A Review of Round Goby Swimming Capabilities, Behaviors, and Habitat Preferences to inform Colonization Deterrence Applications in Waterways

Figure 1. The Round Goby (Neogobius melanostomus) with characteristic black spot on first dorsal fin and its fused pelvic fin (from Figure 1A in Hirsch et al. 2016a).

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Executive Summary

To inform deployment of Round Goby (*Neogobius melanostomus*) deterrence systems at the Menasha Lock on the Fox River, the available science describing the swimming behavior, migrational patterns and habitat preferences of juvenile and adult invasive Round Goby was summarized. The Fox River (a tributary to Lake Michigan in Wisconsin) comprises some 17 locks between Lake Winnebago and Green Bay. Because this invasive species had already colonized the Great Lakes in the early 1990's, the Wisconsin Department of Natural Resources promulgated rules for invasive species prevention measures to thwart range extensions in Wisconsin waters. There is a desire to reopen one of the Fox River waterway structures (Menasha Lock) to regular boat traffic, without incurring the risk of further Round Goby range extensions. Our review addresses the behaviors, migrational patterns and life history habitat requirements of round gobies with this perspective in mind: exploit Round Goby life cycle weaknesses for strategies that can allow lock operation while deterring upstream movements and reducing this species' proclivity for range extensions.

The review was substantive. It examined global sources of information on Round Goby colonizations and their various life history requirements and adaptations. Objectives focus on an improved understanding of Round Goby swimming behaviors and habitats to guide decision-making for potential fish deterrence applications. Our aim in this literature review is to summarize existing knowledge on this species and review its potential for upstream movement at sites such as a proposed electric barrier at Menasha Lock. Thus, we consider the various life-stage adaptations and swimming behaviors of round gobies, their habitat preferences, and known environmental factors that either limit or foster range extensions. A better understanding of this species' biological and physical requirements can help elucidate life history vulnerabilities and/or aid in the development of deterrence strategies and technologies to reduce the risk of range extensions through the subject lock and environs.

Key Findings: Adults. Our review shows that in general, the Round Goby can live up to 5 years, attain maximum total lengths up to 25 cm, and achieve sexual maturity when 1+ to 3 years old. Maximum size differs in various localities, from 12 cm for males and 11 cm for females in the upper Detroit River, to 25 cm for males and 19 cm for females in Europe. A

main taxonomic anomaly is the presence of a fused pelvic fin on round gobies that forms a suction cup or disc for “burst-and-hold” behaviors that aid upstream movement in rivers.

Based on research results of Round Goby swimming behaviors from three published accounts, gobies are quite adept at using “burst-and-hold” or “burst-and coast” strategies to promote upstream movements in strong water velocities. The fused pelvic fin adaptation allows round gobies to “hold-station” in various flow regimes. Therefore, velocity barriers are unlikely to be an effective upstream migration deterrent in waterways.

Round gobies are able to maintain (indefinitely) swim speeds less than 35.5 cm/s but a proportion can maintain speeds >75 cm/s for “burst swims” up to a half-minute in duration (suggesting that with a “burst-and-hold” strategy, these fish could navigate flows, through successive attempts, at levels just less than their maximum-burst swimming capabilities. A swimming endurance model (Tierney et al. 2011) indicated that flow rates would need to be >125 cm/s to prevent upstream movement by round gobies in areas free of refuge recovery habitat. Other swimming speed research showed no significant difference in maximum swimming speed and station-holding endurance capabilities between lake and river-origin fish. Apparently, river fish are not better swimmers than round gobies from lake populations. Maximum speed and endurances were similar, indicating that the unidirectional, higher flows found in rivers are not strong enough to act as dispersal barriers for round gobies. However, we found published evidence (Savino et al. 2001) that an electric barrier successfully deterred round gobies from accessing a Lake Michigan tributary stream. Thus, an electric barrier (leveraged with any natural hindrance effects from water velocity) warrants consideration for the Menasha Lock deterrence application.

Diurnal Behavior: Adult gobies were more active on rocky substrates (as opposed to sandy habitats) during daylight hours than at night. These findings were statistically significant and concluded that the proclivity for daytime activity may lower the risk for predation.

Key Findings: Juveniles. In the Great Lakes region, round gobies spawn from May to October in a range of water temperatures from 9 to 26 ^{o}C. Males prepare and guard the nest from intruders through the incubation and hatching periods. Various physical locations are used for nest construction (each in some form of underwater structure forming a cavity with a single opening).

Data on Round Goby juvenile swimming speeds were quite scarce. However, we found references to an account published in a Russian journal. Initial swimming speeds of newly hatched, 5.5 mm fry were 2 cm/s and swimming speeds of 6 mm fry three days after hatching were 4.4 cm/s. Those unseen data come from a paper by Logachev and Mordvinov 1979, as cited by Marsden et al. 1996. We found no other accounts of larval swimming speeds.

Review findings also underscore the adaptive nature of this harmful and dangerous invader. Its adaptations include repeat spawning every 18-20 days, portion spawning, hidden nest construction, parental brood care, an unusual egg shape having strong substrate attachment capabilities, a very short embryonic development period coupled with relatively fast free-swimming independence, and utilization of varied habitats and water qualities. Canadian modeling studies reinforce such risks and concerns: Round Goby range expansions of 9.3 km/year were predicted in high-quality habitats.

Diurnal Behavior: Of high importance to the purposes of this review, we found evidence for a diel vertical migration pattern among newly hatched, 6.5 to 8.9-mm Round Goby fry. Based on ichyhyoplankton net tows in two separate studies, newly emerged goby fry were present in surface waters **only at night** (virtually none were found during daytime plankton tows). These data suggest a novel dispersal strategy for a species that lacks a swim bladder. The implication is that this negatively buoyant species may be employing a diel surface migration strategy for emergent fry to find and use surface currents for dispersal to new habitats. This unique behavioral adaptation may explain how round gobies found a way to North America in the ballast water of commercial shipping vessels. Relative to the Menasha Lock, the diel pattern does offer the potential to limit dispersal of juvenile Round Goby by enforcing a policy of not operating the lock at night. Also, the lack of any significant upstream current (i.e. flow into the lock from Little Lake Butte Des Morts), especially near the bottom of channel, severely limits the risk of upstream drift of larval gobies during daylight hours when the lock is in operation.

Key Findings: Habitat Preferences. The Round Goby is a bottom-dwelling fish that prefers rock/gravel substrates with interstitial spaces for both escape cover and for spawning in littoral areas of lakes and rivers. Gobies also seem to prefer human-made riprap, breakwaters, and rocky or coarse-gravel in inshore areas with abundant escape cover. Other preferred habitats include stony bottoms, mussel beds, areas near marina-type structures (piers, wharves, etc.) and on occasion, humus-containing bottoms overgrown with marine flora where they can reside with restricted movement.

