each diet type shifted with length. The ontogenetic diet shift observed in this study is consistent with past work that has found reliance on dreissenid mussels to increase with total fish length (Turschak and Bootsma, 2015; Turschak et al., 2019).

An organisms'  $\delta^{15}\text{N}$  value can also provide valuable diet information. Unlike  $\delta^{13}\text{C}$  values that exhibit minimal change between trophic levels, an average trophic enrichment factor (TEF, also called a trophic fractionation constant) of  $3.4\text{‰}$  is widely accepted and applied in  $\delta^{15}\text{N}$  stable isotope studies, although variation in this value has been noted (Minagawa and Wada, 1984; Vander Zanden and Rasmussen, 2001). Based on this information, round gobies'  $\delta^{15}\text{N}$  signature was expected to be enriched by  $3\text{--}4\text{‰}$  in comparison to dreissenid mussel tissue and non-dreissenid benthic invertebrates. However, the observed difference of  $5.44\text{‰}$  on average was outside of the range found by Minagawa & Wada (1984). A possible explanation for the apparently large  $^{15}\text{N}$  TEF is that the prey  $\delta^{15}\text{N}$  values used in the model do not accurately reflect the isotopic signature of what gobies are actually assimilating. This may be true if round gobies are consuming an alternative food source that is not accounted for in mixing models. For example, zooplankton and terrestrial invertebrates have been found in round goby gut content

(Taraborelli et al., 2010; Turschak, 2013). Tissue from fish carcasses (Polačik et al., 2015) or fish eggs (Chotkowski and Marsden, 1999; Lutz et al., 2020) may also be a food source for round gobies. Such tissue would likely be difficult to identify during gut content analysis due to quick digestion but would elevate an individual's  $\delta^{15}\text{N}$  signature (Polačik et al., 2015).

As gobies are reported to migrate offshore during the winter season (Johnson et al., 2005a; Carlson et al., 2021), offshore mussels, which have an enriched  $\delta^{15}\text{N}$  signature compared to nearshore mussels (Turschak, 2013; Hurst, 2020), are also a possible unaccounted for food source. Dreissenid mussels found in gut content analysis were assumed to be nearshore mussels due to round gobies' small home range during the summer season (Ray and Corkum, 2001); however, offshore mussels could be consumed over winter and still be represented in the isotopic signature of gobies collected during the summer if the offshore mussels were assimilated and used for growth. This is supported by a recent study that found offshore mussels to be a larger proportion of the goby diet than nearshore mussels (Turschak et al., 2019).

Assuming that the isotopic half-life does not vary significantly between  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (Vander Zanden et al., 2015), prey sources reflected in a predator's  $\delta^{15}\text{N}$  signature would also be expected to be reflected the predator's  $\delta^{13}\text{C}$  signature. Because offshore mussels  $\delta^{13}\text{C}$  signature is depleted in comparison to nearshore mussels (Turschak, 2013; Hurst, 2020), we would have expected a positive seasonal trend in round goby  $\delta^{13}\text{C}$  values as their isotopic signature equilibrated with the nearshore  $\delta^{13}\text{C}$  enriched food sources, if offshore mussels were a substantial portion of their diet. No such trend was identified despite gut content analysis indicating the consumption of nearshore quagga mussels throughout the sampling season. Other potential pelagic round goby prey species such as Mysis (Mychek-Londer et al., 2013), which have a high  $\delta^{15}\text{N}$  signature similar to offshore mussels but an enriched  $\delta^{13}\text{C}$  signature more

similar to nearshore dreissenids (Turschak, 2013; Hurst, 2020), might result in an enriched  $\delta^{15}N$  signature but have little impact on round gobies  $\delta^{13}C$  signature. Gut content analysis on gobies collected in winter and early spring would be needed to confirm the consumption of Mysis or other offshore prey species by round gobies.

