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Divergent life histories of invasive round gobies (*Neogobius melanostomus*) in Lake Michigan and its tributaries

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Abstract

Round gobies (*Neogobius melanostomus*) have invaded benthic habitats of the Laurentian Great Lakes and connected tributary streams. Although connected, these two systems generally differ in temperature (Great Lakes are typically colder), food availability (*Dreissenid* mussels are more prevalent in Great Lakes), and system size and openness. Here, we compare round goby life histories from inshore Lake Michigan and adjacent tributary systems—an uncommon case study of life-history differences between connected systems. Tributary round gobies grew much faster (average length-at-age of 122.3 vs. 65.7 mm for Age 2+ round gobies), appeared to have shorter life spans (maximum observed age of 2 vs. 5) and had lower age-at-50% maturity (1.6 vs. 2.4 years; females only) compared to gobies from Lake Michigan. In addition, tributary gobies had greater fecundity at Ages 1–2 than lake gobies, but had fewer eggs for a given body size prior to the first spawning event of the summer. We were not able to determine the cause of the observed life-history differences. Nonetheless, the observed differences in growth, maturation and longevity were consistent with known effects of water temperature, as well as predictions of life-history theory for animals at invasion fronts exposed to novel environmental conditions. The high degree of phenotypic plasticity in connected populations of this invasive species has implications for our understanding of invasive species impacts in different habitats.

KEYWORDS

invasive species, life history, Laurentian Great Lakes, Lake Michigan, environmental characteristics, round goby

1 | INTRODUCTION

There is widespread interest in understanding and predicting invasive species spread and impact as part of a broader goal of invasive species risk assessment (Lodge et al., 2006). Abundance and impact of invasive species have substantial spatial variability, making risk assessment challenging (Hansen et al., 2013; Latzka, Hansen, Kornis, & Vander Zanden, 2016). One approach has been to evaluate the match between environmental conditions and species habitat requirements (Thuiller et al., 2005). Other studies have used life-history characteristics to predict the identity of future invasive species in specific locales such as the Laurentian Great Lakes (Kolar & Lodge, 2002; Ricciardi & Rasmussen, 1998).

When introduced into a new region, successful invasive species often spread rapidly and inhabit a wide range of habitats and conditions (Lodge et al., 2006). In addition, environmental niches frequently differ between the native and invasive ranges (Broennimann et al., 2007). It has been argued that invasive species exhibit a high degree

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of phenotypic plasticity—the ability of a genotype to produce different phenotypes in different environments—compared to their native counterparts (Agrawal, 2001; Daehler, 2003; Davidson, Jennions, & Nicotra, 2011). Phenotypic plasticity would be expected to promote invasiveness by allowing adaptation to a broader range of environmental conditions (Davidson et al., 2011). As a result, successful invaders often display diversity in life-history characteristics, as shown in birds (Lockwood, 1999), plants (Daehler, 1998) and fish (Alcaraz & García-Berthou, 2007; Fox, Vila-Gispert, & Copp, 2007). Yet, relatively, few studies have examined variation in life-history traits among connected populations of aquatic invasive species (but see Bøhn, Terje, Amundsen, & Primicerio, 2004 and Masson, Brownscombe, & Fox, 2016). The Laurentian Great Lakes, home to over 180 introduced species and counting (Ricciardi, 2006), and their connected tributaries provide an opportunity for such study.

Round gobies (*Neogobius melanostomus*), small benthic fish native to the Black and Caspian Seas, are prevalent in both the Great Lakes and their tributaries, as well as the Baltic Sea and several European rivers (Kornis, Mercado-Silva, & Vander Zanden, 2012). In North America, round gobies initially invaded inshore benthic habitats of the Laurentian Great Lakes (Charlebois et al., 1997) where they reached high abundances and strongly impacted local fish (Janssen & Jude, 2001; Kornis et al., 2012; Lauer, Allen, & McComish, 2004) and invertebrate (Lederer, Janssen, Reed, & Wolf, 2008) communities. Round gobies also colonised large river systems such as the Illinois River (Irons, McClelland, & Pegg, 2006) and many small Great Lakes tributaries (Campbell & Tiegs, 2012; Kornis & Vander Zanden, 2010; Poos, Dextrase, Schwalb, & Ackerman, 2010). These diverse ecosystems invaded by round gobies differ with regard to water temperature, forage base, habitat and other attributes. In the Laurentian Great Lakes, round gobies typically experience cooler annual water temperatures than in tributaries but are surrounded by *Dreissenid* mussels, a favoured food item for adults (Johnson, Bunnell, & Knight, 2005; Kornis et al., 2012; Walsh, Dittman, & O'Gorman, 2007). By contrast, round gobies forage on a wide assortment of benthic invertebrates in tributaries (Kornis et al., 2012), which are typically absent of *Dreissenid* mussels, and are also exposed to different environmental characteristics including warmer summer water temperature and flowing water. Several populations of tributary round gobies have been reported to reach lower densities than their Great Lakes counterparts, resulting in more subtle effects on local aquatic communities (Kornis, Sharma, & Vander Zanden, 2013).