In the Trent River near Lake Ontario, over 90% of the fish sampled were found in rock or gravel substrates (as opposed to sites composed of sand or macrophytic vegetation). Round Goby habitat preferences in three tributaries to Lake Erie, Pennsylvania were similar: rocky areas having moderate streamflow. But smooth, shallow bedrock areas in upstream portions of these streams were not used, presumably because they contained fewer ledges and crevices than found in deeper, more open stream areas. Shallow bedrock areas appear to act as a barrier to colonization and further upstream movement by round gobies.

Management Implications: Based on our review, the following management implications are offered:

(1) Water-velocity alone is unlikely to be an effective deterrent to halt the spread of adult Round Goby. However, an electric barrier was successful in blocking goby movement in a Great Lakes tributary. Furthermore, the effectiveness of Round Goby deterrence systems such as graduated-field electric barriers may be improved if built on smooth, bedrock-type characteristics void of goby refugia.

(2) Research reviewed on the vertical migrations and diel periodicity of newly emerged Round Goby fry provide additional implications for managers concerned about risks of goby transport at waterway structures. The science we reviewed (especially Hensler and Jude 2007) strongly suggests that larval gobies are only in the water column at night (i.e. in surface waters). Because the swimming abilities of these 6 to 9-mm larvae do not exceed 5 cm/s, and there is strong evidence that their dispersal strategy is to drift with water currents, there is little risk of their upstream movement in an area with no upstream current and occasional strong downstream current (when water is spilled from the lower lock gates). If the lock is operated only during daylight hours when larvae are absent from the water column, there should be no opportunities for upstream transport of larvae, suggesting that deterrence efforts need to instead focus on adult fish.

(3) The localized site fidelity of the Round Goby coupled with its preference for rocky, cobble substrates and underwater structures indicate that transport and colonization risks can be reduced or eliminated when these habitats are unavailable. Because smooth, bedrock-type areas were found to act as a barrier to Round Goby colonization and upstream range extension, the addition of such streambed modifications (replica structures) could serve to minimize goby presence downstream of waterway projects. However, such efforts may be costly and may present stream-bed engineering challenges. Other technologies (e.g. graduated-field, electric fish barriers) can provide better and cheaper solutions for Round Goby deterrence at Menasha Lock or other areas, as this type of electric barrier has achieved Round Goby deterrence success (Savino et al. 2001).

Introduction

A lock system on the Fox River, a tributary to Lake Michigan in Wisconsin, has had a varied history since the 1850's, with multiple operators including the U.S. Army Corps of Engineers. In 2001, the Wisconsin State Legislature created the Fox River Navigational System Authority (FRNSA) to take ownership of some 17 locks between Lake Winnebago and Green Bay. The Menasha Lock is the upstream-most of these locks, providing a boat connection between Lake Winnebago and the impounded part of the Fox River known as Little Lake Butte Des Morts. The Menasha Lock, shown in Figure 2, is typically open from mid-May to early October, and the average annual usage during this period is about 1,500 boats. The lock is only operated during daylight hours.

Figure 2. Menasha Lock from upstream (Lake Winnebago), looking north. Source: Smith-Root, Inc.

In 2009, the Wisconsin Department of Natural Resources promulgated new rules for invasive species that require preventative measures to thwart range extensions into Wisconsin waters. A key target of such legislation was a highly invasive fish species, the Round Goby

(*Neogobius melanostomus*), which had already colonized the Great Lakes. One of the Fox River waterway structures (Menasha Lock) is the focus for this review. Managers want to reopen Menasha Lock to regular boat traffic while simultaneously deterring movements of gobies, without incurring risks of further range extensions through the lock.

The Round Goby is an aggressive bottom-dwelling fish from the Ponto-Caspian region of southeast Eurasia (i.e. Black and Caspian seas) that extended its range to areas of the Baltic Sea (Skora and Stolarski 1993) and the Laurentian Great Lakes (Jude et al. 1992) during the summer of 1990. This invasive species now occurs in both brackish and fresh waters in numerous areas around the world, especially in major river systems and lakes in Europe and North America, where large populations have become established (Kornis et al. 2012; Bonislawska et al. 2014). Various life stages of the Round Goby were likely transported to the Baltic Sea's Gulf of Gdansk and to North America's Great Lakes in the ballast water of Ponto-Caspian shipping vessels in the late 1980's (Corkum et al. 2004). Successful fish invaders are tolerant of environmental change or can survive harsh conditions, as has this euryhaline species throughout the Great Lakes, despite strict ballast water exchange legislation (Ricciardi and MacIsaac 2000). Round Goby species colonized all five U.S. Great Lakes in just 5 years (Jude 1997).

A small, soft-bodied, bottom dwelling fish, the Round Goby can live up to 5 years, attain maximum total lengths up to 25 cm, and achieve sexual maturity when 2 to 3 years old (Bronnenhuber 2010). Maximum size differs in various localities, from 12 cm for males and 11 cm for females in the upper Detroit River (MacInnis and Corkum 2000), to 25 cm for males and 19 cm for females in the Gulf of Gdansk, Poland (Sapota 2012). Although similar in appearance to North American freshwater sculpins (*Cottus* spp.), a main taxonomic difference is the presence of two, distinct pelvic fins on fish in the family Cottidae versus the fused pelvic fin found on round gobies (see Figure 1).

Round Goby characteristics include frog-like eyes, a black spot on the dorsal fin and the fused pelvic fin that helps form a suction disc on the fish's ventral surface (Corkum et al. 2004; State of Michigan, no date). This species is often found on hard substrates in association with another Eurasian invader, the Zebra Mussel (*Dreissena polymorpha*), a major component of goby diets owing to their pharyngeal teeth that can crush mollusk shells as soon as juvenile gobies grow to a length of about 6 cm (French and Jude 2001). Zebra mussels may have facilitated Round Goby invasions by providing an abundant food source (Ricciardi and MacIsaac 2000).

The spread of an invasive species such as the Round Goby is a serious challenge for natural resource managers because once established, containment is difficult, native fish species become threatened, and major shifts in aquatic species' population and ecosystem structure are inevitable. Several studies have shown the harmful effects of Round Goby predation on the eggs of native fish fauna (Sapota and Skora 2005; Kornis et al. 2012) and an ability to outcompete indigenous species for food, shelter and spawning habitat (Lauer et al. 2004; Balshine et al. 2005).

