ROUND GOBY-INDUCED CHANGES IN YOUNG-OF-YEAR YELLOW PERCH DIET AND HABITAT SELECTION

by

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ABSTRACT

ROUND-GOBY INDUCED CHANGES IN YOUNG-OF-YEAR YELLOW PERCH DIET AND HABITAT SELECTION

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Under the Supervision of Professor John Janssen

A critical step in the recruitment of age-0 yellow perch (*Perca flavescens*) to the adult population occurs during their transition to the demersal stage. If larval age-0 yellow perch survive recruitment bottlenecks imposed by alewife (*Alosa pseudoharengus*) and dreissenid mussels, they transition to demersal feeding in late August and early September. In Lake Michigan, demersal age-0 yellow perch seek rock substrate where they begin feeding on benthic invertebrates in late summer. That research preceded the invasion of the round goby (*Neogobius melanostomus*), a species that can have negative impacts on benthic forage. The current study used the spread of round gobies as a natural experiment to assess the competitive interactions between age-0 yellow perch and round gobies. Habitat selection and diet of age-0 yellow perch in relation to round goby abundance were analyzed using fish captured in 6.25- and 8-mm bar micro-mesh gill nets in 2006 and 2007 at six study locations from Sheboygan to Wind Point, Wisconsin. Age-0 yellow perch in this study significantly shifted habitat (from rock to sand) and diet preferences (from benthic invertebrates to zooplankton) with increasing round goby abundance.

Round gobies also significantly altered the benthic community composition. I propose demersal age-0 yellow perch in Lake Michigan face a novel recruitment bottleneck caused by a combination of exploitative competition for benthic prey and interference competition with round gobies.

“When you put your hand in a flowing stream, you touch the last that has gone before and the first of what is still to come” – Leonardo da Vinci

~ For E

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Introduction

Non-indigenous species (NIS) introductions have had negative impacts on terrestrial and aquatic ecosystems worldwide (Strayer, 2010). Freshwater species are being lost at rates similar to those found in tropical forests and invasive NIS have been suggested as one of the likely causes (Ricciardi and Rasmussen, 1999). The magnitude of the impact NIS can have on freshwater systems is facilitated by man-made habitat changes, including connecting watersheds, habitat homogenization, and altering community structure (Ricciardi and MacIsaac, 2011). It has been argued that NIS should be judged by their impact on the ecosystems in which they settle, which can be both positive and negative (Davis et al., 2011). Therefore, it is imperative to understand the fundamental roles NIS play within each ecosystem.

Ecosystems in the Laurentian Great Lakes (henceforth Great Lakes) have been profoundly altered by the introduction of NIS. Some examples include, the introduction of dreissenid mussels (zebra mussel, *Dreissena polymorpha,* and quagga mussel, *Dreissena rostriformis bugensis*) that led to a tenfold increase in the extinction rate of native mussels (Ricciardi et al., 1999), exotic sea lamprey (*Petromyzon marinus*) extirpating some native ciscoes (*Coregonus* spp.) and lake trout (*Salvelinus namaycush*) from the lower Great Lakes (Holey et al., 1995), and overpopulation of non-native alewife (*Alosa pseudoharengus*) leading to declines in planktivore and piscivore fish populations (Smith, 1970). Among the significant invaders is the round goby (*Neogobius melanostomus*), first detected in 1990 (Jude et al., 1992), that is associated with dramatic reductions or extirpations of certain native benthic species such as mottled sculpin (*Cottus bairdi*) (Janssen and Jude, 2001; Lauer et al., 2004), and johnny darters (*Etheostoma nigrum*)(Lauer et al., 2004), with other benthic fishes likely at risk (Poos et al,. 2010). Native faunae in freshwater systems are more likely to be negatively impacted by NIS than in marine systems (Ricciardi and MacIsaac, 2011). Reasons behind this trend are not yet fully understood and need to be further examined.

The likelihood that a NIS will be successful in its transplanted habitat is dependent on a number of biotic and abiotic factors. These factors include availability of underutilized resources, or lack of whole functional groups in the environment, and possession of novel traits giving them a competitive advantage (among many others) (Mittelbach, 2012; Ricciardi and MacIsaac, 2011). The Great Lakes may contain more underutilized niche space than other systems because they are depauperate due to their relatively young age (13,000 yrs bp) which has not allowed enough time for species to diverge and exploit available resources (Jude et al., 2004). Many of the species (i.e., johnny darter, slimy sculpin, *Cottus cognatus*, burbot, *Lota lota*) occurring in the Great Lakes are inherently riverine (Hubbs et al., 2011). These species are adapted for cool water streams and spread into the Great Lakes after the last glacial retreat and fill the same basic niches that they occupied in their original habitats. This inherent riverine origin of many Great Lakes species may have left them vulnerable to exploitative competition with NIS from the Ponto-Caspian that have evolved in a large meso-oceanic system. Coevolved species from the Ponto-Caspian region have also facilitated each other's successful establishment in the Great Lakes (Ricciardi, 2001). The novel competitive interactions between native and non-native species in the Great Lakes may afford us the opportunity to observe and test many aspects of competition theory.

Non-indigenous species introductions can be used to study competitive outcomes between species that have never coexisted in the wild. The resulting outcomes of competition for any niche space (be it prey availability (Bergstrom and Mensinger, 2009), shelter availability (Quinn and Janssen, 1989), or reproductive habitat (Janssen and Jude, 2001), etc.) between an invader and native species are likely key factors in the successful introduction of an NIS. Invasion biology often seeks to determine the factors contributing to a successful invasion by an NIS (Holway, 1998). However, more recently, species invasions have been used as natural experiments to test theories in competition ecology (Bøhn and Amundsen, 2001; Grant and Grant, 2006). Invasions allow researchers to observe interactions between species in their natural environment while being subjected to biotic and abiotic factors that may not be controllable in laboratory or mesocosm experiments. Mechanisms of extirpation or population reduction can be difficult to demonstrate with predation likely the easiest to demonstrate (e.g., sea lamprey predation on lake trout). Competition is more difficult to demonstrate in part because a stressed losing competitor may be more vulnerable to predation. For example, for the Great Lakes, Rice et al. (1987) argued that, for bloater (*Coregonus hoyi*) exploitative competition for zooplankton with alewife could reduce growth and/or predator escape capability and thus render individuals more susceptible to predation.

Lake Michigan's rocky habitat and associated benthic community

Rocky littoral habitats (RLH) are important to a large number of aquatic species in the Laurentian Great Lakes (Auer, 1996; Janssen and Luebke, 2004, Marsden et al., 1995). Rocky littoral habitats are actively sought as spawning, nursery, and feeding grounds for varied fish species (Becker, 1983) and are home to varied invertebrate species. Production potential at RLH is high due to its stability in relation to wave forces, inherent proximity to riverine inputs (Mida et al., 2010), and recent benthification of Great Lakes food webs (Hecky et al., 2004; Lowe and Carter, 2004). In Lake Michigan the extent of RLH is often fragmented and the composition of the substrate varies from glacial till, (ranging in size from gravel to boulder) to various exposed bedrock outcroppings and may be interspersed with sand substrates (Figure 1, Janssen et al., 2005). As a whole, Lake Michigan has relatively more RLH in its north and western sections, with large amounts of sand substrates in the south and east. The major contributing factors to the observed distribution of RLH were the movement of glaciers during the last glacial advance, the underlying Niagran dolomite bedrock that directed the glacial advance, and predominant currents and wind direction that preferentially deposit sand along the Indiana and Michigan coasts. With the emerging importance of RLH in Lake Michigan it is interesting to note that their extent has yet to be assessed in detail (Creque and Czesny, 2012; Janssen and Luebke, 2004).

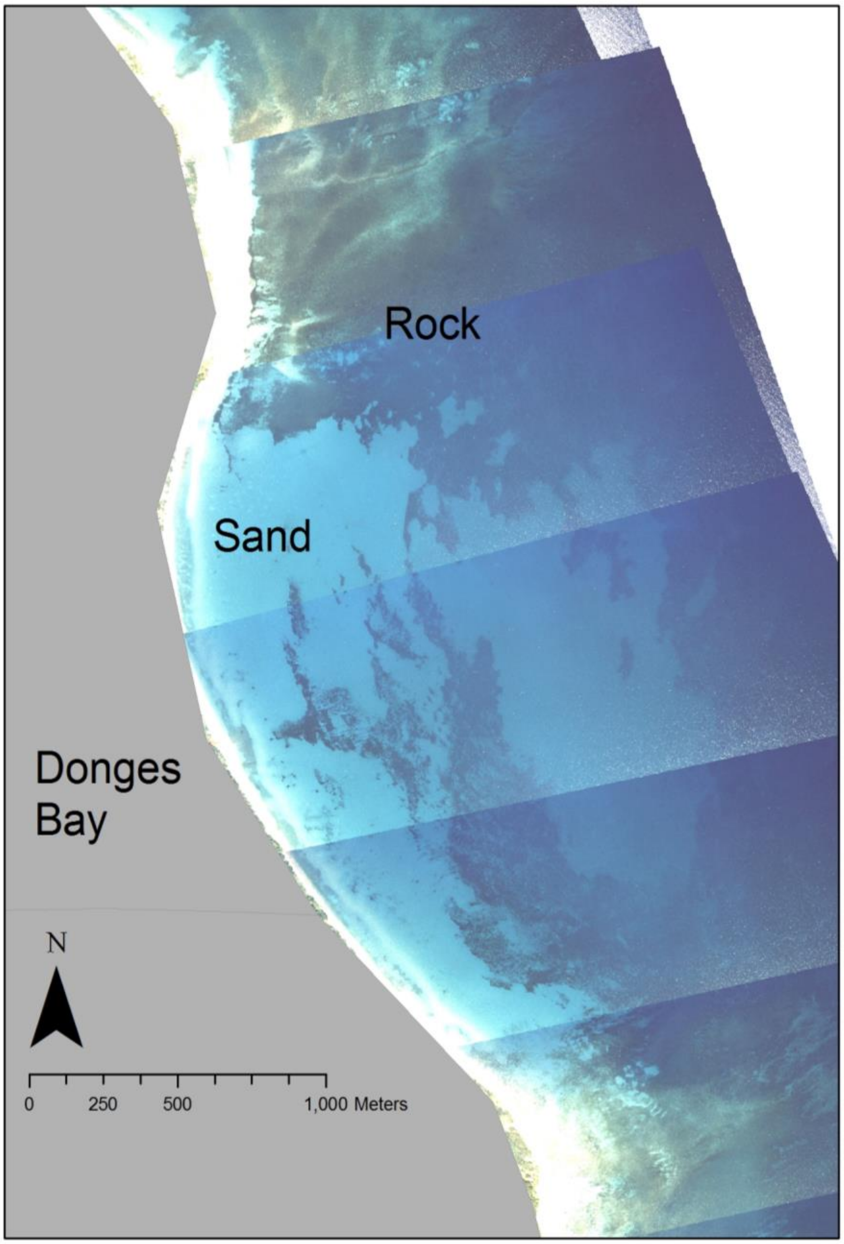

Figure 1. Exposed rocky littoral habitat can be distinguished from sand substrates using georeferenced aerial photographs taken during the summer of 2005. Light blue areas are primarily sand substrate and dark blue and green represent rock substrates (Image center: N 43° 12' 4.8", W 87° 53' 21.9"). Near Milwaukee, Wisconsin.

Since opening of the St. Lawrence Seaway, the repeated introduction of NIS has dramatically changed RLH ecosystem dynamics (Lovell and Stone, 2005). Water filtration by dreissenid mussels, introduced in the mid-1980s, cleared the water column and changed the plankton community (Vanderploeg et al., 2010). Dreissenids now cover most RLH in the lower Great Lakes and have changed benthic invertebrate species composition both at RLH (Kuhns and Berg, 1999) and in the pelagia (Nalepa et al., 2009). Colonies of dreissenids consolidate small RLH by binding the substrate together with byssal threads and have been shown to support higher densities of chironomids (Kornis and Janssen, 2011), and other arthropod species (Pothoven et al., 2001; Higgins and Vander Zanden, 2010). Pseudofeces released by dreissenid beds may concentrate food and nutrients for benthic invertebrates such as chironomids, amphipods, and isopods. The presence of dreissenids also increases interstitial space per unit area which may offer additional shelter from wave action and predators. The recent decline in the deepwater amphipod, *Diporeia* spp*.,* has been largely attributed to the invasion of dreissenids, evidence of the varying impact an invader can have on an ecosystem (Fahnenstiel et al., 2010a). Growth of the nuisance green alga *Cladophora glomera* has also increased due to dreissenids clearing the water column (more available light; Auer et al., 2010), an increase in hard substrata (growth on mussel shells), and possibly a nitrogen/phosphorus shunt that locally increases nutrients available for algal growth (Hecky et al., 2004). Ecosystem effects of the increase in primary production at RLH have yet to be fully assessed.

Newly introduced NIS from the Ponto-Caspian region have taken advantage of conditions created through ecosystem engineering caused by dreissenid mussels at RLH. Successive invasions by other Ponto-Caspian species like *Echinogammarus ischnus* and *Hemimysis anomala*, are certainly anecdotal evidence that dreissenids are facilitating new NIS (Ricciardi, 2001; Simberloff, 2006). One of the newest fish invaders whose expansion has been facilitated by these ecosystem modifications is the round goby.

Yellow perch in Lake Michigan

In Lake Michigan, yellow perch (*Perca fluvescens*) have traditionally been an important commercial and recreational fish species (Francis et al., 1996; Wells, 1977). However, yellow perch populations in Lake Michigan are now at historically low levels (Makauskas and Clapp, 2010; Truemper et al., 2006). During the 1960's yellow perch suffered severe declines due to the introduction of alewife, probably due to alewife predation on larval yellow perch and exploitative competition for zooplankton prey (Shroyer and McComish, 2000). Reductions in alewife densities through the introduction of salmonines resulted in rebounding yellow perch stocks until the late 1980's/early 1990's when their population again collapsed (Marsden and Robillard, 2004). It is thought that a combination of the dreissenid mussels depleting available zooplankton for larval yellow perch and over fishing reduced yellow perch standing stock biomass to levels that were insufficient to replenish the stock (Wilberg et al., 2005).