Rather than a high fractionation constant or alternative food source, it is also possible that the high enrichment factor observed between gobies and their primary consumer food sources could be due to seasonal variation in the  $\delta^{15}N$  baseline. In this project, the baseline was developed from benthic scrapes collected June-October but, due to the long integration time of stable isotopes, round gobies isotopic signature likely reflects a baseline established over a much longer period. Previous research has revealed that Lake Michigan zooplankton have a significantly greater  $\delta^{15}N$  in the winter than in the summer and early fall (Driscoll, 2014). To our knowledge no benthic invertebrates or nearshore mussels have been collected and analyzed for stable isotopes December – January in northern Lake Michigan; however long-term sampling at the reef has resulted in some data collection February – November. Although yearly variation exists, both dreissenid mussels and non-dreissenid benthic invertebrates exhibit a slight depletion in their  $\delta^{15}N$  signatures June – October, suggesting possible seasonal variation similar to that found in zooplankton. Additionally, a slightly negative seasonal trend was observed in round gobies  $\delta^{15}N$  signature (alone and in relation to nearshore quagga mussels) which may represent a delayed reflection of a shifting baseline. Year-round stable isotope analysis on round gobies and their primary consumer food sources is needed but if this hypothesis is supported, it suggests that goby consumption and growth during the winter and/or early spring may be significant bioenergetic factors.

The mixed diet of round gobies and the reliance of small gobies on non-mussel invertebrates is an important consideration for future mussel removal projects. Past work on Lake Michigan has identified a positive relationship between the abundance of non-dreissenid invertebrates and dreissenid mussels (Kuhns and Berg, 1999). Additionally, a large-scale mussel removal project on Good Harbor Reef in 2019, reported a near disappearance of non-dreissenid benthic invertebrates coincident with a 97% mussel mortality rate within the treatment area (LimnoTech, 2020). These results suggest that future large-scale mussel removal projects may also significantly reduce the abundance of non-dreissenid benthic invertebrates and therefore potentially limit round goby population productivity. Future research is needed to determine the size of a project that may have this kind of impact, quantify any resulting losses in round goby productivity, and consider the broader scale implications of a reduced benthic community. Future research should also aim to determine round gobies' capability of limiting mussel recolonization following largescale mussel removal projects.

#### **4.3 Bioenergetic Modeling**

Round goby somatic growth as inferred from otoliths was notably greater at GS10 than predicted by previously published bioenergetic parameters. This may be due to diet composition or an underestimation in the  $C_{max}$  or  $p$  parameters (Equation 2). Round gobies fed a diet composed primarily of dreissenid mussels have been found to experience slower growth rates than those fed a diet dominated by small prey fish and chironomids (Coulter et al., 2011). Current literature defined bioenergetic consumption parameters were determined based on a purely dreissenid mussel diet. As such,  $C_{max}$  and consumption may have been reduced due to satiation resulting from the long gut residence time of mussel shells (Coulter et al., 2011). Experiments measuring  $C_{max}$  of round gobies fed varying diet compositions were attempted as a

side project to this research but were unsuccessful due to natural variation between fish and insufficient resources to perform large scale fish experiments. Future research focusing on quantifying consumption parameters, specifically those associated with  $C_{max}$  (Equation 2), for round gobies consuming both non-dreissenid invertebrates and dreissenid mussels is needed to improve consumption, and thus growth, parameters. These projects should increase the number of fish used in each experiment and work to develop a methodology that minimizes individual stress and competition between gobies.

Additional work should also be done to determine if  $p = 0.35$  is appropriate for round gobies of all sizes. Using reverse modeling while maintaining all other defined parameters, the value of  $p$  needed to support observed growth decreased with fish size from 0.41 to 0.35. Because growth was measured in this study, uncertainty in  $p$  does not alter results. However, productivity modeling using literature-defined consumption estimates was sensitive to this parameter as found by Lee and Johnson (2005).