A very recent publication compared the early and the late phases of the European invasion at the population level in the Danube River between Austria and Germany (Brandner et al. 2018). These authors noted an upstream invasion by the Round Goby of some 30 river km in the Danube within just 4 years. More importantly, this research keyed on the principles of adaptation and genetic plasticity as prime factors in goby colonization success rates. Large-sized pioneering invaders (the earliest colonizers), with greater exploratory behavior, highly adaptive phenotypic plasticity, and increased competitive ability pave the way for colonization success (Brandner et al. 2018).

Such adaptive capabilities and genetic plasticity observations among various Round Goby invasions are strongly supported by other recent research. Kornis et al. (2017) examined the attributes and life history patterns of round gobies that had colonized Lake Michigan versus those living in the lake's adjacent tributaries (stream habitats). Tributary gobies grew much faster, had shorter life spans, and achieved sexual maturity at younger ages compared to those residing in Lake Michigan proper. This Lake Michigan research suggests an additional concern: that divergent life history patterns emerge as a result of local adaptations following initial Round Goby invasions. Adaptive divergences can potentially act as springboards for range extensions by invasive species (Kornis et al. 2017). The observed differences and suggested divergences noted by these authors between lake and tributary round gobies are consistent with life-history theory predicting rapid growth, early reproductive maturity, and a greater investment in reproductive strategies during population establishment in new, low-density habitats (Bøhn et al. 2004). However, and when body sizes were compared among round gobies in an initial colonization location (68 to 77 mm) with those (74 to 92 mm) in newly colonized areas in the Trent River, Ontario, the smaller fish sizes in the initial colonization habitat were thought to be a result of density-dependent factors (Gutowsky and Fox 2011). Round Goby densities reported in some Lake Michigan habitats approach 130 fish/m^2 (Chotkowski and Marsden 1999).

The state of knowledge of these impacts, adaptations and behavioral abilities among invasive Round Goby populations is therefore crucial to our understanding of potential life-cycle vulnerability points; knowledge that can help allocate resources, motivate containment strategies, and implement technologies to deter or arrest range extensions.

The goal of this paper is to focus and present findings on Round Goby life-cycle and behavior-related adaptations from an intensive, global literature review having three objectives:

(1) Describe swimming performance and diurnal behavior of adult round gobies to inform management prospects for potential barrier designs;

(2) Provide a similar review of Round Goby juvenile swimming and diurnal behaviors; and

(3) Describe the types of lacustrine and riverine habitats preferred by juvenile and adult gobies (including their spawning and rearing habitats) to inform which habitats are high-risk for Round Goby transport and colonization..

Methods

Our review was structured to present information on (1) adult Round Goby swimming capabilities and any reported diurnal behaviors or patterns, (2) larval and juvenile swimming behaviors and migration patterns, and (3) the habitat preferences of all life stages. These goals were established in attempts to garner data and information useful to natural resource and engineering managers who approve and/or operate waterway projects where the risk of further Round Goby range extensions is deemed to be high. What types of habitats do round gobies prefer? What types of water velocities can they navigate and overcome? Are there any life history weaknesses that can be exploited to minimize the risk of opening new colonization transport avenues? And are there any diurnal patterns in goby behavior whose knowledge can be used to lower those risks?

We used online commercial databases, literature search tools and colleague contacts to collect and assess information relevant to our objectives. Key search words and phrases were used with prioritization on papers and publications involving Round Goby life history requirements, population dynamics and the unique life history adaptations that have made this species so successful in new environments. However, we focus our review on those results most applicable to the potential reopening and operation of the Menasha Lock on the Lower Fox River in Wisconsin, where deterrence strategies and barriers are now under consideration.

Results

Morphology and Life History Background:

The Round Goby is a prolific, repeat spawner over an extended reproductive season. Research by Jude et al. (1992) suggests that round gobies have the ability to spawn every 18-20 days up to six times per year under favorable reproductive conditions. Thus, potentials exist for production of large numbers of offspring. Males guard the eggs that are typically deposited in nests within a protective cavity. Dr. Lynda Corkum (University of Windsor, Canada) provides a useful summary of Round Goby identification and reproductive traits with a video of Round Goby spawning behavior on her website link: http://web2.uwindsor.ca/courses/biology/corkum/goby/goby.htm

A host of papers provide information on Round Goby size, from pre-hatch egg diameter to adult length and fecundity at reproductive maturity. Several examples are highlighted to provide the reader with perspective on approximate sizes at different life history stages.

Figure 3C (from Hirsch et al. 2016b) depicts the unique shape of Round Goby eggs (described in more detail below) and an adult egg mass (2B).

Hirsch et al. 2016b also studied the resiliency of Round Goby eggs. They found a resistance to physical removal (a 90 mN attachment strength of individual eggs) even if exposed to a rapid water flow of 2.8 m/s for 1 h (and a >95% hatching success after eggs were out of water for 24 h). N (in newtons) is a stress-force value of tensile strength. Round Goby eggs seem to have attachment strengths akin to the byssus threads used by marine mussels for attachment to wave-washed, rocky coastlines (Bell and Gosline 1995).