Yellow perch populations in the southern basin of Lake Michigan are sustained by periodic years of high recruitment, most recently the 1998 and 2005 year classes (Makauskas and Clapp, 2010). The early life history of yellow perch in Lake Michigan is relatively unique. Adult yellow perch spawn on RLH typically less than 15 m in depth (Dorr, 1982). After hatching, larval yellow perch move to the epilimnion where they are current captive (unable to move against predominant currents) and advected offshore where they feed on zooplankton (Dettmers et al., 2005; Beletsky et al., 2007; Graeb et al., 2006). In Lake Michigan, current captive age-0 yellow perch return nearshore and become demersal at around 50-60 mm in total length (typically late August/early September). In smaller lakes this inshore migration can occur at lengths as small as 25 mm (Whiteside et al., 1985). Demersal age-0 yellow perch then undergo an ontogenetic diet shift from feeding on zooplankton to benthic invertebrates (Graeb et al., 2006). Another ontogenetic shift occurs when yellow perch reach a total length of roughly 150 mm and become piscivorous (Clady, 1974). The successful transition of age-0 yellow perch to the demersal phase is an essential step for successful recruitment to the adult yellow perch population and represents a fundamental recruitment bottleneck (Shroyer and McComish, 2000; Dettmers et al., 2005).

Historically, the yellow perch population may have been able to endure multiple stressors from invaders by occupying a generalist niche, allowing them to quickly change feeding strategies or habitats to adjust to new competitive interactions (Weber et al., 2010). However, round gobies were introduced into Lake Michigan during a time when the yellow perch population was already substantially depleted (Redman et al., 2011). If round gobies are a stronger competitor for shared resources with yellow perch, round gobies may have a strong impact on the already stressed yellow perch population.

Round gobies in Lake Michigan

The first observation of round gobies in the Great Lakes occurred in the St. Clair River in 1990 (Jude et al., 1992). They were subsequently spread throughout the Great Lakes via ballast water transport (Hensler and Jude, 2007). Round gobies were first observed in Lake Michigan at Calumet Harbor in 1994 (Janssen and Jude, 2001) and were established in Milwaukee Harbor by 1999 (WI DNR, Milwaukee, Wisconsin).

Round gobies occupy a benthic niche and displaced a number of native benthic fauna, including mottled sculpin (Janssen and Jude, 2001) and johnny darter (Lauer et al., 2004), by occupying preferred spawning habitat and consuming benthic invertebrate prey, which effectively extirpated those species from invaded areas (Janssen and Jude, 2001). Round gobies have a strong affinity for rocky habitats (Ray and Corkum, 2001) which is also the preferred habitat for demersal age-0 yellow perch (Janssen and Luebke, 2004).

Round gobies are primarily invertivores. As juveniles, round gobies prey on benthic arthropods including chironomids, isopods, and amphipods (all of which are the preferred prey of age-0 yellow perch), and can substantially alter density and composition of the macro-invertebrate community where they become established (Lederer et al., 2006). At around 50-60 mm round gobies start to feed on dreissenid mussels and begin to develop specialized, molariform, pharangeal teeth capable of breaking dreissenid shells (Ghedotti et al., 1995; Andraso et al., 2011). Round gobies have also evolved a unique feeding mechanism to break byssal threads through grasping the shell and spinning to create torsion (Djuricich and Janssen, 2001). Adult round gobies typically prey on mussels with valve lengths between 7 and 12 mm and are one of few fish species that prey heavily on dreissenids in the Great Lakes (Ghedotti et al., 1995; Janssen and Jude, 2001). As a result of round goby predation size distributions of dreissenids are often skewed (Djuricich and Janssen, 2001; Lederer et al., 2008) and dreissenid establishment and spread can be dependent on round goby presence (Houghton and Janssen, 2013).

Round gobies are antagonistic toward other species and conspecifics, especially during mating (Dubs and Corkum, 1996; Ray and Corkum, 2001). Bergstrom and Mensinger (2009) found that in artificial streams round gobies competitively dominated native species when competing for amphipod prey. In trials against slimy sculpin, spoonhead sculpin, *Cottus. ricei*, and logperch, *Percina caprodes*, round gobies did not appear to have a sensory advantage but were much more aggressive than the native species, and posed a threat to many native species because they could dominate resources. Research in test aquaria has shown round gobies will exclude similarly sized smallmouth bass from lower portions of tanks and exclude them from preferred shelter (Winslow, 2010). However, the interspecific interaction between round gobies and smallmouth bass is likely variable over both species' development (Winslow, 2010). Research on the competitive interactions of yellow perch and round gobies in Lake Erie suggested little competitive interaction between the two species due to the presence of, and the yellow perch's affinity for, macrophyte beds (Duncan et al., 2011). The shared affinity for rocky habitat, similarity in diet of juvenile individuals of both species, and the round goby's antagonistic nature are indications that yellow perch and round gobies may interact competitively in western Lake Michigan which is lacking the macrophyte beds present in Lake Erie. If round gobies are the competitively strong species for a given resource they may have negative impacts (i.e., reduced growth and fitness) on age-0 yellow perch and thus their survival and recruitment.

Objectives and overview

To continue to explore the consequences of competition among species in the wild, I used a natural field experiment to demonstrate a general hypothesis that round gobies can compete with yellow perch under the conditions of western Lake Michigan. Competing species may coexist in the same habitat by limiting their similarity of resource utilization (Schoener, 1974). Chesson (1983) argued that species may coexist by differing utilization of, or presence in, four niche dimensions; time, habitat, predators, and prey. Of the four niche dimensions, prey, habitat, and time are likely the most important (Schoener, 1974).

One potential consequence of competition, hence a potential test, is niche shifts (ecological character displacement) between competing species. This has been used to assess competition in relatively easily observed organisms such as birds (Diamond, 1970), lizards (Schoener, 1975), and plants (Grace and Wetzel, 1981). Fishes are less easily observed than plants and diurnally active vertebrates, but the observational challenge does not mean that niche shifts do not exist. Interspecific competition in fishes has been assessed using nonindigenous species (NIS; sensu Chisolm, 2009) introductions and resulting niche shifts as natural experiments in the Laurentian Great Lakes (Crowder, 1986) as well as the African Great Lakes (Wanink and Witte, 2000). Wanink and Witte (2000) documented niche shifts in habitat utilization and prey preferences in dagaa (*Rastrineobola argentea*), by following the dagaa population before the Nile perch introduction as well as through the Nile perch's spread and population boom in Lake Victoria. In Lake Michigan, Crowder (1986) used the introduction of nonindigenous alewife as a natural experiment to infer competition with bloater. Crowder (1986) theorized that interspecific exploitative competition for zooplankton prey was the driving factor behind observed habitat and prey shifts of bloater after the alewife's introduction.

While observational studies of niche shifts are an important tool to assess interspecific competition in the wild, they lack the ability to distinguish what competitive mechanisms are causing observed differences (Matthews, 1998). Experimental manipulation of the densities of competing species and limiting resources in enclosed systems have offered researchers the ability to assess these underlying mechanisms. Studies on interspecific competition between fish species often utilize experimental ponds (Werner and Hall, 1977) and enclosures (Duncan et al., 2011) that allow species densities and habitats to be manipulated and controlled. Manipulative studies allow researchers to precisely control the factors being assessed. However, mesocosm experiments can introduce undetected novel actors that can affect the study’s outcomes. Such enclosure experiments are more likely to show competition than unenclosed experiments (Schoener, 1983) and a common concern is that controlled nature of enclosure experiments does not accurately represent conditions in the wild (i.e. unreal fish densities or habitats). On the other hand, studies of competition in the wild, often due to their inherent size, are criticized for not controlling enough factors to adequately assess contributing factors.

The goal of the present study was to use the population density gradient at a round goby invasion front as a natural experiment to assess interspecific competition between the NIS, round goby, and a native species, yellow perch. This study was performed during the initial invasion of the round goby to the western shores of Lake Michigan around Milwaukee, Wisconsin. Round gobies were first observed in Milwaukee harbor in 1999. They were first seen outside of the harbor in 2004 and slowly radiated north and south along the coastline from this initial introduction site (Houghton, pers. obs.). The progression of the round goby invasion presented a unique opportunity to assess possible changes in two niche dimensions of age-0 yellow perch, habitat and prey, along a gradient of round goby densities in the wild. Previous work using similar sampling methods (micro-mesh gill nets set on rock versus sand substrates) showed a strong site affinity of age-0 yellow perch toward rock substrates (Janssen and Luebke, 2004), also the preferred habitat for round gobies (Kornis et al., 2012).

The current study focused on two shared resources of age-0 yellow perch and round gobies, habitat and prey. Resource utilization of age-0 yellow perch along an active round goby invasion front were used to determine the effect of round gobies on age-0 yellow perch in the wild. Effects of round goby abundance on rock associated benthic invertebrates were also assessed with the goal of determining if ecological character displacement of age-0 yellow perch may be resulting as a consequence of interspecific competition. I therefore had four general hypotheses:

Hypothesis 1: Age-0 yellow perch habitat utilization shifts from rock to sand with increasing numbers of round gobies at rock sites.

Hypothesis 2: There is evidence of exploitative competition for prey: round gobies decrease the number of benthic invertebrates found at rock sites.

Hypothesis 3: Age-0 yellow perch undergo a diet shift: age-0 yellow perch feed on lower amounts of benthic invertebrates when round gobies are present at rock sites.

Hypothesis 4: Yellow perch grow more slowly as a result of competition with round gobies at rock habitats.

Ecological character displacement in the form of a reduction of habitat or prey utilization of age-0 yellow perch as a response to increasing round goby abundance would provide evidence consistent with interspecific competition between the two species (Hypotheses 1 and 2), while a decrease in benthic invertebrate abundance due to the presence of round gobies may indicate that prey is a limiting resource in the interaction. A decrease in growth of yellow perch would be expected if round gobies are a strong competitor with demersal age-0 yellow perch and the yellow perch preying upon less optimal prey.

Methods

Hypothesis 1: Effect of round gobies on age-0 yellow perch habitat utilization

Habitat utilization of age-0 yellow perch was assessed at six locations along western Lake Michigan. Each study location consisted of a rock substrate and sand substrate pair of sites. Western Lake Michigan's littoral habitat is composed of a mosaic of different rock, sand, and clay outcroppings (Janssen et al., 2005). Sampling locations were chosen for their proximity to both rock and sand substrates by analyzing aerial photographs of the coastline captured in 2005 (Table 1, Figure 1). Promising locations determined from the photographs were ground-truthed for suitable substrate type by wading, snorkeling, and scuba diving. Final study locations, from north to south, were: Sheboygan, Donges Bay, Fox Point, Whitefish Bay, Milwaukee, and Wind Point, a longitudinal distance of 112 km (Table 1, Figure 2). Across the study locations "rock" sites were composed of a range of different types of hard substrate consisting of bedrock (Silurian-dolomite limestone and Devonian mudstone) and clay outcroppings overlain by glacial till ranging in size from cobble to boulders. "Sand" sites at all locations were composed almost entirely of sand deposited from coastal moraine bluffs, with only occasional rocks present. Only six suitable locations for sampling were discovered and the yellow perch population becomes scarce north of our most northern locations, Sheboygan (P. Hirethota, pers. comm., WI DNR 600 E Greenfield Ave. Milwaukee, WI 53204).

Table 1. Geographic coordinates for rock and sand sites at each of six study locations for yellow perch-round goby studies in western Lake Michigan during 2006 and 2007.

Location	Rock Site	Sand Site
Sheboygan	N 43° 45.85'	N 43° 45.52'
	W 87° 41.69'	W 87° 42.15'
Donges Bay	N 43° 12.50'	N 43° 12.20'
	W 87° 53.54'	W 87° 53.63'
Fox Point	N 43° 10.06'	N 43° 07.54'
	W 87° 52.87'	W 87° 53.99'
Whitefish Bay	N 43° 06.48'	N 43° 06.98'
	W 87° 52.75'	W 87° 53.36'
Milwaukee	N 43° 03.62'	N 43° 03.22'
	W 87° 52.19'	W 87° 52.73'
Wind Point	N 42° 46.92'	N 42° 45.86'
	W 87° 45.31'	W 87° 46.63'

Habitat utilization of age-0 yellow perch was estimated using catch-per-unit-effort (CPUE) from micromesh gillnetting performed at each of the six study locations (replicates). Age-0 yellow perch and round gobies CPUEs were defined as the total number of each species captured in overnight gill net sets. Within each location two gill nets were set at the rock and sand sites (paired sites), totaling 12 gill net sets per sampling bout for the six locations (Figure 2). Pairs of rock and sand sites were within 5 km of each other (most within 1 km, Table 1). Gillnet sets were performed in late August and early September, 2006 and 2007. GPS coordinates for both ends of a net were recorded and the between-year variation in study site position was generally less than 50 m.