In the light of these environmental differences, we sought to describe round goby life-history attributes in Lake Michigan and connected tributaries. To do this, we present empirical estimates of length-at-age, longevity, maturation age and fecundity of round gobies from two tributaries and from Lake Michigan itself. Our objective was to describe phenotypic variability among populations of a harmful invasive species inhabiting considerably different ecosystems. Understanding system-specific differences in round goby life history may provide insight into why the abundance and ecological role of this invasive species varies among habitats.

2 | MATERIALS AND METHODS

2.1 | Fish collection

We made every attempt to collect fish from tributary and Lake Michigan sites not likely influenced by one another. Round gobies were collected from two tributary sites (Kewaunee River, WI, USA, at 44.462577, −87.558976, and West Twin River, WI, USA, at 44.175897, −87.650124) and one Lake Michigan site not likely influenced by any major tributary (Bailey's Harbor, WI, USA, at 45.062616, −87.121367, approximately 60 km from the mouth of the Ahnapee River, the nearest tributary with a drainage area >65 km^2; Fig. 1). Both tributary sites were shallow (1-m maximum depth), cobble rich and upstream of the confluence with Lake Michigan (11.4 and 9.6 river km for the Kewaunee and West Twin sites, respectively) such that round gobies were unlikely to have spent any time in lake conditions. Round gobies likely overwintered at both tributary sites based on their abundance during ice break-up (15 March 2011, considered late winter in the study area). The Lake Michigan site was located approximately 200-m offshore at 3–8-m depth. Fish collected at these three primary sites were used in all analyses (Table 1). To supplement

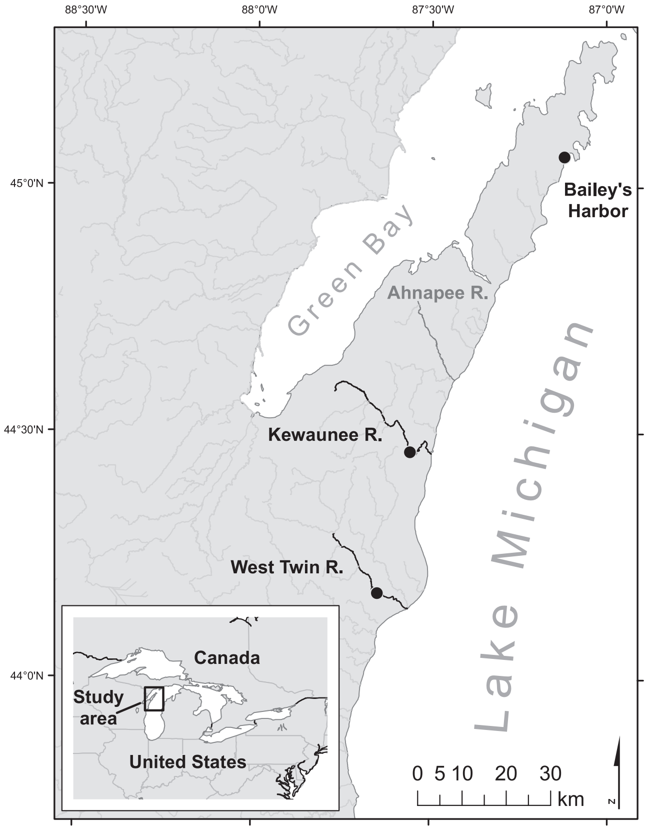

FIGURE 1 Map of the study area. The three primary sample sites are shown with black circles. Two auxiliary Lake Michigan sites located outside of break walls near the mouths of the West Twin and Kewaunee Rivers were used to supplement the fecundity analysis. No fish were collected from the Ahnapee River; it is shown for reference as the closest major tributary (drainage area > 65 km^2) to the Bailey's Harbor Lake Michigan site