Lower growth rates using defined consumption parameters may also be a result of the high energetic costs of consuming mussels due to their hard shell and the low energy density of mussels compared to non-dreissenid food sources (Coulter et al., 2011). In this study, round gobies GCE was estimated to be 20%, a value within the range observed by Lee and Johnson (2005) and in line with the GCE of winter flounder (Chesney and Estevez, 1976), juvenile fish (Brett and Groves, 1979), and non-native species including chinook and coho salmon, brown trout, and rainbow smelt (Matthias et al., 2021). However, round goby GCE was higher than reported alewife GCE estimates which range from 7.5-12.7% for young of the year and decrease to less than 2% as alewife age (Stewart and Binkowski, 1986; Stewart et al., 2010). A strong positive relationship existed between round goby GCE and the proportion of the diet composed

of benthic invertebrates but it is difficult to determine if this is a reflection of diet composition or a byproduct of a general decrease in conversion efficiency as fish age (MDNR, 2000; Lee and Johnson, 2005).

#### 4.4 Nearshore Bioenergetics

Mussels 2-4 mm in length were prevalent throughout the sampling season. However, a low density of mussels 7-21 mm indicates that many mussels were not surviving to maturity. A similar pattern has been observed in Lake Ontario (Karatayev et al., 2020). While mussel survivorship may be related to round goby predation, other factors such as competition for food with larger mussels may also be responsible (Karatayev et al., 2018). Ongoing research at GS10 aims to isolate the impact of round goby predation by excluding round gobies from a designated area. Results from these studies will be important in connecting changes in mussel populations with round goby feeding behavior.

Nearshore mussel carbon grazing rate in Lake Michigan was estimated to be  $267 \frac{mg\ C}{areal\ m^2*day}$  by Tyner et al. (2015), just over half of the rate estimated in this study. Here, mussel grazing rate was estimated from areal mussel density accounting for substrate rugosity and mussel populations on both the top and sides of rocks. Alternatively, Tyner's estimates only accounted for mussel populations on the top of rocks. As such, mussel density estimates in this study were nearly double those used by Tyner. If accounting for mussel density only on the top of rocks, mussel grazing rate at the GS10 site during the 2020 sampling season was

$$248 \frac{mg\ C}{areal\ m^2*day}.$$

Lake Michigan's lake-wide phytoplankton production has been estimated to range from 214 to  $312 \frac{mg\ C}{areal\ m^2*day}$  (Fahnenstiel et al., 2016; Sayers et al., 2020). Based on our estimates,



this would mean mussels in the nearshore zone are, on average, clearing organic carbon more quickly than it is produced in the overlying water column. However, as currents and mixing patterns move nutrient-rich water into the nearshore areas, mussels gain access to greater amounts of carbon than what is produced in their immediate area. Therefore, mussel clearance rates do not necessarily reflect phytoplankton productivity, but rather the advection of energy into the nearshore zone in the form of phytoplankton (Waples et al., 2017).

Energy and biomass production by primary consumers in the rocky nearshore zone was dominated by dreissenid mussels, which accounted for just under 95% of total productivity. Although mussel productivity is high, less than 3% of mussel production is estimated to be consumed by round gobies. This does not necessarily indicate a complete trophic “dead end” though for the remaining energy. Other species may connect the benthic nearshore food web with upper trophic levels on a smaller scale. For example, lake whitefish have incorporated dreissenid mussels as a substantial proportion of their diet (Pothoven and Madenjian, 2008) and have been modeled to consume 109kt of mussels annually in Lake Michigan (Madenjian et al., 2010). Diving ducks have also been found to feed on dreissenid mussels in some environments albeit at a much lower rate (Mitchell et al., 2000).