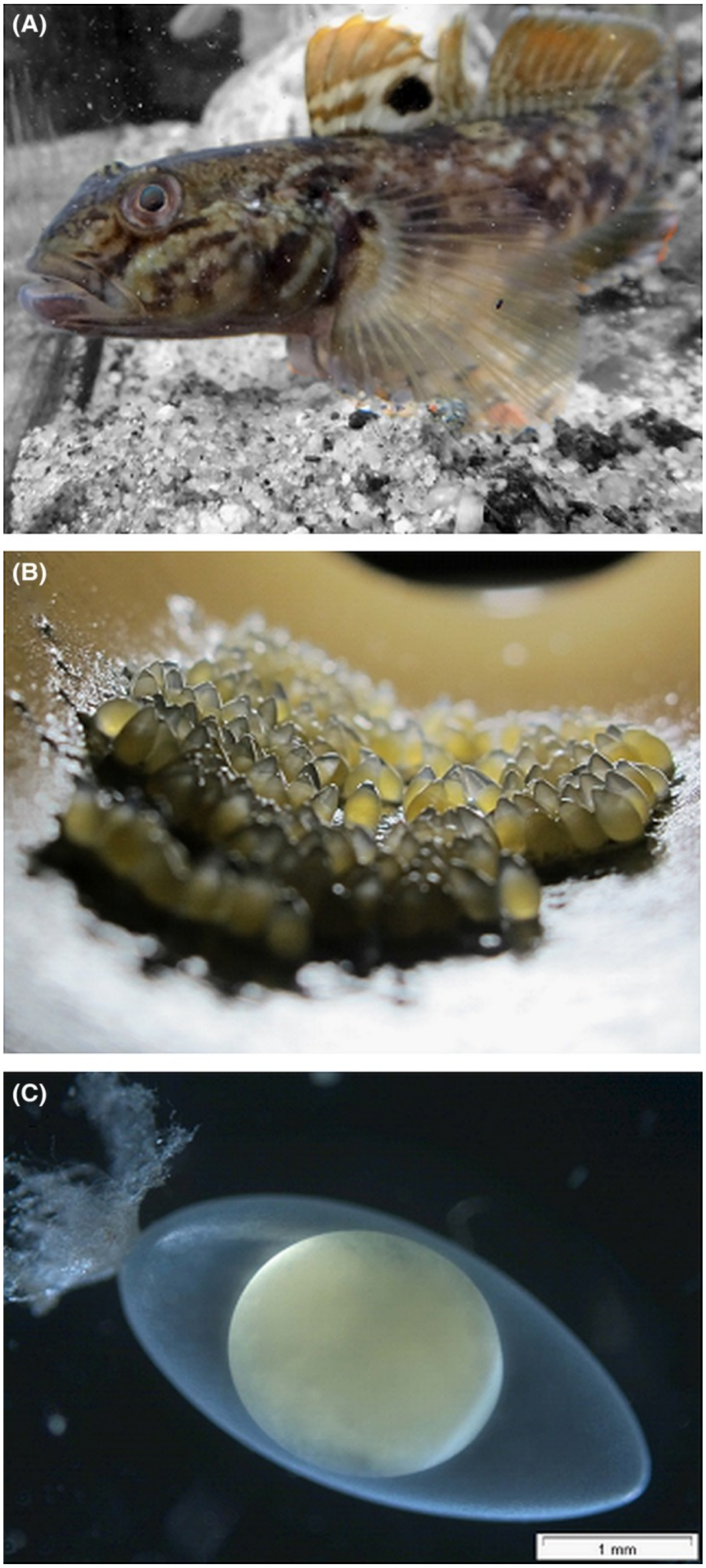

Figure 3 (from Hirsch et al. 2016b). The invasive Round Goby and its adhesive egg mass deposited inside a pipe trap (2B) and showing the adhesive attachment filaments on a single, ellipsoid egg (2C).

In a Round Goby study at a university in Poland, Bonislawska et al. 2014 collected sexually mature fish from an area in the Baltic Sea known as Puck Bay. Males (average length about 15 cm) and females (average length 12.4 cm) were transported to tanks having sand and stone bottoms with water quality conditions (e.g. dissolved oxygen, temperature and salinity) similar to those in capture locations.

The fish collected by Bonislawska et al. spawned naturally in confinement, with newly laid eggs (uncharacteristically ellipsoid or "pear-shaped" in nature) attached to tank substrates. Egg height approximated 2.7 mm and egg width ranged from 1.3 to 1.9 mm. Resulting fry began active feeding 5 days after hatching (average larval length 10.3 mm), when yolk sacs were reabsorbed. After 90 days, mean length was 24.8 mm and mean weight was 0.18 g.

In the Great Lakes region, round gobies spawn from May to October but require a range of water temperatures from 9 to 26 ^{o}C for spawning success (MacInnis and Corkum 2000). Unlike reports from Europe and the findings of Bronnenhuber 2010 (that female Round Goby mature at age 2), MacInnis and Corkum found sexually mature, female round gobies at just 1 year of age in the upper Detroit River. Whereas fecundity appears to be much higher in European round gobies (Bonislawska 2014), MacInnis and Corkhum noted mean fecundities of only 198 eggs per nest, with nests in the upper Detroit River being used more often by more spawning females than in European goby nests. Phillips et al. 2003 also found female round gobies maturing at 1+ years of age in Pennsylvania tributaries to Lake Erie, with fecundities ranging from 86 to 591 eggs. Apparently, males migrate from deeper water to establish spawning areas (dig out nests) in shallow water before females arrive at spawning locations (MacInnis and Corkum 2000).

Round Goby reproduction involves five stages: territory establishment, nest preparation, courtship behavior, spawning, and parental care of the eggs. Male gobies construct the nest (Marsden et al. 1996). European data suggest that males die after spawning (when nest guarding activities are complete), but females can reproduce in subsequent years and more than one female can spawn in a given nest (Sapota 2012). Also, the reported life span of the Round Goby is somewhat short: 3 to 4 years in the Gulf of Gdansk (Sapota 2012) and up to 5 years in the Great Lakes region (Bronnenhuber 2010).

Various physical locations are used for nest construction (each in some form of cavity with a single opening). Using cement gland excretions, nest substrates are coated by the male whereupon females “glue” each egg to the nest cavity’s roof (Marsden et al. 1996). These authors report that nests are generally built under stones, logs or other protective cover where males guard and fan the eggs to promote aeration and reduce fungus. Marsden et al. 1996 cite additional reproduction-related information (unseen) in difficult-to-obtain Russian papers (Logachev and Mordvinov 1979; Moiseyeva 1983; Moskal’kova 1989):

- Round Goby eggs are 3.4 to 3.8 mm in diameter and develop in 14 to 15 days at 19-21 ^{o}C or 18 to 20 days at 17.5-19 ^{o}C under laboratory conditions.
- Round gobies lack a true larval stage (most researchers instead refer to “fry”).
- Fry emerge from eggs at 5.5 to 5.7 mm in length, begin feeding on prey (such as juvenile brine shrimp) within a couple of days of hatching, and are 6 mm in length by day three.
- Newly hatched fry are capable of swimming speeds averaging 2 cm/s. After 3 days, they can swim at speeds of 4.4 cm/s. These data come from Logachev and Mordvinov 1979, as cited by Marsden et al. 1996.

Other difficult-to-obtain publications in Russian (Berg et al. 1949 and Nikolsky 1954, as reviewed and cited in Bonislawska et al. 2014) provide further data on reproductive behaviors. Those Bonislawska-cited sources mention spawning times from April until August for round gobies in Black and Caspian Sea-related habitats. Egg fecundities ranged from 300 to about 6,000 eggs laid in masses in portions (i.e. multiple egg deposits) at water depths from 0.5 to 6 m at 15 to 16 ^{o}C. Hatching occurred within 4 to 7 days as water temperatures rose (but larvae remained attached for several more days to the adult male-guarded nest via their ventral suction discs). Different thermal regimes and water quality conditions undoubtedly contribute to reproductive timing and physical size differences among the varied habitats used by the Round Goby. In research conducted by Kornis et al. 2017, gobies residing in Lake Michigan tributaries grew much faster (122.3 mm at age 2+) versus 65.7 mm for lake-residing gobies at the same age (with tributary fish attaining reproductive maturity in just 1.6 years versus 2.4 years for lake-residing fish). Kornis et al. 2017 suspect that the warmer water temperature profile in their tributary study streams (versus a colder thermal regime in Lake Michigan) was a key driver of the divergent life histories they discovered. But some very important points and management implications can be drawn from studies like the Kornis et al. work:

- Life history divergence is likely when introduced species spread into suboptimal, novel habitats. The more a species spreads, the greater its adaptive requirements.