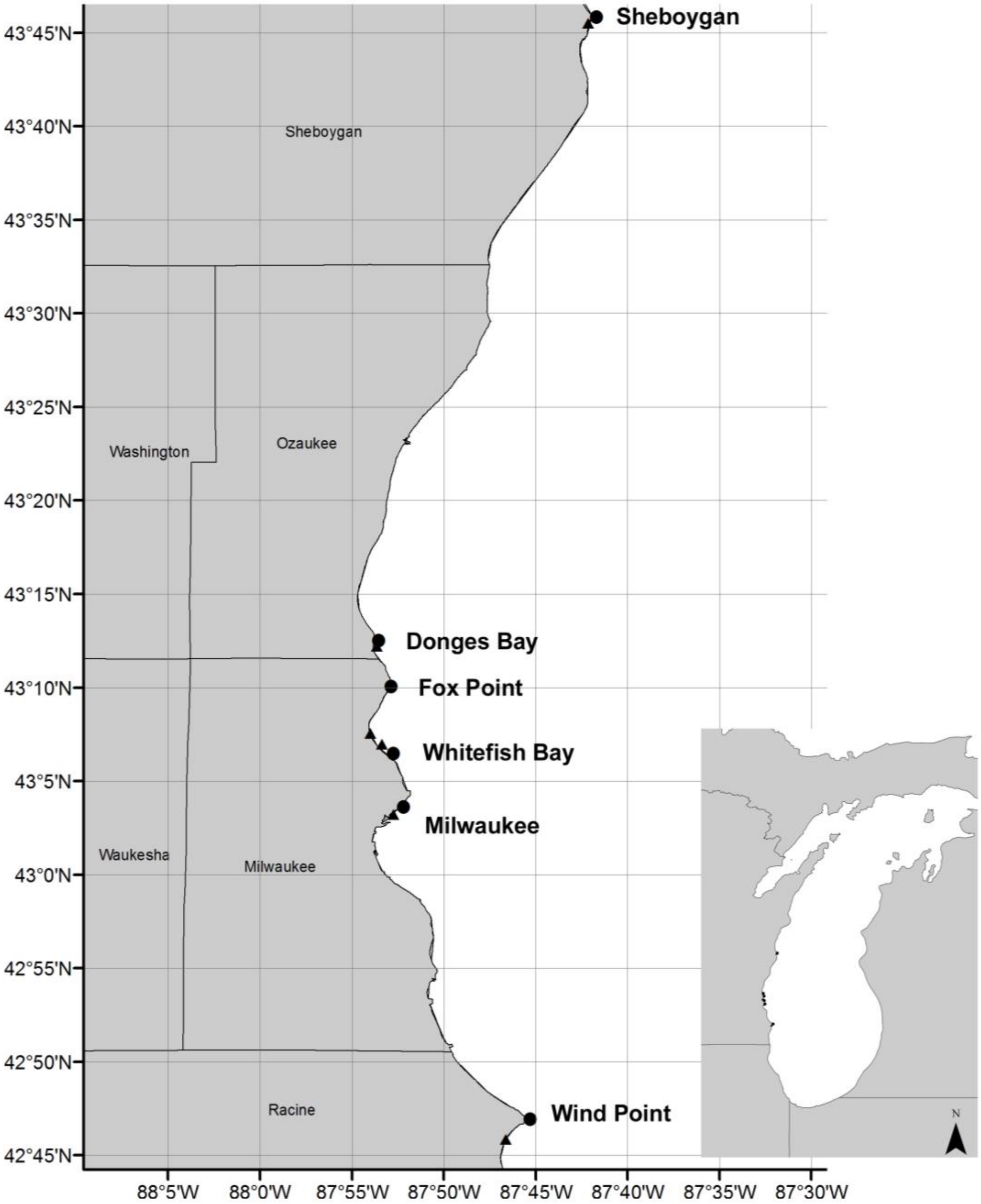

Figure 2. Study locations for evaluating yellow perch-round goby interactions along the Wisconsin shoreline of Lake Michigan; Circles = Rock sites, Triangles = Sand sites.

Each study location was sampled using two gangs of 6- and 8-mm bar monofilament, micromesh gill net. Gangs consisted of two 1.2-m high by 30-m long panels of each mesh size tied together (60 m total length). At shallow water locations (Sheboygan, Fox Point, Whitefish Bay, and Wind Point) gill nets were set in ≈1.5 m of water by wading from shore. These four locations had very large boulders or blocks of bedrock making operating from a power boat dangerous. Gill nets were set in ≈4 m water depth at locations accessed by boat (Donges Bay and Milwaukee). Gill nets were typically set within ≈1 hour before sunset and pulled ≈1 hour after sunrise the next morning (total time in water ≈12 hours). Age-0 yellow perch and round gobies were immediately removed from the net upon retrieval and enumerated; fish were also preserved for diet analysis (see Hypothesis 3). Similar gill nets are now used around Lake Michigan for yearly age-0 yellow perch assessment, and are known to catch age-0 yellow perch and round gobies (Janssen and Luebke, 2004; Diana et al., 2006).

In 2006 and 2007, round goby abundance estimates from gillnetting were supplemented with video strip transects conducted by scuba divers. Round goby abundance estimates using video strip transects were important for two reasons. First, they allowed me to confirm the relative abundance of round gobies at rock sites by comparing the two methods, and visual estimates had been used previously by others (Diana et al., 2006; Ray and Corkum, 2006). Second, they allowed me to record the spatial distribution of round gobies within rock sites, which may have an effect on the round goby-yellow perch interaction.

Video transects were completed by two scuba divers. One diver used a video camera in an underwater housing and recorded the transect, while the second diver aided in moving the transect line. The transect line was a 10 m long section of ≈10-mm diameter cotton line that was weighted at both ends and placed haphazardly (swimming with eyes closed) on the bottom by the divers. Diver separated the transect by ≈ 10 m by swimming the transect at least 2 m above the bottom to avoid disturbing round gobies on the substrate. The diver with the camera then swam down the transect line with the camera held ≈ 1 m (with a weighted line spacer) off the bottom facing down toward the substrate. Width was determined by measuring the cameras field of view underwater when held at 1 m. Transects lasted between 45 seconds and 90 seconds and the captured video covered a swath ≈ 1 m wide. Five or more transects were recorded at each site. Transect swims were reviewed using computer video software. Round goby CPUE from video transects (Video CPUE) was defined as the total number of round gobies observed in each transect. Mean video CPUEs were then calculated for each rock site for statistical analysis.

To better visualize benthic habitat and round goby distribution at each site I entered the video strip transects into Microsoft Corp's Image Composite Editor (ICE) version 1.4.4.0 software. ICE creates a composite image of individual frames from within the video transect file. The resulting high resolution image allowed me to magnify specific portions of video transects (Figure 3). Future projects using video strip transects may be able to utilize this method to assess microhabitat use of benthic fish and invertebrate species.

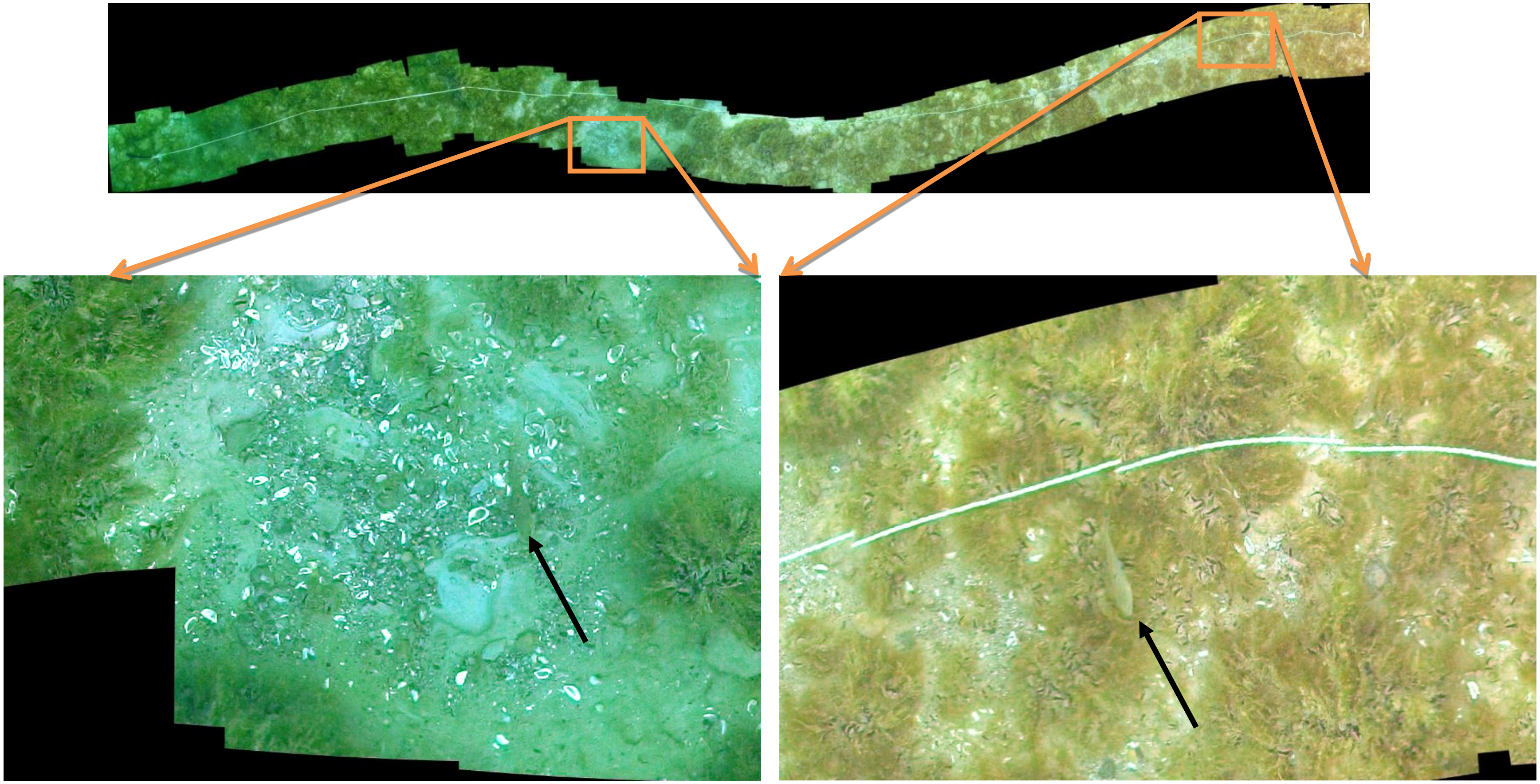

Figure 3. Composite image from a round goby video transect produced using Microsoft Corp's Image Composite Editor. The composite image can be magnified and the image processed to better resolve the image of round gobies, and may be useful in future benthic microhabitat studies. Round gobies can be seen at the end of black arrows.

Hypothesis 1- Statistical methods

A paired t-test comparing mean round goby gill-net CPUE at rock sites was calculated to determine if round goby numbers increased between 2006 and 2007. Data for each pair came from the same site over the 2-year period.

Round goby CPUE from video transects was used to determine the spatial distribution of round gobies at rock sites. First, Index of Contagion (IoC, the variance to mean ratio, Elliot, 1971) for round goby video CPUE was calculated for each site in 2006 and 2007, separately. Then a one sample t-test with IoC values from each year was used to determine if the round goby IoC values significantly differed from 1.0, a Poisson distribution. IoC values close to 1.0 would indicate round gobies were distributed randomly and IoC values greater than 1.0 would indicate round gobies were distributed in patches (Elliott, 1971; Steel and Torrie, 1980). Pearson's correlation coefficient (r) was calculated to compare the similarity between video strip transect CPUE and micromesh gill-net CPUE. In 2006 and 2007 gill nets were set at the six sites resulting in 12 round goby gill-net CPUE estimates, with five video transects performed at each site and date.

To determine whether rock habitat utilization of age-0 yellow perch was affected by round goby presence at rock sites I correlated the percentage of age-0 yellow perch utilizing rock habitat with round goby CPUE from gill nets. Percent habitat utilization was used because I expected that the concept of the Ideal Free Distribution applies, i.e., fish will proportionately distribute themselves among the two habitats with respect to relative profitability of prey resources in accordance with encounter rates, prey visual acuity, escapability, etc. (Fretwell and Lucas, 1970). The concept was recently applied to northern pike (*Esox lucius*) in Lake Windermere, England (Haugen et al., 2006). Age-0 yellow perch in the current study were likely becoming demersal and therefore in the process of assessing the relative profitability of littoral habitats (Miehls and Dettmers, 2011). Percentage of age-0 yellow perch utilizing rock habitat was calculated for each location, by dividing age-0 yellow perch CPUE from gill nets set at rock sites, by the total age-0 yellow perch CPUE caught at both sites and multiplying by 100. Round goby CPUE values were Log_{10}+1 transformed and percent age-0 yellow perch rock habitat utilization values were arcsine square root transformed (Zar, 1999). Pearson's correlation coefficient (r) was computed for 2006 and 2007 separately, because the locations (and their sites) were not independent between years. A temporally combined Pearson's correlation coefficient that included age-0 yellow perch habitat selection data from 2002 (Janssen and Luebke, 2004) and a preliminary sampling conducted in 2005 at Fox Point, Milwaukee, and Wind Point was also calculated. Janssen and Luebke (2004) performed sampling using identical methods in 2002 at four of my study locations before round gobies were present. The temporally combined correlation resulted in 20 different age-0 yellow perch rock habitat utilization values between 2002 and 2007.

Hypothesis 2: Effect of round gobies on benthic invertebrate abundance

Rock samples were collected by divers for invertebrate prey abundance estimates at each study location within 20 m of the gill net locations and at the same time as the gill net sets. Rock invertebrate collections consisted of divers retrieving a cobble-sized rock from the bottom by closing their eyes and randomly selecting a rock approximately 250 mm in diameter from the bottom by feel, enveloping it in a cloth bag, and tying it shut. Five rocks were retrieved at each rock site. Bags were then brought to the surface and placed in a water-filled cooler for transit to the lab. In the lab, rocks were scraped clean onto a 3.5-mm screen to separate dreissenid mussels and other large invertebrates. The resulting filtrate was then washed through a 500-um sieve and remaining invertebrates were enumerated under a dissecting microscope. Non-dreissenid invertebrates that remained on the large screen were added to the small invertebrate tallies. Invertebrates were identified to the same taxonomic level as for stomach content analysis.