The other 5% of primary consumer productivity was comprised of non-dreissenid benthic invertebrate productivity, 100% of which was consumed by round gobies. Due to variation in reported P:B ratios of benthic invertebrates, some uncertainty exists in productivity estimates. However, even if the P:B ratio of non-dreissenid invertebrates was increased by 100%, dreissenid mussels would still account for the majority of primary consumer productivity in the benthic nearshore zone. Over the past decade, a positive long-term trend in benthic invertebrate density has been observed at GS10, coincidental with a negative trend in round goby density

(Bootsma, unpublished). Additionally, long-term data suggests that round goby density increases between May and October while benthic invertebrate populations decline over the same period, though data from the 2020 season did not reflect this pattern. Similar opposing trends have been identified in southern Lake Michigan and Green Bay (Kuhns and Berg, 1999; Lederer et al., 2008). These relationships, along with the conclusion that nearly all benthic invertebrate production is consumed by round gobies, suggest that there is strong top-down regulation of benthic invertebrates by round gobies and that round gobies are eating non-dreissenid invertebrates as their desired prey, resorting to dreissenids as an alternative food source when needed.

The low efficiency of trophic transfer between dreissenids and round gobies indicates that the majority of the energy sequestered by mussels is not making its way up to higher trophic levels via round gobies. However, findings suggest that mussels are needed to support the goby population, even if they are only consumed to fill a void in the diet when other food sources are unavailable (Coulter et al., 2011). Despite round gobies consuming only a small fraction of total mussel productivity, round gobies may still act as an important conduit of some energy transfer, as the energy that they consume in the form of mussels would otherwise likely remain unused in the benthic region. Additionally, mussels may indirectly supply food for round gobies by supporting benthic invertebrate productivity by providing habitat for non-dreissenid benthic invertebrates (Kuhns and Berg, 1999).

Round goby population structure, growth, and density are expected to be heterogeneous in the nearshore area due to temperature, substrate type, and depth, but lake-wide biomass and productivity can be approximated using the results of this and other studies. The optically shallow area of Lake Michigan with submerged aquatic vegetation (SAV) is estimated to be

1220 km<sup>2</sup> using Landsat satellite data (Brooks et al., 2015). As SAV, primarily *Cladophora*, is known to grow on hard substrate, this area can serve as a conservative estimate of the rocky littoral zone that round gobies inhabit. Assuming that lake-wide round goby density is within the range observed at ATW and GS10, the total round goby population is estimated to be  $\sim 1.65 * 10^9 - 3.48 * 10^9$  individuals. This equates to a biomass estimate of  $\sim 5.61 * 10^9 - 16.5 * 10^9$  g WW. This is likely a conservative estimate, as it assumes there are no gobies in nearshore areas with soft substrate, and it does not account for gobies that inhabit depths deeper than those that can be viewed remotely (e.g. Carlson et al. 2021). Recent prey fish biomass surveys, done with bottom trawls on Lake Michigan by USGS estimate round goby biomass to be  $7.25 * 10^9$  g WW (Bunnell et al., 2019a), a value on the low end, but within the range estimated above. This value was estimated from bottom trawls at depths >9m and therefore is also a conservative estimate. It is possible, that true round goby biomass in Lake Michigan is closer to the combined estimates from this study (nearshore rocky zone) and USGS (depths greater than 9 m) rather than the average of these estimates. In comparison to round goby biomass estimates, Lake Michigan's alewife population, a critical prey source for many salmonid species, has declined from a long term (1973- 2018) mean biomass of  $4.62 * 10^{10}$  g WW to  $3.13 * 10^9$  g WW in 2018 (Bunnell et al., 2019a).

By scaling the per area round goby productivity estimates from GS10 up to the area of SAV in the nearshore zone, lake-wide round goby productivity was estimated to be  $1.13 - 1.70 * 10^{10}$  gWW·year<sup>-1</sup>. By comparison, assuming that alewife have an annual P:B ratio of about 1 (Stewart et al., 1981, 2010), alewife productivity in 2018 was  $3.13 * 10^9$  gWW · year<sup>-1</sup>. Hence, while the round goby productivity estimate presented here accounts for about 25% of the long-term alewife productivity in Lake Michigan, it is nearly 4 times that of 2018 annual alewife

productivity. While there is a large degree of uncertainty in the above estimates, it is clear that round gobies are a substantial portion of prey fish biomass in Lake Michigan and their productivity could be an important energy source for upper trophic levels.