- This propensity (for local adaptations) also requires a high degree of phenotypic plasticity. Gradual genetic changes (via natural selection) are undoubtedly a reason for what may otherwise appear to be conflicting life history data from various authors evaluating different study sites.

- Also, divergent life histories may be prevalent among invasive species that are now engaged in secondary invasions into connected habitats.

Our review found what is purportedly an incidence of intersex (simultaneous occurrence of both male and female gonadal tissue) among round gobies in Europe (two harbors in Poland). Gonad analysis of two male fish from separate harbors displayed the presence of female gametes in histological examination of testes. However, and as pointed out by the authors (Guellard et al. 2015), these anomalies could be the result of the improper discard of estrogenic endocrine disruptors in harbor waters (compounds known to induce sex-changing influences in other fish species). In fact, Marentette et al. (2010) found similar evidence among male round gobies from Hamilton Harbour, Canada. However, additional concerns (that round gobies have a propensity to concentrate pollutants in their tissues and thus promote ecosystem food-web contamination in apex predators) may be the greater risk.

In Lake Erie, Smallmouth Bass (*Micropterus dolomieu*) males vigorously defend (guard) their nests from the Round Goby’s propensity to prey on eggs of other species. This heightened activity among bass can cause significant declines in their weight and energy (Steinhart et al. 2004). Therefore, increased parental care costs (owing to the presence of round gobies) can affect future growth, reproduction, and survival when Smallmouth Bass approach critically low energy reserves.

From an overall perspective, newly colonized round gobies in the brackish waters and lakes of North America are smaller, mature earlier, have a male biased operational sex ratio and are more short-lived compared with round gobies from Ponto-Caspian native habitats (Corkum et al. 2004).

Our review findings underscore the adaptive nature of this harmful and dangerous invader. Its adaptations include repeat spawning every 18-20 days, portion spawning, hidden nest construction, parental brood care, an unusual egg shape having fast substrate attachment capabilities, a very short embryonic development period coupled with relatively fast, free-swimming independence, and utilization of varied habitats and water qualities. Canadian modeling studies by Brownscombe et al. 2012 reinforce such risks and concerns: their research model predicts a range expansion of 9.3 km/year in high-quality habitats in the Trent-Severn Waterway in Ontario, with a 5% probability that highly mobile round gobies could disperse up to 27 km/year.

<u>Objective 1</u>: Round Goby Swimming Speeds and Patterns (Adults)

In comparison with the numerous papers and publications on occurrence, colonization and life history information, comparatively fewer research studies and reports have been undertaken to assess and quantify the swimming speeds and patterns of round gobies. Two of the best, however, are studies published by Tierney et al. 2011 and Gilbert et al. 2016, using stepped velocity tests where fishes are brought to fatigue through incremental increases in water flow and the speed at fatigue is considered the critical swimming performance (described as U_{crit}; see Gilbert et al. 2016). The U_{crit} test (Brett 1964) was pioneered for research on salmonid swimming performance. In fishes that employ alternate strategies to advance or maintain positions in flowing water, the point of fatigue will relate to water flow speed, but will result from a combination of energy exerted in substrate holding *and* swimming (Gilbert et al. 2016). Fortunately, we are not dealing with various species of Hawaiian gobies (they also use a fused pelvic fin as a suction disc). Hawaiian gobies can gradually “climb” 350-m high waterfalls to reach upstream spawning grounds (Blob et al. 2007)! The fused pelvic fin is a unique adaptation among gobiid fishes that plays a very important role in Round Goby migration and dispersal (Jude et al. 1992).

The Gilbert et al. 2016 Swimming Speed Study:

In swimming performance tests of 23 adult gobies from the upper Detroit River (mean mass 16.9 g and mean total length 11.2 cm), Gilbert et al. 2016 used a modified respirometer comprised of a 1-m square tube with internal dimensions of 10 x 10 cm as their test apparatus. A rear gate made of stainless steel was electrified with low voltage (<5 V) to prevent gobies from resting at the rear of the flume. Fasted adult gobies (no juveniles used) were selected for testing and acclimated to the minimum flow in the test chamber (17.9 cm/s). Fish were brought through stepped increases in flow until they were unable to remain off the electrified rear grid for 5 s. Each step "height" was 7.5 cm/s and each step length was 10 min. Swimming behaviors (holding, "sliding," or swimming) were video-recorded and visually scored. Substrate holding was a primary behavior noticed in this research. The critical substrate holding velocity ($U_{hold)}$ was the last flow speed at which holding accounted for >50% of total goby activity.

In the Gilbert et al. study, the U_{crit} critical swimming performance value (the water speed in which a position can be maintained for a prolonged time period) was measured at 34.8 cm/s. The last flow speed at which round gobies were able to hold the substrate for a majority of the time (U_{hold}) was 28.6 cm/s, with swimming as the primary behavior once fish were unable to hold the substrate. Results suggested that substrate holding ability was largely responsible for test fish to reach U_{crit} but with substantial, individual variation (e.g. some fish reached U_{crit} by using a "burst-and-coast" gait with greater than three bursts per min). In coarse, natural, stream substrates, round gobies may perform better because resting refugia could be used to replenish energy reserves during arduous, upstream dispersal forays.

The Tierney et al. 2011 Swimming Speed Study:

Round Goby swimming behavior was also evaluated by Tierney et al. 2011, who recorded activity in a 2-m flume using "critical swimming" (U_{crit}) and burst tests in both still and flowing water. Similar to the Gilbert et al. work, study fish also came from the Detroit River near Windsor, Ontario and were captured by hook and line and subsequently held for recovery at the University of Windsor for 6 months or more. The authors evaluated 24 female and 23 male fish having an average mass of 15 g and a mean total length of 11 cm. Goby swimming ability was measured and video-recorded in three ways: (1) by chasing (startling) fish in static water to ascertain maximum burst speed, (2) allowing volitional choice by fish to swim upstream or downstream, and (3) by motivating fish to swim in flowing water in a swim tunnel. Minimum flows in the flowing water tunnel trials were set at 17.9 cm/s and incrementally raised to 2x the maximum achieved by each goby tested. Like the Gilbert et al. study, a rear removable gate in the swim tunnel was electrified with low voltage (5 V) to prevent test fish from resting at the rear of the flume. Salient findings from Tierney et al. are as follows:

- Fish chased in still water exhibited average burst swimming speeds of about 1 m/s (97 cm/s) for either sex, corresponding to 9.3 body lengths (BL) per second, with individual speeds ranging from 15 to 162 cm/s (1.7 to 16 BL/s).