Hypothesis 2 - Statistical Methods

IoC was calculated for chironomid larvae and amphipods within rock sites to determine whether these prey occurred in patches. Patchiness could lead age-0 yellow perch to use search behaviors effective at finding clusters of prey (Humphries et al., 2012).

The effect of round goby presence on the abundance of benthic prey was assessed by calculating Pearson's correlation coefficients for round goby gill-net CPUE and the mean of summed chironomid larvae + amphipod. The two prey items were summed because the biological question was whether yellow perch feeding on benthic prey was impacted by round goby density. Presumably a yellow perch searching among rocks will consume either chironomid larvae or amphipods, but, given prey patchiness I found, I did not attempt to estimate relative selectivity for chironomid larvae or amphipods.

Hypothesis 3: Effect of round gobies on age-0 yellow perch diet

Stomach content analysis was performed on age-0 yellow perch and round gobies captured from gillnetting to assess possible diet shifts of age-0 yellow perch where round gobies were present. Captured fish were picked from gill nets immediately after retrieval and live fish were euthanized in an overdose of MS-222. Fish were enumerated, labeled, and stored in 95% ethyl alcohol with their body cavities opened to allow quick and thorough saturation of the carcasses. Yellow perch up to 115 mm total length were considered age-0, comparable to the size range used in previous studies of age-0 yellow perch in southwestern Lake Michigan (Marsden and Robillard, 2004). Few age-0 yellow perch captured in the micromesh gill nets were greater than 80 mm total length (16% of dissected fish), therefore the operational definition of age-0 yellow perch was determined by the size range of yellow perch that the gill net captured. Stomach contents of age-0 yellow perch and round gobies were analyzed by removing the stomach and identifying its contents to the lowest practical taxon using a dissecting microscope and Pennak's Freshwater Invertebrates of the United States (Elliott, 2002). For round gobies, which lack a defined stomach, the entire digestive track was analyzed.

Individual taxa were enumerated and clustered into functional groups of taxa. The four taxa analyzed were Chironomidae (both chironomid larvae and pupae), Amphipoda, Isopoda, small benthic invertebrates, and zooplankton. The small benthic invertebrate group contained Chydoridae, Ostracoda, Hydracarina, and harpacticoid Copepoda. The zooplankton group consisted of Cladocera (*Daphnia* sp., *Polyphemus* sp., *Bythotrephes* sp., and *Bosmina* sp.) and cyclopoid and calanoid Copepoda, as well as emergent chironomid adults. While emergent chironomids are not typical zooplankton, they are indicative of fish feeding at the water's surface (Kornis and Janssen, 2011). Whole or partially digested prey items were counted for numerical abundance, including chironomid head capsules. Prey weight and volume were not estimated.

Stomach content analysis was performed on subsamples of 10 or more age-0 yellow perch and 10 round gobies from each sample site. If fewer than ten individuals of each species were captured, all fish stomachs were analyzed. Total number of each prey eaten was tallied for individual age-0 yellow perch and round goby stomachs from all sites (Macdonald and Green, 1983).

Hypothesis 3 - Statistical Methods

To determine if the presence of round gobies had an effect on the diet of age-0 yellow perch, I first calculated the amount of dietary overlap between the two species using the Schoener index (α) (Schoener, 1974). I then determined if age-0 yellow perch prey selectivity was affected by round goby density using Chesson's α (Chesson, 1983). I used modified Costello graphs to visually compare distributions of prey items between age-0 yellow perch at rock and sand sites, as well as the diet of round gobies at rock sites (Amundsen et al., 1996; Costello, 1990). IoC was also calculated to determine the patchiness of prey in the diets of round gobies and age-0 yellow perch. Finally, I used Pearson's correlation coefficient to determine if there was a relationship between consumption of prey items by age-0 yellow perch and round goby abundance at rock sites. Below, is a detailed description of all analyses performed.

Dietary overlap between age-0 yellow perch and round gobies was used as an indicator of possible competition for prey between the two species at rock habitat. Dietary overlap was assessed using the Schoener index (α) (Schoener, 1974).

$$\alpha = 1 - 0.5\left(\sum_{i=1}^{n} \left| P_{xi} - P_{yi} \right| \right)$$

Where P_{xi} is the proportion of the *i*th prey item in species *x*, and P_{yi} is the proportion of the *i*th prey item in species *y*. The Schoener index compares the amount of dietary overlap on a scale from 0 to 1 (0 = no overlap, 1 = complete overlap), with an α value of 0.6 or higher indicating significant overlap in diet composition between species (Wallace, 1981). Significant dietary overlap between round gobies and age-0 yellow perch may indicate competition for available food resources. However, for competition to occur between species that consume similar prey, the prey must also be limiting. Resource depression with varying round goby abundance at rock habitats is addressed in Hypothesis 2.

I used Amundsen's modified Costello method (Costello, 1990) for graphically interpreting stomach content data to visualize the major prey contributions, importance of prey groups, and feeding strategy of round gobies and age-0 yellow perch (Amundsen et al., 1996). The modified Costello method plots frequency of occurrence (F_i; x axis) against prey-specific abundance (P_i; y axis).

$$F_i = (N_i / N)$$

$$P_i = \left(\sum S_i \middle/ \sum S_{ti}\right) \times 100$$

Where N_i is the total number of individuals having consumed prey i and N is the total number of individuals with prey in their stomachs. For prey-specific abundance (P_i); S_i is the total number of prey i in all stomachs and S_{ti} is the total stomach content of only those fish with prey i in their stomach.

The feeding strategy and prey importance of round gobies and age-0 yellow perch can be observed by the placement of prey items along the three axes presented in Figure 4. Prey importance is represented along the axis from lower left to upper right hand corner of the figure. Abundant prey is positioned in the upper right and less abundant prey is in the lower left. A specialist feeding strategy on a prey item is higher in the figure, with a generalist feeding strategy lower. A point positioned in the upper left hand corner would indicate that individual round gobies and age-0 yellow perch are specializing, whereas a point in the lower right portion of the figure indicates that the entire population is preying upon similar items (Welker and Scarnecchia, 2003).

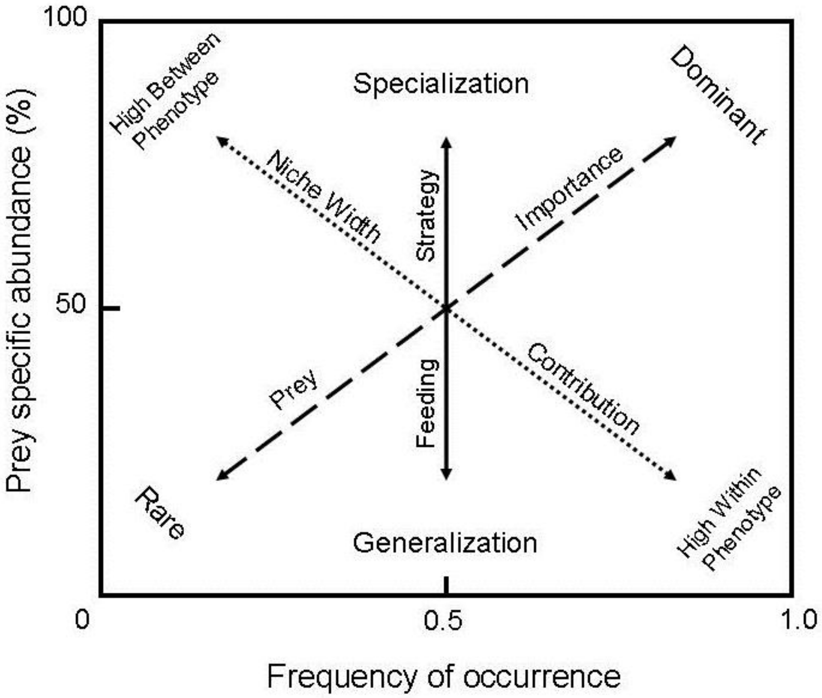

Figure 4. Explanatory diagram of modified "Costello Graph" redrawn from Amundsen et al. 1996. See methods for explanation of prey specific abundance and frequency of occurrence axis.

For age-0 yellow perch in 2006 and 2007, IoC of prey items in age-0 yellow perch stomachs were calculated to assess prey item distributions in stomach contents from fish caught at the same site. IoC greater than one may indicate age-0 yellow perch are feeding on patches of prey when they are encountered (Elliott, 1971). If prey is shown to occur in patches within the environment it may also be expected that prey occur in patches within the stomach contents of age-0 yellow perch and round gobies.

Hypothesis 3, decreased benthic prey consumption by yellow perch related to round goby density, was assessed similar to Hypothesis 2. Pearson's correlation coefficient was calculated using the mean of summed chironomid and amphipods per stomach, $\text{Log}_{10}+1$ transformed, correlated with round goby gill-net CPUE. A significant negative correlation may indicate round gobies decreased invertebrate prey availability at rock sites (for rock counts), and that round gobies negatively impacted the feeding of age-0 yellow perch at rock habitats (for age-0 yellow perch stomach contents). I considered the mean of the two summed benthic prey by year and location as conservative because it assumed that individual year and location were the replicates. If I can consider rocks collected at a particular location to be independent, then the number of replicates increases so there is more statistical power. The IoCs that were found (see Results) may justify this because it would suggest little correlation among rocks for prey types. Hence, I also present this non-conservative statistical analysis. Similarly, for the diet comparison, I also present the correlation analysis using individual yellow perch as independent within a location.

Differences in zooplankton consumption by age-0 yellow perch at rock and sand sites were also evident in the Costello graphs. To assess the impact of round goby abundance on age-0 yellow perch consumption of zooplankton I calculated the percent abundance (by number) of zooplankton prey in age-0 yellow perch stomachs containing prey at sand sites in 2006 and 2007. To determine sites where round goby abundance was "high" and "low", an equation for the line of best fit, drawn between percent age-0 yellow perch habitat utilization and the gillnet round goby CPUE (using Microsoft Excel's graphing function), was used to calculate the point at which 50% of age-0 yellow perch were utilizing sand habitats over rock habitats. Round goy abundance was considered "high" at rock sites when the mean round goby CPUE in gillnets at a rock site was 7 or more, and "low" with less than 7. Pearson's correlation coefficients between percent zooplankton abundance and round goby CPUE at rock sites were then calculated to determine the relationship between round goby abundance and age-0 yellow perch zooplankton consumption, to assess the effect of round goby presence at rock sites on the consumption of zooplankton by age-0 yellow perch.

Hypothesis 4: Yellow perch growth has decreased as a result of increasing round goby abundance in western Lake Michigan

An historical data set of length-at-age of yellow perch in western Lake Michigan maintained by the Wisconsin Department of Natural Resources (WDNR) was used to search for possible impacts of round goby on yellow perch growth. During late December and early January of each year the WDNR performs a yellow perch stock assessment at Green Can Reef, located ~10 km east-southeast of Milwaukee Harbor (N 42° 57' 6", W 87° 43' 33"). They use 300-m lengths of graded-mesh monofilament gill net to capture adult (2+ years old) yellow perch. Nets are set over night for a period of around 12 hrs. All captured yellow perch are measured for length and aged using either scales or spines. From 1986 to 2001 scales were used to age adult fish. In 2001, the WDNR transitioned to using dorsal spine sections to age yellow perch due to the ability to more accurately estimate the age of captured fish from spine sections. A time series of mean length–at-age was plotted for both male and female yellow perch from spine sections of captured fish from 1999 to 2012. Pearson's correlation coefficient was then calculated between mean length-at-age for each male and female year class and year. Significant correlations may indicate a decrease in the growth of age-0 yellow perch in Lake Michigan.

Results

In total 2,124 age-0 yellow perch were caught in 24 separate gill net sets in 2006 and 2007; sand sites accounted for 1,522 of the total and rock sites accounted for 602. Total lengths of dissected age-0 yellow perch ranged from 52-111 mm (mean = 68 mm, S.D. = 15.2) at sand sites and from 54 to 115 mm (mean = 71 mm, S.D. = 10.5) at rock sites. There were 318 round gobies caught at rock sites with a total length range of 48-101 mm (mean = 65 mm, S.D. = 11.1). Lengths were measured from dissected individuals; not all captured fish were measured. Round gobies were predominantly captured on rock habitat, with only 55 of 373 (15%) gillnetted specimens captured at sand sites (85% on rock habitat), and those round gobies captured on sand were likely among hard substrate scattered at sand sites (based on exploratory snorkeling/scuba observations, next paragraph).

Hypothesis 1: Effect of round gobies on age-0 yellow perch habitat utilization

Paired t-test comparing round goby gill-net CPUE at rock cites indicated round gobies increased in abundance from 2006 to 2007 (t_5 = 3.776, P = 0.013;

Figure 5), shows the progressing invasion front of round gobies was captured during the study period.