#### **4.5 Conclusion**

At both study sites and throughout the sampling season, round gobies were observed to be the dominant fish species in the rocky nearshore zone. Their abundance (which is commonly underrepresented in prey biomass estimates), competition with other prey fish, and potential to recycle phosphorus and energy, has made round gobies an important aspect of the nearshore food web, and a recent report by the International Joint Commission (Hecky and DePinto, 2020) has highlighted the need to better understand their role. The research presented here aimed to quantify the production of energy and biomass by round gobies that could potentially support higher trophic levels. In doing so, it aimed to determine the pathways and flow rates of energy from primary consumers to round gobies, allowing for estimates of trophic transfer efficiency. In agreement with past research, round gobies were found to be more reliant on benthic invertebrates than dreissenid mussels. However, gut content and stable isotope data indicated that round gobies were reliant on mussels for just under half of their diet. This, along with the observation that round gobies consume nearly all non-dreissenid benthic invertebrate production, suggests that some mussel production is needed to support the goby population at the observed densities. Although total transfer efficiency was low and the majority of energy sequestered by mussels appears to not be moving up the food web to higher trophic levels (at least not through round gobies), gobies still likely serve as an important energetic link between the benthic region and upper trophic level piscivores due to their abundance, high productivity, and inclusion in the diet of predators.

Although round goby biomass and productivity are expected to be heterogeneous in the nearshore area, lake-wide approximations of these parameters suggest that round gobies are a substantial source of potential energy for upper trophic levels. Because round goby predators likely feed in variable environments, the spatial distribution of round goby productivity should be considered when examining round gobies as a potential prey source; however, the recorded incorporation of gobies into the diet of numerous fish, bird, and snake species suggest existing overlap. Results from this study found round goby productivity on Good Harbor Reef to be significantly higher than would be estimated based on previously published bioenergetic parameters (Lee and Johnson 2005). These results highlight the importance of more accurate measurements of round goby abundance, bioenergetics, and their role in the nearshore and offshore food webs.

The findings of this study and future work on this topic are especially important for predator-prey models, invasive mussel removal projects, and the management of commercial and sport fisheries. Because round gobies appear to have higher productivity than some other popular prey species (i.e., alewife), they make a significant contribution to prey biomass estimates which could potentially impact stocking and fishing regulations. This is of particular significance for species that rely heavily on round gobies such as brown trout, although it is equally as important for species such as Coho salmon which rely predominantly on alewife but feed periodically on round gobies. Additionally, because of the reliance of gobies on both dreissenid mussels and non-dreissenid benthic invertebrates that live in mussel colonies, large-scale mussel removal may have the potential to limit round goby population productivity and the amount of potential energy that they make available to upper trophic levels.

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## APPENDIX A: Bioenergetic parameters

Value of bioenergetic model parameters determined by Lee and Johnson (2005) that are incorporated in the Fish Bioenergetics 4.0 application.

Description	Parameter	Estimate
Respiration	R	$R = 0.00094 * W^{-0.157} * e^{0.061*T}$
Proportion of consumed energy used for specific dynamic action	s	0.175
Proportion of consumed energy lost as fecal matter	f	0.150
Proportion of assimilated energy lost as nitrogenous waste	u	0.100
Female spawning losses as a percent of body weight	G	6.8
Consumption	C	$C = C_{max} * 0.350 * f(t)$
Maximum consumption	$C_{max}$	$C_{max} = 0.192 * W^{-0.256}$
Functional temperature response function	$f(t)$	$f(t) = K_A * K_B$ $K_A = \frac{(0.113 * e^{0.312(T-5.594)})}{1 + 0.113(e^{0.312(T-5.594)} - 1)}$ $K_B = \frac{(0.419 * e^{1.07(28.992-T)})}{1 + 0.419(e^{1.07(28.992-T)} - 1)}$

\* W represents total wet weight (g), T represents temperature (°C).

## APPENDIX B: Conversion rates

Conversions between wet weight, dry weight, carbon content, and energy content.