- Tests in still water further showed that round gobies (regardless of sex) became fatigued and unresponsive to stimuli in just over 2 min, with successive series of bursts at lower speeds. However, males exhibited 2x the number of bursts seen in female fish and males covered twice the total distance (about 12.2 m) traveled by females (5.7 m) in burst tests (about 110 versus 63 BLs).

- Volitional movement trials showed that gobies chose to move in the test flume under low-flow conditions after a period of some 4 hr. No sex-based movement differences were observed but fish covered considerable ground in the test environment (about 81.3 m, or 722 BL).

- Flowing water trials used the well-known "critical swimming performance" (U_{crit}) test to evaluate Round Goby behavior when forced to swim in a swim tunnel. In these trials, gobies used either a "burst-and-hold" or a "burst-and coast" strategy to deal with velocity. These trials soon became "critical station holding" abilities because all gobies retarded rearward movement by contacting the tunnel's substrate. Burst-and-hold distances averaged 35.5 cm/s (3.2 BL/s) whereas burst-and-coast distances averaged 65.8 cm/s (5.8 BL/s). In either case, behaviors were unrelated to fish sex.

- The majority of test fish spent greater time upstream than in downstream locations but the difference was not statistically significant. Researchers found no significant overall diurnal difference in the number of upstream versus downstream trips made by gobies (day: 36.4; night: 41.4). However, gobies made significantly more short trips at night (in an upstream direction) and were less active during the day (i.e. they exhibited a nocturnal bias).

- Maximum swim speeds of round gobies were unrelated to those that fish could perform when forced (with travel distances similarly unrelated to those observed when fish were forced). Results indicate that **gobies are able to sustain speeds of up to about 38 cm/s (3.4 BL/s) for indeterminate periods but that a marked and steady decrease in swimming duration occurs at swim speeds above 40 cm/s (about 3.6 BL/s).**

The research from Tierney et al. 2011 suggests that round gobies can choose to be very active swimmers, with daylight having only a marginal influence. When coerced, gobies can be formidable swimmers with somewhat powerful burst swimming capabilities and an ability to "hold-station" in fairly strong currents. Round gobies appear to be able to maintain (indefinitely) swim speeds less than 35.5 cm/s. About 18% of the gobies tested by Tierney et al. maintained speeds >75 cm/s for "burst swims" up to a half-minute in duration (suggesting that with a "burst-and-hold" strategy, these fish could navigate flows, through successive attempts, at flows just less than their maximum-burst swimming capabilities). **The authors provide a swimming endurance model indicating that flow rates would need to be >125 cm/s to prevent upstream movement by round gobies in areas that are free of refuge recovery habitat.**

The Hoover et al. 2003 Swimming Speed Study:

An additional paper on goby swimming speeds was reviewed. This comprised some earlier work by Hoover et al. 2003. These authors also examined critical swimming and holding behaviors during water velocity tests to quantify the maximum sustained swimming speed of the Round Goby in a somewhat smaller flume than used by Tierney et al. 2011. Hoover et al. tested 63 males and 34 females (total lengths ranged from 7.2 to 15.4 cm for males and 7.5 to 13.6 cm for females). They reported mean station holding speeds of 20.7, 42.4, and 52.5 cm/s on Plexiglas, sand, and gravel substrates respectively. In all experiments, round gobies spent very little time (<20%) swimming in the water column and preferred to stay on or in close proximity to the bottom substrates that were evaluated.

The Hoover et al. research subjected round gobies to a variety of flow rates from 15 to 75 cm/s, recording time to fish fatigue. Their research noted burst, prolonged, and sustained station holding at speeds from 15 to 20, 20 to 50, and 55 to 75 cm/s, respectively. At 17 ^{o}C, small gobies exhibited sustained station holding at 15 cm/s, prolonged station holding (from 0.5 to 44 min) at 20 to 50 cm/s, and burst station holding at 55 to 75 cm/s. Large gobies exhibited sustained swimming at 20 cm/s, prolonged swimming (0.5 to 72 min) at 20 to 50 cm/s, and burst station holding at 55 to 75 cm/s (larger fish having greater endurance than smaller cohorts). At 20 ^{o}C, small gobies exhibited prolonged station holding (0.5 to 61 min) at 15 to 55 cm/s, with burst station holding behavior at 60 cm/s.

However, and as noted above, 18% of the gobies tested by Tierney et al. 2011 maintained speeds *>75 cm/s* for burst periods as long as a half minute. And in still water, the Tierney et al. data show that 87% of fish maintained a speed >75 cm/s for at least 0.5 s. For Round Goby management and deterrence purposes, the Tierney et al. 2011 data seem to call into question those reported by Hoover et al. 2003 who suggested that flow speeds >75 cm/s would be a sufficient hydraulic barrier for Round Goby containment.

Other Data on Round Goby Swimming Speeds:

MS thesis research by Bronnenhuber 2010 also looked at maximum swimming speeds and station holding endurance for round gobies collected from both lake and river populations (encompassing habitats in or adjacent to Erie, Huron and Ontario Great Lakes). The author described methodology issues with her data and her interpretations for absolute U_{crit} and U_{hold} values (in obtaining data showing swim speeds that were over 100 cm/s and thus double or triple those reported by other researchers). Thus, these data may be questionable. But since the same methodology was used between all sample sites, one result should hold. **Bronnenhuber found no significant differences in maximum swimming speed and station holding endurance capabilities between lake and river fish.** Apparently, river fish were not better swimmers than round gobies from lake populations, as originally hypothesized. Maximum speed and endurances were similar, indicating that the unidirectional, higher flows found in rivers are not strong enough to act as dispersal barriers for round gobies (Bronnenhuber 2010).

Adult Diurnal Behavior:

In regard to potential diurnal behavioral patterns among adult round gobies, Ray and Corkum 2001 found adult fish to be most active on rocky substrates (as opposed to sandy habitats) during daylight hours than at night. Their findings were statistically significant and highly so. The authors concluded that the proclivity for daytime activity was geared towards lowering the risk for predation on adult round gobies. Belanger and Corkum 2003 attached tethers (25-cm monofilament lines) under the dorsal fin of round gobies (mean weight 8.5 g; mean total length 8.6 cm) to evaluate predation in sandy habitats with and without shelters. Results showed that 17 of 120 round gobies were missing from the sand habitats having no shelters whereas only 7 of 120 gobies went missing from the sand habitats *with* shelters. Such findings support the need for refugia and shelters (e.g. rocky cobble, crevices, shipwrecks, etc.) by round gobies to reduce their predation risk in newly colonized habitats.