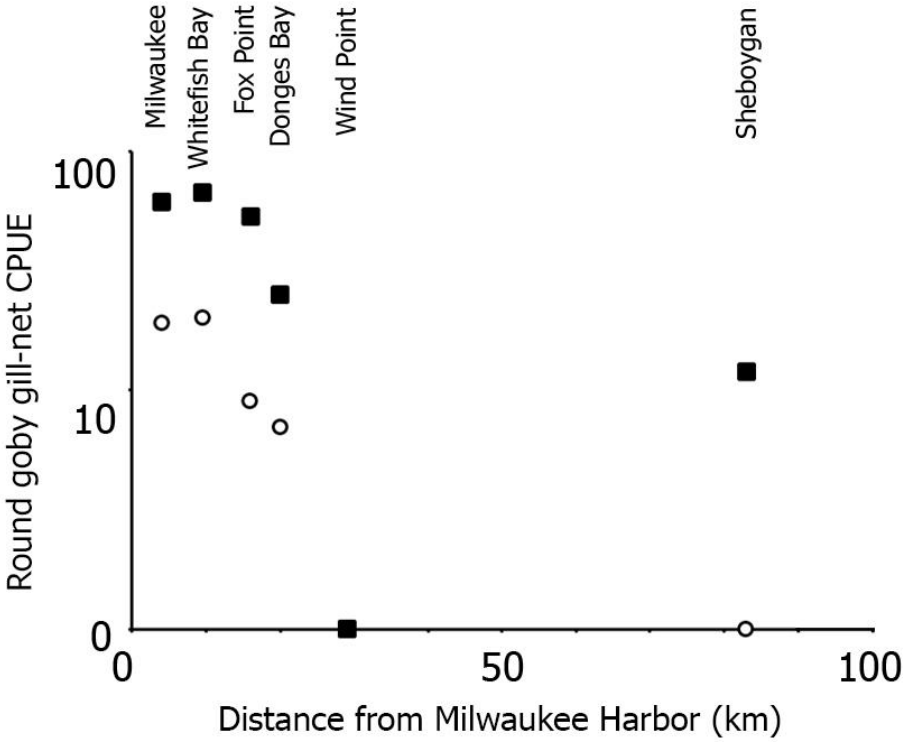

Figure 5. Scatterplot of round goby gill-net CPUE at six study sites in 2006 (circles) and 2007 (squares) versus study site distance from Milwaukee Harbor, the location of the initial round goby introduction in 2004. No round gobies were collected in either year at Wind Point. Paired t-test indicated round goby CPUEs were significantly higher in 2007 than 2006 ($t_5 = -3.776$, $P = 0.013$), showing the ongoing invasion was captured during the study period.

Video transects recorded round gobies only on rock habitat. A broader non-recorded exploratory search at sand sites found a few round gobies off transects, but only associated with scattered rocks. Round gobies exhibited a spatial distribution within rock sites not distinguishable from poisson in 2006 and 2007. Mean IoCs for round goby CPUEs from video transects at rock sites were not significantly different from 1.0 in either 2006 (t_4 = -2.256, P =0.087) or 2007 (t_3 = 2.106, P = 0.126). There was a significant correlation between gill-net CPUE and mean video transect CPUE for each site and date (r = 0.76, df = 20, P = 0.0016; Figure 6).

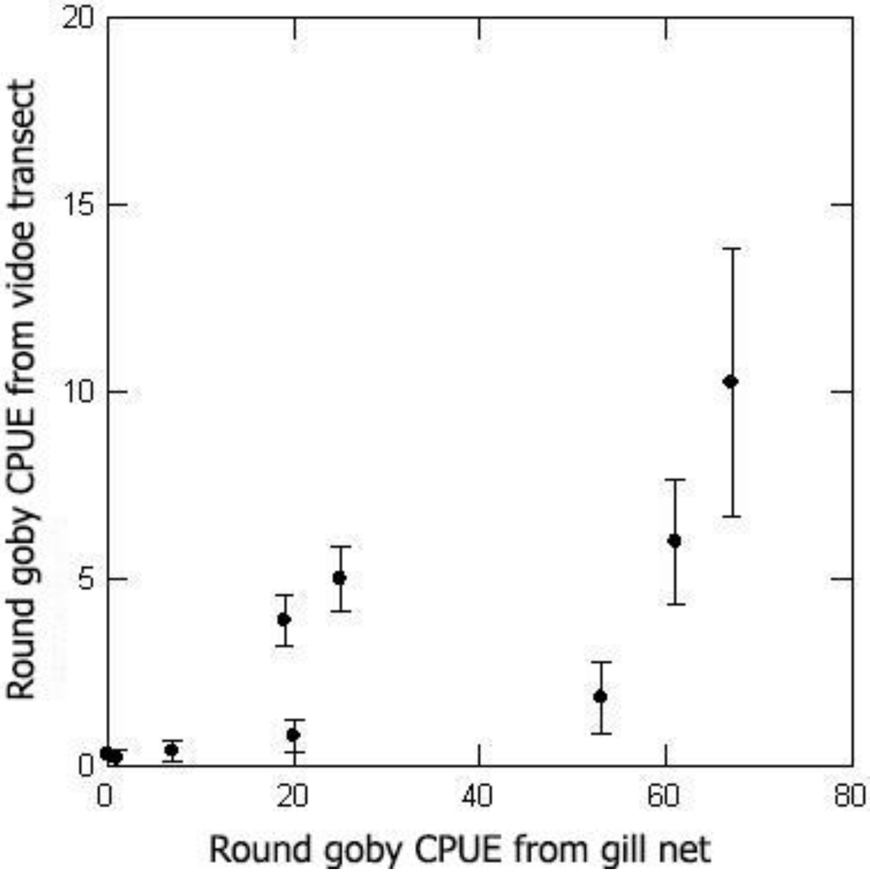

Figure 6. Round goby CPUEs at six rock sites in western Lake Michigan during 2006 and 2007 estimated using log-transformed round goby CPUE from video strip transects and log-transformed round goby gill net CPUE. Both estimates returned similar results across study locations (all video transect CPUEs included, r = 0.705,

df = 66, P < 0.001; mean video transect CPUEs, r = 0.76, df = 10, P = 0.0016). 68 video transects were conducted among the 12 gill net sets in 2006 and 2007. Gill nets returned a single value each year, whiskers represent standard error for multiple video transects.

There was a negative correlation between percentage of age-0 yellow perch captured at rock habitat versus round gobies gill-net CPUE for both 2006 (r = -0.94, df = 4, P = 0.005) and 2007 (r = -0.87, df = 4, P = 0.025). The correlation coefficients for the 2 years were not statistically distinguishable (using z-transformation of correlation coefficients as described by Zar (1998)). These results cover only 2 years but the extended correlation that includes the 2002 data from Janssen and Luebke (2004) and preliminary 2005 data (Figure 7) was consistent (r = -0.85, df =18, P = 0.001).

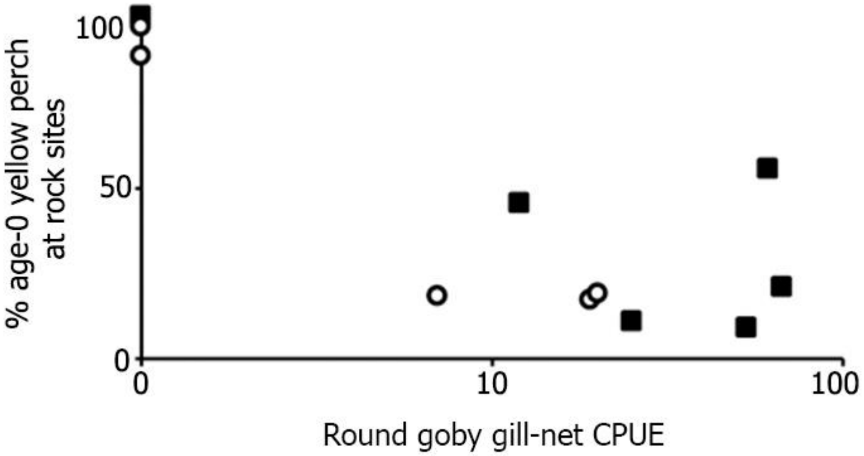

Figure 7. Age-0 yellow perch rock habitat utilization versus round goby gill-net CPUE at all study sites in 2006 (circles) and 2007 (squares). Correlation analysis indicates a negative relationship in 2006 (r = -0.94, df = 4, P = 0.005) and 2007 (r = -

0.87, df = 4, P = 0.025), separately. Pooling data from both years, preliminary data collected in 2005, and Janssen and Luebke's (2004; collected in 2002) data also show a strong negative relationship (r = -0.85, df = 18, P = 0.001).

Hypothesis 2: Effect of round gobies on benthic invertebrate abundance

The most abundant prey items in round goby diet contents in 2006 and 2007 were chironomid larvae (34.3%), amphipods (19%), and isopods (13.7%). Age-0 yellow perch also consumed large numbers of chironomid larvae (41%), amphipods (8%), with very few isopods (2.6%) so prey overlap was primarily with chironomid larvae and amphipods at rock sites. Therefore I focused my preliminary analysis on the relationship among round gobies, chironomid larvae and amphipods, both in the environment at rock sites and in yellow perch diets (Hypothesis 3).

Chironomid larvae and amphipods were the most abundant invertebrates enumerated. Mean abundance from both years combined ranged from 5- to 230- chironomid larvae and 4- to 285- amphipods per rock (Table 2). In the environment, chironomid larvae and amphipods were abundant at all rock locations (Table 2). IoCs in 2006 and 2007 were greater than 1.0 for all locations (range 2.7 to 569.7) except Wind Point chironomid larvae in 2006 (IoC = 0.3), an indication that chironomid larvae and amphipods occur contagiously within the rock study sites.

Table 2. Mean (x̅) and Index of Contagion (IoC) for invertebrate counts from rocks collected at six sites in western Lake Michigan in 2006 and 2007. Five rocks were collected from each site; Fox Point 2006 was excluded due to missing rocks.

		Sheboygan		Donges Bay		Fox Point		Whitefish Bay		Milwaukee		Wind Point	
Year	Taxa	x̅	IoC	x̅	IoC	x̅	IoC	x̅	IoC	x̅	IoC	x̅	IoC
2006	Chironomid larvae	33	**4.9**	33	**569.6**			10	**260.8**	24	**12.4**	38	0.3
	Amphipod	27	**26.3**	156	**33.2**			90	**11.3**	26	**17.6**	35	**3.6**
2007	Chironomid larvae	91	**6.6**	47	**6.8**	146	58.4	55	**32.5**	21	**7.0**	230	**22.6**
	Amphipod	31	**7.5**	18	**8.8**	16	64.8	9	**11.9**	25	**4.6**	90	**10.6**

The mean of summed amphipod and chironomid larvae collected on rocks (N = 5) for each site versus round goby gill-net CPUE. There was a strong negative relationship in 2007 (r = -0.97, df = 4, P =0.001; Figure 8). If we consider the rocks to be independent then the correlation coefficient decreases due to inter-rock variability, but is still highly significant (r = -0.51, df = 28, P =0.001). I did not detect a correlation for 2006, likely because round goby numbers were significantly lower the first year of the study.

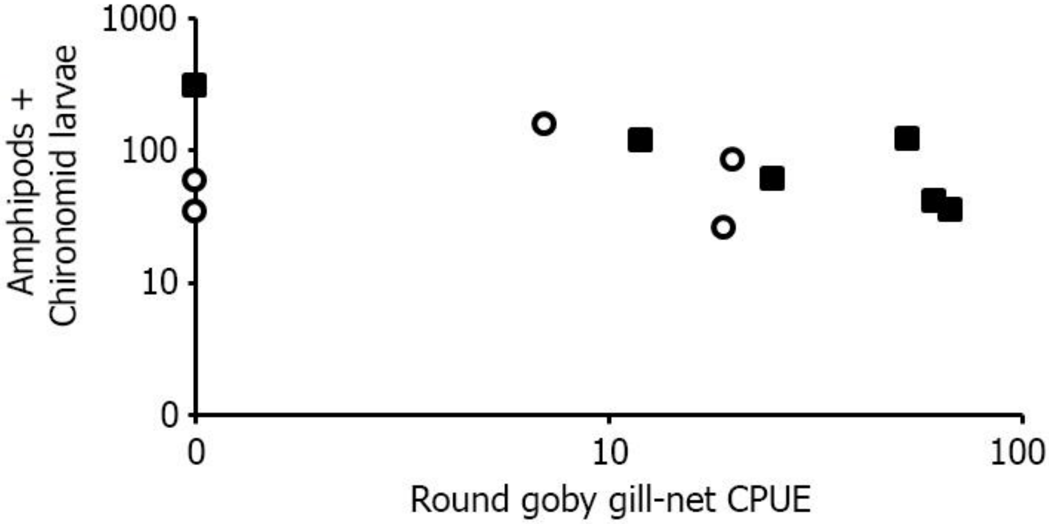

Figure 8. The mean of summed amphipod and chironomid larvae collected on rocks for each site versus round goby gill-net CPUE in 2006 (circles) and 2007 (squares). There was a strong negative relationship in 2007 (r = -0.97, df = 4, P = 0.001), and non-conservative estimate for 2007 of summed chironomid larvae and amphipods also showed a negative relationship (r = -0.51, df =28, P = 0.001). Both axis are $\log_{10}$ scaled.

Hypothesis 3: Effect of round gobies on age-0 yellow perch diet

During 2006 at rock sites, age-0 yellow perch primarily preyed upon chironomids, amphipods and isopods, which composed 81.6% of identified prey items by number (Table 3). At sand sites in 2006, age-0 yellow perch diet was split among all four groups. Zooplankton prey became more important in 2007, with age-0 yellow perch at rock sites consuming a high percentage of zooplankton and chironomid prey (55.8% and 38.9% respectively). Zooplankton prey accounted for 84.7% of total identified prey items in age-0 yellow perch captured at sand sites in 2007 (Table 3). Percentages may be biased toward zooplankton prey due to their small size.

Table 3. Percentage of total prey items and sum of prey identified in age-0 yellow perch diets at rock and sand sites in 2006 and 2007.

	2006				2007			
	Rock		Sand		Rock		Sand	
Prey Taxa	%	N	%	N	%	N	%	N
Chironomid larvae	75.6	684	9.6	40	38.9	250	6.4	173
Amphipods and isopods	16.0	145	22.8	95	3.1	20		
Small benthic invertebrates	0.8	7	16.3	68	0.8	5	8.8	239
Zooplankton	4.9	44	14.7	61	55.8	359	84.7	2278

Amphipods (23.9%), isopods (21.2%), and dreissenid mussels (19.8%) were most abundant in round gobies caught on rocks in 2006. During 2007 the percent contribution of prey items in round goby diets was 45.6% chironomid larvae, 17.1% chironomid pupae, and 9.8% amphipods (Table 4).