	Carbon (mg)	Dry Weight (mg)	Wet Weight (mg)	Energy (J)
Phytoplankton*	0.1	0.2	1.0	
Quagga mussel tissue	0.066	0.15	1.0	2427**
Non-dreissenid benthic invertebrates	0.042	0.15	1.0	3327**
Round gobies	0.11	0.24	1.0	Equation 11

\*Conversions for phytoplankton are from Hecky and Kling (1981). \*\*Energy density values for quagga and non-dreissenid benthic invertebrates are from Schneider (1992). All other coefficients were developed as part of this study.

## APPENDIX C: Historical stable isotope data

Mean lipid-corrected  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of *Cladophora*, benthic invertebrates, nearshore dreissenid mussels, and round gobies. 2002-2003 and 2010-2012 data are from Turschak (2013), 2019 data are from Hurst (2020), and 2020 data are from this study.

Taxon	Year	n	Mean lipid-corrected $\delta^{13}\text{C}$ *	Lipid-corrected $\delta^{13}\text{C}$ s.e.*	Mean $\delta^{15}\text{N}$	$\delta^{15}\text{N}$ s.e.
<i>Cladophora</i>	2002-2003	9	-18.54	0.25	2.71	0.59
	2010-2012	21	-17.76	0.62	0.89	0.14
	2020	17	-16.46	0.50	0.62	0.18
Benthic Invertebrates	2002-2003	6	-15.98	0.20	4.25	0.36
	2010-2012	11	-16.09	0.37	3.54	0.20
	2020	26	-17.70	0.20	3.37	0.18
Nearshore Dreissenids	2002-2003	10	-22.37	0.51	4.10	0.12
	2010-2012	219	-23.05	0.11	4.41	0.05
	2019	6	-24.47	0.14	4.08	0.20
	2020	24	-25.18	0.17	3.82	0.13
Round Goby	2002-2003	15	-21.38	0.15	10.52	0.22
	2010-2012	504	-19.38	0.08	8.75	0.03
	2019	8	-20.59	0.37	9.51	0.22
	2020	65	-20.48	0.13	9.26	0.05

\* No lipid correction was applied to  $\delta^{13}\text{C}$  values of *Cladophora*.

## APPENDIX D: Variables and parameters used in this study

Description and units for variables and parameters used throughout this study. All parameters are also defined with units in the text.

Equation	Parameter	Description	Units	Reference
	WW	Wet weight	<i>g</i>	
	DW	Dry weight	<i>g</i>	
1 and 2	C	Consumption		Lee and Johnson, 2005
	$C_{max}$	Maximum consumption under ideal conditions		
	P	Proportionality scaler		
	i	Intercept of the allometric function	$\frac{g \text{ food}}{g \text{ WW} * \text{ day}}$	
	j	Slope of the allometric function		
	$f(T)$	Function temperature response		Thornton and Lessem, 1978
3 and 4 12 and 13	L	Round goby total length *Subscript of i and f indicate initial and final respectively	<i>cm</i>	Taraborelli et al., 2010
	a	Length -weight coefficient		
	b	Length-weight exponent		
5	K	Fulton's condition factor	$\frac{g}{cm^3}$	Ricker, 1975
6	$f(L)$	Relative frequency of gobies of a certain length		
7	$L(t)$	Length or wet weight of round goby at age t	<i>cm</i> or <i>g</i>	
	$L_{\infty}$	Asymptotic size' maximum theoretical length or weight that a round goby will tend towards	<i>cm</i> or <i>g</i>	
	$L_0$	Size at age 0	0.73 <i>cm</i>	Leslie and Timmins, 2004
	k	Growth coefficient	$\frac{1}{years}$	
	t	Age	<i>years</i>	
11	ED	Round goby energy density	$\frac{kJ}{g \text{ WW}}$	Bunnell et al., 2019
16	TE	Transfer efficiency		Lindeman, 1942
	$\lambda_n$ $\lambda_{n-1}$	Productivity of trophic level n or n-1	$\frac{g \text{ C}}{m^2 * \text{ day}}$	