Management Implications:

The subject of Round Goby swimming capabilities necessitates consideration of at least two key points regarding the findings for adult fish:

(1) The unusual, fused pelvic fin on round gobies (that distinguishes this fish from most other non-gobiid species) can be used as an effective suction disc in high, turbulent flows or while ascending inland rivers (Marsden et al. 1996; Bronnenhuber 2010) and even high waterfalls by some Hawaiian gobiids (Blob et al. 2007). This morphological adaptation allows for the successful “burst-and-hold” behaviors observed by Hoover et al. 2003, Tierney et al. 2011 and others (making water velocity barriers all the more challenging).

(2) Clean smooth substrates can minimize opportunities for adults to rest and recover when attempting to use “burst-and-hold” strategies to ascend upstream areas in rivers. For goby containment and/or deterrence applications, resource managers should consider all options to eliminate coarse cobble and rocky substrates in waterway projects where goby transport and colonization risk must be eliminated or reduced. **Rocky cobble substrates and underwater structures are preferred habitats for invasive round gobies because they offer refugia that promote rest-and-burst or rest-and-coast behaviors.**

Water-velocity barriers are unlikely to halt the spread of this invasive species. However, and if applications such as graduated-field electric barriers are being considered for goby deterrence, it may be possible to include some of the smooth, bedrock-type characteristics explained by Phillips et al. 2003 (see below) to reduce the risk of upstream transport and further range extensions if preferred rocky habitats cannot be removed or altered downstream of a waterway project site. A graduated-field electric barrier successfully blocked downstream Round Goby migrations in a Michigan stream (Savino et al. 2001). Whereas control fish moved repeatedly across a non-electrified barrier within 20 min time periods, movements were blocked when electric gradients up to 4.9 V/cm were applied (and only a single, dead goby was found below the barrier). Electric barriers have been highly successful at deterring various fish movements in many applications (Burger et al. 2015).

<u>Objective 2</u>: Round Goby Post-Hatch Behavior and Movements (Fry)

The offspring of round gobies typify a pattern of ontogeny and development common among livebearers and nest guarders: direct development. That is, the young emerge functionally and morphologically similar to adults and thus, lack a true larval stage (Marsden et al. 1996). For this reason, and as mentioned previously, newly emerged round gobies greater than about 6 mm in length (attained within a few days after hatching) are referred to as fry.

The embryonic development of the Round Goby is described by Bonislawska et al. 2014 (egg size and morphology information was previously presented, above). Newly hatched fry are about 5 mm in length. Yolk sac reabsorption is fairly rapid and occurs within 5 to 7 days, when the fry commence feeding on zooplankton (larger sizes of zooplankters are consumed through day 30).

Initial swimming speeds of newly hatched, 5.5 mm fry (2 cm/s) were reported above, as were the swimming speeds of 6-mm fry 3 days after hatching (4.4 cm/s). Those unseen data come from Logachev and Mordvinov 1979 (as cited in Marsden et al. 1996). Additional published data on the behavior and movements of Round Goby juveniles were limited

Diel Periodicity and Vertical Migrations of Newly Hatched Fry:

Earlier in our review, round gobies seem to be active during daylight hours when they avoid sand-laden substrates (Ray and Corkum 2001). A study by Hensler and Jude 2007 found quite the opposite when they sampled Round Goby fry in the Muskegon Harbor channel leading to Lake Michigan and at subsequent sites in Lake Michigan and Lake Erie. Collections relied on ichthyoplankton net tows at all sites from June through August, where catches resulted in Round Goby fry that were 7 to 8 mm in length (98% of fish sampled).

The most interesting part of the Hensler and Jude report is that Round Goby fry were most prevalent during nighttime collections at the water surface (with virtually no goby fry found during daytime tows and none longer than 8.9 mm in the surface nighttime collections).

These results constitute a very significant diel difference between nighttime and daylight plankton tow collections. The authors note that surface sampling sites were located some 2 km from known spawning habitat. **Hensler and Jude thus hypothesize that this finding (fry collections in surface areas remote from spawning habitat and only at night) is evidence for a diel vertical migration pattern** — which may be a Round Goby dispersal strategy for a species that lacks a swim bladder. The implication is that this negatively buoyant species may be employing a diel surface migration strategy for optimally sized fry (those 6.5 to 8.9 mm in length) to find and use surface currents for dispersal to new habitats. This unique behavioral adaptation may explain how round gobies found a way to North America (i.e. in nighttime ballast water extractions in estuaries by ocean-going vessels).

Results from Hensler and Jude 2007 are a somewhat surprising find, but not necessarily unique among gobiid fishes. Schultz et al. 2003 found a similar behavioral pattern for a cousin to the Round Goby, the Naked Goby (*Gobiosoma bosc*) in the Hudson River estuary, New York. Using plankton trawls, Schultz et al. also caught goby fry (having a mean length of 5.8 mm) in nearshore surface areas at night, particularly during neap tides. Their conclusion for this diel periodicity result was the promotion of transport for Naked Goby fry.

Management Implications:

The research we reviewed on vertical migrations and diel periodicity of newly emerged Round Goby fry has potential implications for managers concerned about goby transport risks at waterway structures. The science provided by Hensler and Jude 2007 (with support from Schultz et al. 2003 for a related gobiid fish) strongly suggests that larval gobies are only in the water column at night and utilize a nocturnal dispersal strategy where surface water currents and wind promote range expansion, similar to the strategies used by some marine species. Upstream water flows are not likely at Menasha Lock and lock openings for boat transport would occur only during daytime. Coupled with known larval swimming capabilities (<5 cm/s) and assuming that discharges from the lock when it is operated will typically exceed 5 cm/s, it is unlikely that Round Goby fry could ever navigate upstream during lock openings. If lock openings occur only during daytime hours, the risk of any upstream larval transport is thus precluded, and management should instead direct its focus on the deterrence of upstream-moving, adult round gobies (a very achievable goal based on the electric barrier results obtained by Savino et al. 2001).