Table 4. Summed round goby diets from 2006 and 2007 at rock sites. Total occurrence of each prey item is on the right, percentage on left.

	2006		2007	
Prey Taxa	%	N	%	N
Chironomid larvae	26	57	63	121
Amphipods and isopods	45.0	100	10.4	20
Small benthic invertebrates	2.3	5	13.5	26
Zooplankton	6.8	15	3.6	7

Schoener α values (Schoener, 1974) between round gobies and age-0 yellow perch caught on rock varied among sites, Schoener's α ranged from 0.15 at Whitefish Bay to 0.74 at Wind Point with an average 0.42, among all sites. An indication that the two species prey upon the same resources. Low Schoener's α values at rock habitats could be an indication that age-0 yellow perch remaining at rock sites where round gobies are present are utilizing different prey items than age-0 yellow perch at rock sites without round gobies.

I used modified Costelllo graphs to search for patterns in prey consumption of age-0 yellow perch at rock and sand sites and round goby diets at rock sites (Figure 9). At rock sites age-0 yellow perch specialized on chironomids while at sand sites chironomids were still frequent in the diet but less abundant (Figure 9a). Zooplankton were more abundant in age-0 yellow perch diet at sand where they were preyed upon by roughly 50% of the sampled fish. The downward shift in chironomid prey combined with the shift upward of zooplankton is an important observation when comparing the age-0 yellow perch Costello graph with the round goby Costello graph of fish caught at rocks sites.

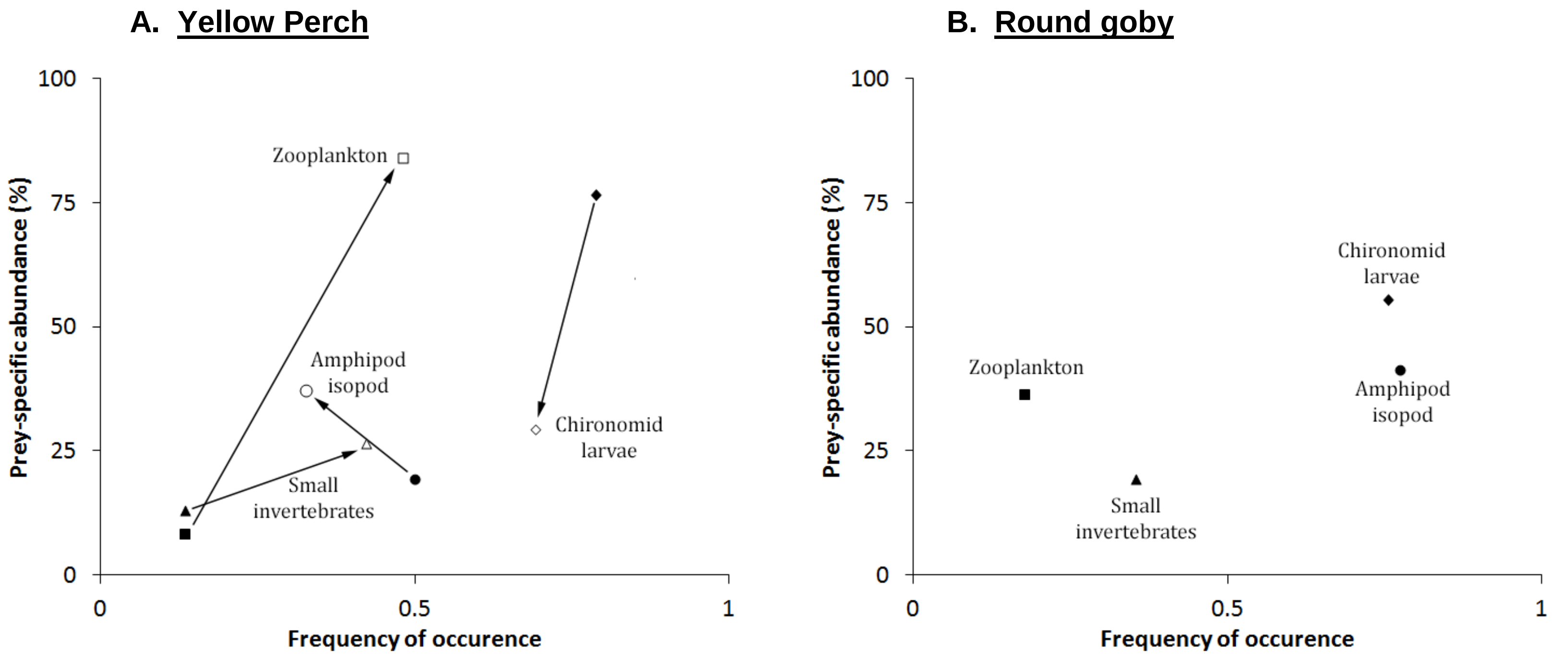

Figure 9. Modified Costello graphs for (A) age-0 yellow perch on rock (black symbols) and sand (hollow symbols). Arrows indicate changes in feeding strategy of age-0 yellow perch from rock to sand habitats. (B) Modified Costello graph for round gobies captured at rock sites. See methods for explanation of prey specific abundance and frequency of occurrence axis.

Calculated IoC for prey items in age-0 yellow perch stomachs indicated a high amount of contagion (IoC greater than one) for zooplankton and chironomids in 2006 (Table 5) and 2007 (Table 6); IoC of prey items in diets are often similar to those prey items distributions in the wild (Sparling et al., 2007).

Table 5. Mean number ($\bar{x}$) and Index of Contagion (IoC) of prey items in age-0 yellow perch diets captured in western Lake Michigan during 2006.

	YEAR - 2006	Sheboygan		Donges Bay		Fox Point		Whitefish Bay		Milwaukee		Wind Point	
Site	Prey Item	$\bar{x}$	IoC	$\bar{x}$	IoC	$\bar{x}$	IoC	$\bar{x}$	IoC	$\bar{x}$	IoC	$\bar{x}$	IoC
SAND	Chironomid larvae			1	3.7			1	2.6	1	3.9	< 1	0.8
	Amphipod and isopod			3	22.6	< 1	1.0	< 1	1.0			3	18.8
	Small benthic invertebrate			1	14			5	24.4	< 1	0.9		
	Zooplankton			7	29.2					< 1		4	27.7
ROCK	Chironomid larvae	11	43.8	< 1	1.5			4	21.5			39	84.5
	Amphipod and isopod	1	0.5	7	28.9			< 1	1.2	< 1	1.2	4	25.8
	Small benthic invertebrate	< 1	1.0					1	1.9				
	Zooplankton							3	34			1	11

Table 6. Mean number ($\bar{x}$) and Index of Contagion (IoC) of prey items in age-0 yellow perch diets captured in western Lake Michigan during 2007.

	YEAR - 2007	Sheboygan		Donges Bay		Fox Point		Whitefish Bay		Milwaukee		Wind Point	
Site	Prey item	$\bar{x}$	IoC	$\bar{x}$	IoC	$\bar{x}$	IoC	$\bar{x}$	IoC	$\bar{x}$	IoC	$\bar{x}$	IoC
SAND	Chironomid larvae			< 1	2.3	1	4.4	20	17.9	4	9.7		
	Amphipod and Isopod												
	Small Benthic Invertebrate			1	4.4	1	4.4	7	6.3	20	20.8		
	Zooplankton			124	572.2	69	225.8	4	36	33	36.2		
ROCK	Chironomid larvae			2	1.8	7	20.6	2	2.3	1	1.6	34	11.1
	Amphipod and Isopod			< 1	1.0	< 1	2.0	< 1	1.0			2	4.9
	Small Benthic Invertebrate					< 1	1.0			< 1	2.0	< 1	2.0
	Zooplankton			18	120.1	< 1	0.9					< 1	1.0

Correlation analysis also indicated a negative relationship between the mean of summed amphipod and chironomid larvae in age-0 yellow perch diets at each site versus round goby gill-net CPUE in 2006 (r = -0.92, df = 3, P = 0.026) and 2007 (r = -0.92, df = 3, P = 0.027; Figure 10). The relationship persists if age-0 yellow perch are considered to be independent foragers for both 2006 (r = -0.370, df = 49, P = 0.008) and 2007 (r = -0.510, df = 79 P < 0.001). As with the rock samples, the correlation coefficient decreases due to between fish variation.

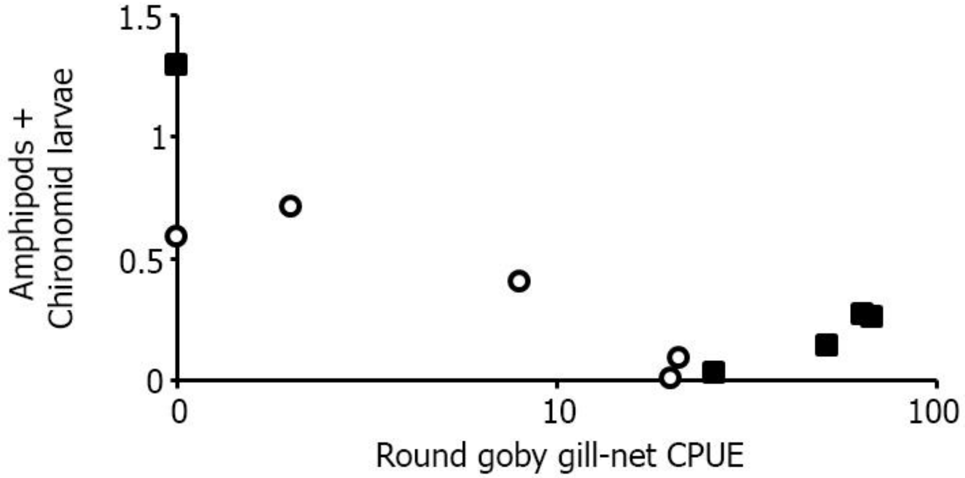

Figure 10. A correlation analysis between the mean of summed amphipod and chironomid larvae in age-0 yellow perch diets at each site versus round goby gill-net CPUE in 2006 (r = -0.92, df = 3, P = 0.026) and 2007 (r = -0.92, df = 3, P = 0.027). The relationship persists if age-0 yellow perch stomach contents are considered as independent for all sites in 2006 (r = -0.370, df = 49, P = 0.008) and 2007 (r = -0.510, df = 79, P < 0.001). All count data were $\log_{10}$+1 transformed for analyses; points are presented on a $\log_{10}$ scale along the X axis.

A two sample t-test was performed using transformed percent zooplankton contribution to age-0 yellow perch diet as the dependent factor and round goby abundance as the independent factor, to determine the effect of round goby abundance on age-0 yellow perch predation on zooplankton prey. Age-0 yellow perch consumed a higher percentage of zooplankton prey at rock sites with high round goby abundance using CPUE from gill nets (t = 3.42, df = 51, p = 0.001). When there were fewer than seven round gobies (low abundance) present age-0 yellow perch consumed a lower percentage of zooplankton prey at rock sites (Figure 11).

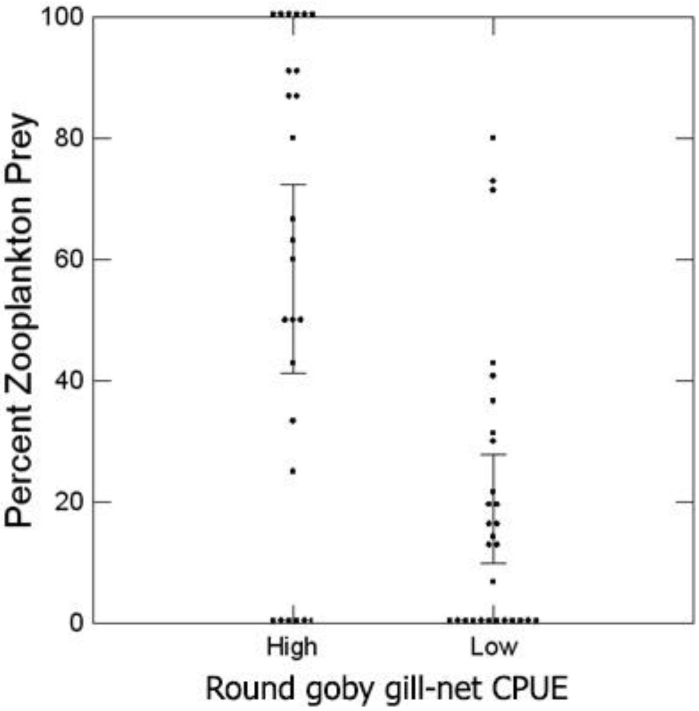

Figure 11. Percent contribution of zooplankton to the total stomach contents of age-0 yellow perch at rock sites with high and low round goby gill net CPUE. Dots represent the percentage of zooplankton contribution to each age-0 yellow perch

captured. Bars represent standard error around mean percent zooplankton prey contribution at sites with high and low round goby abundance.

Hypothesis 4: Decrease in growth of yellow perch with increasing round goby abundance

Yellow perch in Lake Michigan have a decrease in length-at-age of age-2 ($r = -0.692$, $df = 7$, $p = 0.039$) and age-3 ($r = -0.905$, $df = 10$, $p < 0.001$) males between 1999 and 2012. This downward trend in length-at-age is apparent in the graded mesh gill net assessment performed yearly by the WIDNR. The decrease in length of age-2 and age-3 yellow perch from 1999 to 2012 is over 50 mm or 25% of the overall length of yellow perch (Figure 12). Dub and Czesny (2013) showed size-selective mortality in young yellow perch likely occurred between the ages of 1 and 2, likely when they are still feeding on benthic invertebrates in the littoral zone of Lake Michigan. It is likely that the decrease in length-at-age is from before the fish's second year.

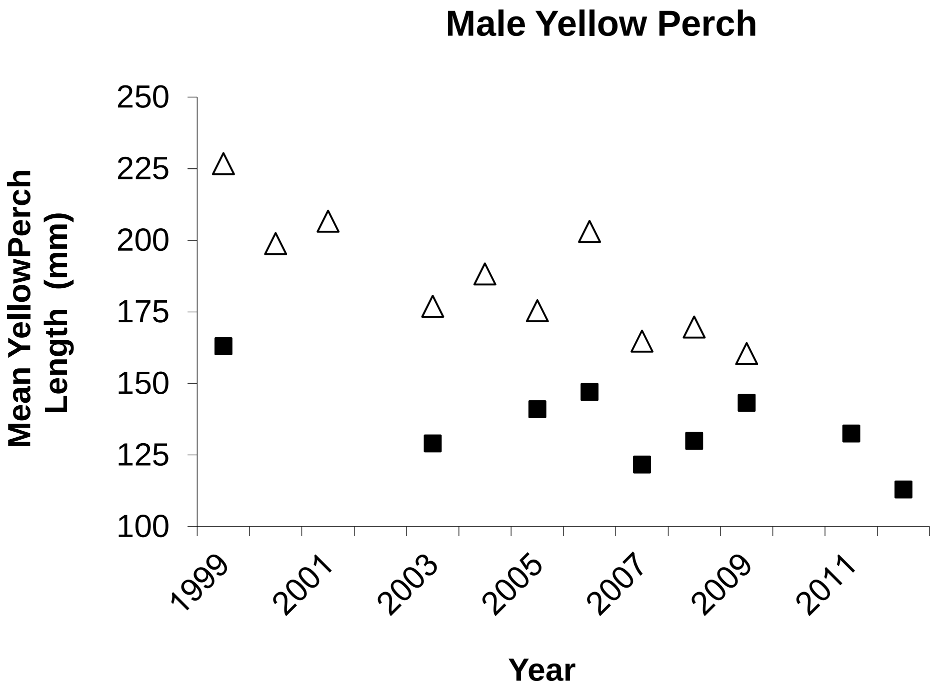

Figure 12. Length-at-age of yellow perch (squares = age-2; triangles = age-3) caught between 1999 and 2012 from WDNR yellow perch population survey. Since 1999 there has been an overall decrease in length-at-age of age-2 and age-3 yellow perch in western Lake Michigan.

Discussion

Results for the four tested hypotheses, habitat shift by yellow perch, diet shift by yellow perch, evidence of resource depression by round gobies, and a decrease in yellow perch growth in western Lake Michigan are consistent with my overall hypothesis that round gobies may exert competitive pressure on age-0 yellow perch at RLH. None of my findings refute the overall hypothesis.

Hypothesis 1, that preferred habitat of age-0 yellow perch has shifted away from rock substrates to sand substrates was supported by the strong negative correlation of round goby densities with percent yellow perch collected on rock habitat. A longer time series for habitat utilization of age-0 yellow perch would have provided stronger data for my analysis. However, the techniques used in the current study, as well as the extent of RLH in western Lake Michigan, were only just being explored during the time of sampling. Further, additional surveys within the study area since the time of the study revealed no other suitable sites which could have been added to the sampling locations.

The correlations among age-0 yellow perch habitat utilization and diet with round goby CPUE does not necessarily indicate round gobies are the causal agent because a third factor could be driving the response of both observations. However, evidence of an underlying mechanism does make it less likely that there is a third agent. The second hypothesis tested, that round gobies can depress food resources, was also supported by my analyses and this provided a potential mechanism for the observed change in age-0 yellow perch habitat selection. Increased round goby densities at rock habitats decreased the abundance of key benthic invertebrate prey for age-0 yellow perch i.e. amphipods and chironomid larvae. A negative relationship between round gobies and the density of invertebrate prey across a round goby invasion front was also shown by Lederer et al. 2006 and Kuhns and Berg, 1999.

Hypothesis 3, that there was a diet shift for age-0 yellow perch correlated with increasing round goby density at rock habitats, was also supported in this study. At rock substrate sites, where round gobies were present, age-0 yellow perch fed less on chironomid larvae and amphipod prey, the two invertebrates that were negatively correlated with round goby CPUE at rock site (Hypothesis 2). Schoener indices indicated a range of diet overlap between age-0 yellow perch and round gobies at rock sites, lending support for the hypothesis that round gobies and age-0 yellow perch may compete for prey.

The relative contribution of different prey items to the diet of age-0 yellow perch at rock and sand sites became apparent by looking at the Costello graphs. At rock sites age-0 yellow perch fed more on chiromonid larvae and amphipods while at sand sites age-0 yellow perch fed on more zooplankton and less chironomid larvae. This was confirmed statistically by comparing the percent contribution of zooplankton prey to the diet of age-0 yellow perch caught at sand sites with the number of round gobies captured at the rock site pair. While not sampled due to logistical difficulties created by shallow water and rock habitat, zooplankton would have been available at both rock and sand sites; whereas, the other important prey items, amphipods and chironomids were primarily associated with rock habitat (Kornis and Janssen, 2011; Kuhns and Berg, 1999). The combined observation of resource depression in Hypothesis 2, and an age-0 yellow perch diet shift in Hypothesis 3 for the same prey items in the same year, are strong evidence for competition between age-0 yellow perch and round gobies at rock sites. Hypothesis 4, that yellow perch growth has significantly decreased with increasing round goby abundance was also confirmed. However, these results need to be interpreted within the context of other ecological perturbations occurring within Lake Michigan over the course of the WI-DNR yellow perch surveys. The introduction and spread of round gobies was also coincident with the expansion of quagga mussels (Houghton et al., 2013), changes in the zooplankton community (Fahnenstiel et al., 2010a), and variation in the abundance of alewife (Bunnell et al., 2013), to name a few.

This study served as a natural experiment, where round goby densities were "manipulated" via their natural spread along the invasion front. As a result of round gobies spreading from their source populations to newly invaded areas, possible competitive interactions and effect on age-0 yellow perch were assessed. The current experiment was unique for the Great Lakes, in that it captured the competitive interactions between round gobies and age-0 yellow perch over a short amount of time during the round goby's population expansion.

Controlled experiments in the Great Lakes are difficult to conduct due to the Lake's large size. In Lake Michigan there is a limited history of using NIS species invasions and resource partitioning as natural experiments to assess the effect of competition between native species and NIS (Crowder, 1986). Crowder (1986) assessed competitive interactions between non-indigenous alewife and bloater by comparing resource use patterns and trophic morphology of bloater before and after the introduction of alewife. Crowder (1986) found that bloater shifted prey preference to benthic prey earlier in life as well as exhibited character displacement with fewer and shorter gill rakers which Crowder attributed to decreased reliance on zooplankton prey, as a result of competition with non-indigenous alewife. By using datasets with observations from before and after the introduction of an NIS, competition could be inferred. My study similarly relies on an observational design, but is unique in that it focused on niche shifts that occurred over 2 years.

The spread of round gobies during this study afforded me the opportunity to estimate the habitat utilization of age-0 yellow perch across a gradient of round goby densities. These results indicated the realized niche (i.e., utilization of preferred rock habitat and prey) of age-0 yellow perch decreased when competing against round gobies at rock habitat sites. From 2002 to 2007, the average age-0 yellow perch rock habitat utilization fell over 50%, including data from Janssen and Luebke (2004). The habitat shift of age-0 yellow perch correlated with increasing round goby CPUE at rock habitats and indicated age-0 yellow perch may be an inferior competitor for benthic invertebrate prey when competing with round gobies at RLH in western Lake Michigan.

Generally, in a system with two competitors, the realized niche of an inferior competitor in a sympatric system will be smaller than that of their allopatric counterparts, which occupy a larger range of their fundamental niche. Habitat shifts, as a result of interspecific competition, have been demonstrated in a number of systems including New Guinea mountain dwelling birds (Diamond, 1970), Caribbean *Anolis sp.* lizards (Schoener, 1975), and *Typha* spp*.* cattails in the Midwest (Grace and Wetzel, 1981). The effect of competition between two species can be observed by quantifying their realized and fundamental niches in allopatric and sympatric populations. Diamond (1970) showed that allopatric populations of New Guinea bird species increased their habitat utilization by moving to higher and lower elevations (thus increasing their realized niche) on islands compared with islands with sympatric populations of the three bird species. Similarly, Grace and Wetzel (1981) found that two cattail species (*Typha latifolia* and *T. angustifolia*) occupied larger depth gradients when grown in allopatric plots compared with sympatric plots. The observed habitat shift, resource depletion, and diet shift of age-0 yellow perch, all correlated with increasing densities of round gobies, are indicators that age-0 yellow perch may have shifted their realized habitat and prey niches as a result of the round goby invasion (Mittelbach, 2012).

Exploitative competition between age-0 yellow perch and round gobies

In the present study, dietary overlap between age-0 yellow perch and round gobies on rock was moderate (Schoener's $\alpha = 0.42$) indicating the two species utilize similar prey resources. The Costello graphs indicated age-0 yellow perch change feeding strategies once they move from rock to sand habitats with increasing round goby densities at rock habitats. These are all indications of exploitative competition between the two species.

Research on the interaction between round gobies and yellow perch in Lake Erie mesocosms also found the highest amount of dietary overlap between the two species was for small individuals (Duncan et al., 2011). They found zooplankton, dipterans, amphipods, and isopods were important forage for small yellow perch and round gobies, especially before round gobies grew large enough to prey on dreissenids.

The present study's findings of increased reliance on zooplankton prey are corroborated by recent research that found small yellow perch have increased their utilization of offshore energy sources since the invasion of quagga mussels in Lake Michigan (Turschak et al., 2014). Turschak et al. (2014) used stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes of 10 fish species captured in 2002 and 2012 to assess nearshore and offshore energy contributions to the food web. Their results showed that, out of the 10 fish species analyzed, yellow perch was the only species to change from a more nearshore to more offshore (pelagic) energy source. Separation of yellow perch into three size classes; small (<70 mm), medium (70-150 mm), and large (>150 mm) indicated that, of the three sizes, small yellow perch shifted the most to offshore-pelagic energy sources. They determined the source of offshore energy in yellow perch diets was likely zooplankton. Yellow perch are primarily a littoral species and the fish captured in their study were captured in the nearshore zone. Therefore, it is likely that yellow perch were feeding on offshore zooplankton that had moved inshore via advected water masses. They theorized that the overall shift of the other nine fish species, to more nearshore/benthic energy sources, was likely caused by quagga mussel-induced benthification of primary production (sensu Hecky et al., 2004).

Foraging generalists are often better competitors when resources are abundant but are less effective against specialists when resources are scarce (Mittelbach, 2012). Round gobies transition to a specialist molluscivore as they grow from about 50 to 100 mm with shell-crushing molariform, pharangeal teeth, and unique feeding mechanics (Ghedotti et al., 1995; Andraso et al., 2011; Houghton and Janssen, 2013). The exploitative impact on age-0 yellow perch would likely be due to small round gobies (mean TL = 67mm, S.D. = 11.1) caught during our sampling. The impact of larger round gobies, not easily captured in the micromesh gillnet used in this study, would more likely be due to increased aggression in territorial adults.

The observed diet shift of age-0 yellow perch at rock substrates is an important observation because diet shifts often occur in systems where an inferior competitor relies on the same resource as a competitively superior species. A classic example of diet shifts in fish species as a result of competition is demonstrated by Werner and Hall (1977). They showed that bluegill sunfish (*Lepomis macrochirus*) shifted habitat and prey utilization when competing with green sunfish (*L. cyanellus*) for invertebrate prey in 18 experimental ponds. They hypothesized this shift was due a combination of resource depletion and aggression caused by the green sunfish, which led to the green sunfish competitively excluding bluegill from cattail associated invertebrate prey (Werner and Hall, 1977).

Comparing the results of the present study with those of Werner and Hall (1977) reveals similarities between the two model systems. In both studies the competitively inferior species (bluegill sunfish/age-0 yellow perch) switched to new habitats to feed in the pelagia on zooplankton when competing against a superior benthic invertebrate predator (green sunfish/round goby). As with our study, Werner and Hall (1977) did not determine whether the mechanism of habitat displacement was via exploitation or interference. They also noted that exploitative competition and interference competition are not mutually exclusive. It may be that round gobies are negatively affecting age-0 yellow perch through two competitive mechanisms, both of which could result in age-0 yellow perch changing habitat utilization and diet.

Variation in prey distribution and stomach contents of yellow perch

The combined IoC and correlation statistics indicated benthic invertebrates at rock sites occurred in patches. Benthic invertebrates are often distributed in patches within the environment (Elliott, 1971) however, the negative correlation between chironomid larvae and amphipod prey with round goby CPUE, may indicate that round gobies preferentially deplete amphipods and chironomid larvae from rock habitats. The distribution of prey items in diets often mirror the distribution of prey items in the environment. The patchy distribution of prey items in age-0 yellow perch diets may be explained by the patchy distribution of prey within rock sites and/or the patchy distribution of round gobies within rock sites.

It is very likely that I conducted insufficient rock sampling to adequately assess impacts of round gobies on potential prey. As is typical of rock habitat, invertebrates showed great contagion, making statistical analyses difficult without extensive sampling (Elliot, 1971). However, the patchiness itself is biologically important because fish searching for prey are likely primarily searching for patches of prey. This can contribute to great variation in diet among individuals. That I found statistically detectable effects on prey densities and yellow perch diets indicates a more extensive study of prey and fish microdistribution is necessary for a better understanding of the round goby-yellow perch interaction. If there are patches of invertebrates on rock and yellow perch need to move between rock and sand to find those patches we would expect there to be high amounts of contagion within the stomach contents of the yellow perch. Yellow perch could be modifying their feeding strategy to seek out these patches of prey, both as a consequence of reduced prey abundance at rock sites with round gobies and possibly territoriality of round gobies.