<u>Objective 3</u>: River and Lacustrine Habitats Favored by the Round Goby

The Round Goby is a bottom-dwelling fish that prefers rock/gravel substrates with interstitial spaces for both escape cover and for spawning in littoral areas of lakes and rivers (Hirsch 1998). Gobies also prefer human-made riprap, breakwaters, and rocky or coarse-gravel inshore areas with abundant escape cover. In the Gulf of Gdansk, preferred habitats of round gobies include sandy, stony bottoms, mussel beds, areas near marina-type structures (piers, wharves, etc.) and even muddy, humus-containing bottoms overgrown with marine flora where they reside with restricted movements (Sapota 2012). In the Trent River near Lake Ontario, Gutowsky and Fox 2011 sampled 607 round gobies from upstream and downstream colonization sites. The predominant habitats selected by round gobies constituted rock and gravel (over 90% of fish found in these habitats) as opposed to sites principally composed of sand or macrophyte vegetation.

In regard to habitats used for reproduction, all solid elements of an estuary, lake or river bottom can be used as a foundation for round goby nests including stones, rocks, parts of wood, roots of vascular plants, and even dumped waste (Sapota 2012). In contrast to European findings, **round gobies in streams such as the St. Clair River (a Great Lakes tributary and site of the first invasion colonization in North America) occur in habitats that offer cover. These include cobble substrates to 3 m depth (Jude et al. 1992), riprap, and vegetation in nearshore areas where substrates offer large interstices for refuge and spawning** (Jude and Deboe 1996; Ray and Corkum 2001). Round Goby catches are generally lower in wetland macrohabitats than in adjacent lake macrohabitats where gobies seem to prefer areas dominated by submersed aquatic vegetation (Cooper et al. 2007). Round gobies are also known to visit sandy habitats near beaches at night. This is especially true of juveniles in search of zooplankton and other small macrophytic-based prey items whereas adults are less abundant on sand substrates (Jude et al. 1992; Jude and Deboe 1996).

Round gobies may migrate to deeper water in winter (Miller 1986; as cited in Hirsch 1998). Their diet consists of micro- and macroinvertebrates including amphipods, polychaetes, chironomids, cladocerans, bivalve mollusks, and occasionally other small fish and fish eggs (Jude et al. 1992). **The Round Goby prefers shallow waters up to 3 m and they avoid surf zones** (Kornis et al. 2012). They are generally sedentary, with home ranges estimated at just 5 to 6 m or so, however there is evidence (see below) that some gobies are capable of fairly long-distance movements up to a couple km (Wolfe and Marsden 1998; Ray and Corkum 2001). Commercial shipping, however, is the main culprit that influences in-lake dispersal (Kornis et al. 2012).

Phillips et al. 2003 examined Round Goby habitat use in three tributaries to Lake Erie in Pennsylvania. Habitat preferences were similar in each of the three streams (rocky areas having moderate streamflow). An important observation was made. **Smooth, shallow bedrock areas in upstream portions of these streams were not used,** presumably because they contain fewer ledges and crevices than found in deeper, more open stream areas. Thus, shallow bedrock areas appear to act as barriers to colonization and further upstream movement by round gobies.

Additional research on habitats used by round gobies have noted their ability to perch on rocks and other substrates in shallow areas, yet flourish in a variety of habitat types that may include open sandy areas where favorite prey items (aquatic macrophytes) are abundant (Jude and DeBoe 1996; Clapp et al. 2001). This goby also has a well-developed sensory system that enhances its ability to detect water movement. This allows round gobies to feed in complete darkness, providing an advantage over other fish species in the same habitat (Wisconsin Sea Grant 2008).

In a mark-recapture study of Round Goby in three Great Lakes tributaries, Ray and Corkum 2001 estimated fish densities, site fidelity and habitat preferences over time. Perhaps not surprisingly, mean goby densities were highest in their St. Clair River site (the original area of Round Goby colonization in North America), with lower densities of small gobies (≤ 5 cm) at their Detroit River site near Peche Island (an area most recently colonized by round gobies). However, the fairly high percentage (58%) of round gobies recaptured at or near study-site release locations (Ray and Corkum 2001) indicated a strong tendency for site fidelity (for both males and females) in rock-substrate habitats as opposed to sandy habitats, with adults most active during the day than at night (likely an adaptation to avoid predation).

Wolfe and Marsden 1998 found similar site fidelity in a tagging study of 308 round gobies they conducted in Lake Michigan. With the exception of a single fish caught by an angler 2 km from its release site, Wolfe and Marsden observed all tagged-fish recaptures within 67 m of the tagging site. As for habitat preferences, Ray and Corkum 2001 found round gobies to be more abundant in rock than in sand habitats, with younger age classes more prevalent during daytime than at night (suggesting that large-sized gobies were in refugia during daylight). Although gobies were somewhat common in sand substrates in the Ray and Corkum study, they suggest that habitat complexity at rock substrates likely corresponds to an increase in refuges (accounting for the higher densities found in rocky substrates). Because juveniles seem to be more prevalent in sandy substrates, the authors hypothesized that adults may displace juveniles into sub-optimal habitats.

Discrepancies and apparent data conflicts were found among the reports of habitat preferences cited by various authors included in our review. Such differences may be reflective of local adaptations by different populations to specific habitats. However, and as noted by others (Gutowsky and Fox 2012, Kornis et al. 2012, Thompson and Simon 2015), the Round Goby exhibits high intraspecific variations in age and growth (local adaptations) that are related to site specificity and factors such as density, food, predation, competition and water quality.

Management Implications: The Round Goby shares several life-history characteristics present in successful invasive species colonizers: a tolerance for a wide range of environmental conditions, a broad diet, aggressive behavior, high fecundity, repeat spawning capabilities within a season, cavity nesting for egg protection, nest guarding by males, and a fairly large body size compared to species having a similar benthic lifestyle. These attributes have allowed the Round Goby to quickly establish populations in all of the Great Lakes and many of their tributaries. They pose a bona fide challenge for invasive species management.

The localized site fidelity of the Round Goby coupled with its preference for rocky, cobble substrates and underwater structures indicate that transport and colonization risks can be reduced or eliminated when these habitats are unavailable. Because smooth, bedrock-type areas were found to act as a barrier to Round Goby colonization and upstream range extension in one Lake Erie study, the addition of such streambed modifications (replica structures) could serve to minimize goby presence downstream of waterway projects. Such efforts may be costly and may present streambed engineering challenges. However, if technologies such as electric fish barriers are considered for Round Goby deterrence at Menasha Lock and other Fox River areas, these barriers should be effective deterrents and it may be possible to include design modifications that discourage goby presence.

In summary, the likelihood that discharges from Menasha Lock will naturally exceed the poor swimming abilities of larval round gobies, the strong preference of larval gobies to remain at the bottom of the channel during daylight hours when the lock is operational, and the preference of larval gobies to rise in the water column at night when there is no upstream current and the lock is not operational should all act synergistically and counter to any argument in support of juvenile transport at the lock. If an electric barrier is designed having the characteristics described in Savino et al. 2001, upstream movement by adult Round Goby is also precluded.

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