In the pelagia, fertile waters with abundant planktonic prey are not evenly distributed in space or time, due to prey habits and currents (ex. upwelling) (Beaudreau and Essington, 2011). Benthic invertebrates are also distributed unevenly and often exhibit high contagion due to preferential habitat use, predation, and other biotic and abiotic factors (Elliott, 1971). My results indicate that age-0 yellow perch feed on a higher percentage of zooplankton prey at rock sites and that round gobies deplete benthic amphipod and chironomid larvae numbers where round gobies occur in high abundance. Yellow perch are more likely to consume zooplankton prey where round gobies are present on rocks. However, patches of benthic prey may allow age-0 yellow perch to continue to feed at rock habitats, resulting in the observed high amount of contagion for prey items found in age-0 yellow perch stomachs. If the distribution of round goby patches and benthic invertebrate patches does not fully overlap, age-0 yellow perch could take advantages of fringing areas and opportunistically use them as prey refuges.

Studies have shown that switching between feeding strategies is dependent on the relative profitability of those prey items to the fish (Graeb et al., 2004; Wu and Culver, 1992). Graeb et al. (2004) showed that 20-mm yellow perch selected for zooplankton while 40- and 60-mm yellow perch began to feed on benthic invertebrates in mesocosm experiments. They theorized that while 20-mm yellow perch were able to feed upon benthic invertebrates (chironomid larvae in their study) they likely continued to feed on zooplankton due to differences in relative foraging cost. Thus the shift from zooplankton to benthic invertebrate prey is determined by foraging efficiency and energetic gain rather than simple prey availability (i.e. zooplankton prey availability decreases in later summer to the point of being inefficient to capture). Similarly, Wu and Culver (1992) found that 50-mm TL age-0 yellow perch would only shift to benthic prey if prey zooplankton abundance dropped below 50/L, and this can happen at a range of yellow perch sizes. This shift to benthic prey is then determined by loss of zooplankton in the water column. The tradeoff between foraging efficiency and energetic gain for age-

0 yellow perch in the current study was complicated by the presence of round gobies, and the general lack of zooplankton prey, especially large cladocerans preferred by age-0 yellow perch, in western Lake Michigan. It is likely that the habitat switch and continued reliance on zooplankton prey by age-0 yellow perch larger than 50 mm is detrimental to their growth. While age-0 yellow perch may be able to take advantage of the inherent patchiness of prey at rock habitats by opportunistically preying on benthic invertebrates during rock habitat feeding excursions, the act of switching between foraging modes can take time and it is difficult for fish to switch back and forth between foraging modes (Murdoch et al., 1975).

Interference competition between age-0 yellow perch and round gobies

While my study offers strong evidence for exploitative competition as a factor leading to the observed habitat and diet shift of age-0 yellow perch, interference competition can also lead to habitat and prey shifts (Duncan et al., 2011; Winslow, 2010). Interference competition has been implicated in habitat shifts of sunfishes (Werner and Hall, 1977) and several salmonines (Fausch, 1998; Hindar et al., 1988; Jonsson et al., 2008; broader review in Ross, 2013). Age-0 yellow perch will avoid aggressive interactions with round gobies, which both are metabolically costly, due to increased locomotion, and also inhibit age-0 yellow perch from successfully feeding on the benthos (Duncan, 2006). Duncan (2006) found that yellow perch in mesocosms with conspecifics grew less than yellow perch in mesocosms with round gobies. However, in their mesocosm studies yellow perch had access to macrophytes to shelter them from round goby aggression. They concluded that since yellow perch in mesocosms with round gobies exhibited lower activity and aggression compared with yellow perch with conspecifics, that round gobies would not hinder yellow perch growth in Lake Erie (Duncan, 2006). However, caution should be taken when comparing studies between Lake Michigan and Lake Erie as the main basin of Lake Michigan lacks macrophyte beds (Jude et al., 2004) that buffered competitive interactions between round gobies and yellow perch in Duncan et al.'s experiments.

Similar research performed on round gobies and smallmouth bass (*Micropterus dolomieu*) in Lake Erie mesocosms showed age-0 smallmouth bass grew less in the presence of round gobies (Winslow, 2010). Winslow (2010) also showed that round gobies displaced smallmouth bass <33 mm, from the benthos likely via interference competition. They found that Lake Erie age-0 smallmouth bass preyed more on zooplankton as a result of interference competition with round gobies. However, the interspecific effect of round gobies on age-0 smallmouth bass was similar to the intraspecific effect with similar densities of all age-0 smallmouth bass in their mesocosms (Winslow, 2010). Winslow noted that in the wild, densities of round gobies are often much higher than age-0 smallmouth bass densities and hypothesized that the interspecific effect of round gobies would likely exceed the intraspecific effect of age-0 smallmouth bass.

However, smallmouth bass in Lake Erie are also becoming piscivorous earlier in life due to the presence of age-0 round gobies (Steinhart et al., 2004; Winslow, 2010). Piscivores tend to grow more quickly once they begin preying on other fish. Availability of juvenile round gobies as prey for age-0 smallmouth bass may help mitigate the negative effects of early life history competitive interactions with larger round gobies. A similar interaction could also occur for age-0 yellow perch and age-0 round gobies in western Lake Michigan (discussed below).

If one consequence of competition is decreased growth, then the smallest yellow perch may succumb to overwinter starvation, as Bystrom et al. (1998) found for Eurasian perch (*Perca fluviatilis*) competing with roach (*Rutilus rutilus*). Even if there is not mortality due to starvation, direct mortality could be due to predation. For example, Rice et al. (1987) argued that predation on age-0 bloater would likely increase if the bloater larvae grew too slowly to escape predation, due to exploitative competition. In such a case there is a combined competition and predation effect. Competition and predation can combine for interference competition also. Quinn and Janssen (1989; Lake Michigan), Garvey et al. (1994; Wisconsin lakes), and Soderback (1994; European lakes) argued that less aggressive crayfish species were more vulnerable to predation because they are less likely to access quality shelters.

Age-0 yellow perch predation on round gobies

Recent research focused on interactions between adult yellow perch and round gobies has concentrated on predation (Weber et al., 2010, 2011). The predominant interaction between adult yellow perch and round gobies is predation of the former on the latter. Historically, yellow perch in Lake Michigan become piscivorous at around 150 mm in total length, and round gobies can be heavily selected, especially in complex habitat (Weber et al., 2010). Weber et al. (2011) also showed their smallest group of yellow perch (240-259 mm) preferentially consumed the smallest round gobies (50-55 mm). Presence of age-0 round gobies (although only a few) in the diet of age-0 yellow perch in this study may confound the effect of round gobies on the overall perch population. Steinhart et al. (2004) showed smallmouth bass grew faster in Lake Erie if they switched to round goby prey earlier in their life. Yellow perch generally undergo higher growth when feeding on fish prey. Graeb et al. (2005) theorized that the switch of yellow perch to piscivory was likely due to an interaction between successful foraging and gape width. Yellow perch as small as 80 mm will select for bluegill sunfish when offered them in mesocosms, however larval fish small enough for age-0 yellow perch to consume in the wild are typically not abundant during the right time (Graeb et al., 2004).

The presence of age-0 round gobies during the age-0 yellow perch switch to demersalism may lead yellow perch to become piscivorous earlier, and could allow yellow perch to grow more quickly, similar to a study of pikeperch (*Sander lucioperca*) in southern Sweden (Persson and Brönmark, 2002). This switch may be reinforced by the shift of age-0 yellow perch away from their preferred benthic forage due to its depletion by round gobies. Perrson et al.'s (2007) research documented the eventual outcome of early competition during juvenile stages and subsequent predation as adults on a given competitor is dependent on a number of variables and can easily change. The outcome of interactions between size-structured communities depends on the relative strengths of both the competitive and predatory interactions (Persson et al., 2007). What effects the dietary change of yellow perch will have on growth and survival of age-0 yellow perch, and subsequent recruitment, are not yet known. Further analysis of length-at-age data obtained from yellow perch spines and otoliths may help elucidate these effects.

In fishes, growth can be used as an index of resource availability and is usually positively related to fitness (Hall et al., 1970). The effect of a habitat and diet shift in age-0 yellow perch is expected to manifest itself as a reduction in growth, fecundity, or survival in the overall population (Mittelbach, 2012). Recent WDNR length at-age-data of yellow perch captured around Milwaukee show a consistent decline in size at age of 2- and 3- year old yellow perch in Lake Michigan starting around 1999 and continuing until 2012 (Hypothesis 4). The apparent decrease in length-at-age of age-2 and age-3 yellow perch may be attributed to a number of factors, including interspecific competition between round gobies and age-0 yellow perch. If another factor, such as decreased zooplankton abundance due to alewife and mussels, or predation by alewife, it would be expected that over the course of their survey the decrease in length-at-age of yellow perch would have found a new equilibrium. It is beyond the scope of my study to parse the factors contributing to the continued decline in length-at-age of yellow perch in western Lake Michigan. However, from the WIDNR data, it does not appear age-0 yellow perch have reached such an equilibrium point. Given that round gobies are now the most abundant forage fish in Lake Michigan (Bunnell et al., 2013), the magnitude of the impact round gobies could have on age-0 yellow perch at rock habitats is very high. My evidence suggests round gobies may now be a large contributor to the decreased growth of juvenile yellow perch.

The future of yellow perch in Lake Michigan

Many proposed theories for the yellow perch decline in Lake Michigan have implicated non-indigenous alewife (Wells, 1977; Forsythe et al., 2012) and dreissenid mussels (Marsden and Robillard, 2004). Most of these competitive scenarios impact yellow perch during their first recruitment bottleneck as planktonic larvae. Alewives compete with age-0 yellow perch for zooplankton in the pelagia and also prey directly on age-0 yellow perch larvae. Evidence suggests that direct predation on larval yellow perch by alewife is likely the best theory presented that explains yellow perch year class failure (Wells, 1977; Shroyer and McComish, 2000). Shroyer and McComish (2000) predicted that alewife numbers would need to be reduced to levels lower than during the 1980s for yellow perch recruitment to increase. However, alewife abundance in Lake Michigan is now at levels lower than the 1980s and there has been no apparent increase in yellow perch recruitment (Bunnell et al., 2013).

The recent invasion of dreissenids (Cuhel and Aguilar, 2013; Houghton et al., 2013) has also likely negatively impacted age-0 yellow perch during their planktonic stage. First, quagga mussels have sequestered pelagic energy by filtering algae and microplankton from the water column thus reducing zooplankton prey abundances (Fahnenstiel et al., 2010b). Second, filtration and subsequent release of feces and pseudofeces into the benthos has increased available energy for primary production (i.e., benthic invertebrates) (Bootsma and Liao, 2014; Cuhel and Aguilar, 2013). By itself, the increase in available energy in the littoral zone should benefit age-0 yellow perch recruitment by providing more invertebrate prey once fish become demersal. However, my evidence shows that round gobies are now excluding age-0 yellow perch from rock habitats.

I propose that, in Lake Michigan, round gobies may have produced a new recruitment bottleneck for age-0 yellow perch during their second stage of life. This new recruitment bottleneck would occur after age-0 yellow perch have survived the planktonic stage and transition to become demersal in the littoral zone. During this period round gobies depress prey abundance and competitively exclude age-0 yellow perch that have survived the planktonic bottlenecks imposed by alewife and dreissenid mussels. Given the increasing populations of both dreissenids and round gobies in Lake Michigan since the present study was conducted, the combined effect of round gobies, dreissenids, and alewife will likely continue the trend of poor yellow perch year class recruitment in Lake Michigan.

Assuming that round gobies do drive a habitat shift in age-0 yellow perch, the broader scale consequences are not certain. The present study was limited to Wisconsin waters which are predominantly rocky (Janssen et al., 2005) and the western side of Lake Michigan tends to be colder due to upwellings (Beletsky et al., 2001) and has many fewer tributaries. This combination of factors likely led to regional differences in growth of both age-0 and older yellow perch (Horns, 2001), so the impact of round gobies likely varies by region. Broad-scale approaches to the round goby yellow perch interactions should be encouraged in the future to determine how variation among regions could affect the yellow perch population as a whole. However to perform broad-scale analyses significantly more detail on the distribution and biota of Lake Michigan's diverse nearshore habitats will be required.

Future directions

The current study, like most fisheries research, was limited in temporal and spatial scale. While my data were primarily collected in 2006 and 2007, preliminary data from 2005 and Janssen and Luebke (2004) were instrumental in constructing a timeline to assess the competitive interaction between round gobies and age-0 yellow perch in western Lake Michigan. Further temporal scale could be achieved by returning to the study locations and repeating the sampling effort. It would be interesting to determine if round goby densities have reached equilibrium and if their current densities are high enough to sustain the proposed demersal bottleneck for age-0 yellow perch. If the proposed bottleneck is a strong selective pressure upon the yellow perch population of Lake Michigan we may also expect a phenotypic response in character displacement. Hjelm et al. (2000) found that for the Eurasian perch gill raker density was negatively correlated with planktivorous fish biomass in eight European study lakes. If multiple generations of age-0 yellow perch are dependent on zooplankton later in their life we may expect to find increased gill raker density in response. Finally, while it was beyond the scope of the present study, back calculated length-at-age from WIDNR collected spines could likely be used to determine if there has been an effect of round gobies on yellow perch now that round gobies have become fully established.

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SELECTED PUBLICATIONS

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Houghton, C.J. and J.Janssen. (2013) Variation in predator-prey interactions between dreissenid mussels and round gobies. In T.F. Nalepa and D. W. Schloesser [eds.] Quagga and Zebra Mussels: Biology, Impacts and Control. CRC Press: Boca Raton FL.

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PRESENTATIONS

Houghton, C.J., (2013). Impacts of round goby on diet and distribution of age-0 yellow perch. International Conference on Great Lakes Research. (Oral presentation)

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