TABLE 1 Sample sizes and size ranges of round gobies collected at various study sites. The range and average of round goby total length, as well as the sample size, are provided for fish collected in each sample event. The "overall" column reflects all round gobies captured during a given event, whereas the "length at age" and "fecundity" columns reflect the fish selected for use in those analyses

Site	Date	Length at age	Fecundity	Overall
Bailey's Harbor	26 August 2010	47–175 mm Average = 89.8 mm *n* = 23		42–175 mm Average = 81.4 mm *n* = 103
	11 May 2011		67–150 mm Average = 96.1 mm *n* = 28 mature *n* = 0 immature	62–167 mm Average = 95.0 mm *n* = 48
West Twin River	18 April 2010	51–111 mm Average = 73.2 mm *n* = 18	70–105 mm Average = 84.1 mm *n* = 13 mature *n* = 2 immature	34–111 mm Average = 61.8 mm *n* = 90
	14 July 2010	112–136 mm Average = 122.4 mm *n* = 5		23–139 mm Average = 79.5 *n* = 133
Kewaunee River	19 April 2010	56–105 mm Average = 77.8 mm *n* = 16	68–101 mm Average = 84.8 mm *n* = 21 mature *n* = 5 immature	56–105 mm Average = 79.6 mm *n* = 34
	14 July 2010	111–135 mm Average 122.2 mm *n* = 5		50–135 mm Average 83.6 mm *n* = 205
L. Michigan Kewaunee break wall	19 April 2010	n/a	102–104 mm Average = 103 mm *n* = 2 mature *n* = 0 immature	73–155 mm Average = 98.5 mm *n* = 10
L. Michigan Two Rivers break wall	18 April 2010	n/a	80–105 mm Average = 89 mm *n* = 9 mature *n* = 8 immature	39–145 mm Average = 83.0 *n* = 26

the fecundity analysis, additional round gobies were collected from two Lake Michigan sites located outside of break walls at Kewaunee (44.458176, −87.497579) and Two Rivers (44.143291, −87.563149), WI, USA, near the mouths of the Kewaunee and West Twin Rivers (Table 1). Finally, large sample sizes of measured fish (*n* = 103, 133, and 205) were recorded from the three primary sites during summer 2010 during a related study (Kornis et al., 2013). These collections enabled a comparison of length–frequency distributions of round gobies from the three main sites. Length–frequency distributions were compared using kernel density estimation to plot probability densities of round goby length from each site ("stats" package in R, version 3.1.1).

Two collection methods were utilised to cover a range of habitats and maximise the range of specimen lengths. Gee-style cylindrical minnow traps were set overnight at all sites and baited with liver contained in sealed, punctured plastic canisters to allow scent to escape while preventing consumption of the bait. A battery-powered backpack electrofishing unit with pulsed DC current was also used where possible (all sites except Bailey's Harbor, Lake Michigan) because it selected for smaller individuals than minnow traps. All specimens were immediately placed on ice and placed in a −20°C freezer upon return to the laboratory.

2.2 | Length-at-age analysis

Round gobies used in the length-at-age analysis were collected from Bailey's Harbor, Lake Michigan on 26 August 2010 (*n* = 23 gobies), and from the two tributary sites on 18–19 April (*n* = 34 gobies) and 14 July 2010 (*n* = 10 gobies). Collected gobies were subsampled from a larger number collected on each sampling date, deliberately taken to represent the size distribution of the broader population (Table 1). The five fish collected from each of the two river sites on 14 July of 2010 were an exception—larger fish were targeted in an attempt to capture age 3 or older fish, which were not found during the main collections in April. Ages were estimated from whole sagittal otoliths extracted from at least four fish in each of four size classes from each site (<60 mm, 60–85 mm, 86–110 mm, and >110 mm). Five recently hatched round gobies (8–14.5-mm total length) were captured in Sunset Bay, Lake Ontario, using a 400-µm Wisconsin-style plankton net in June and July 2010 to help estimate length at hatching for all sites. Whole-mounted sagittal otoliths have been previously used to estimate age from round gobies (Gümüs & Kurt, 2009) and are considered a reliable structure for age estimation on fish that have <6 visible annuli (Maceina & Sammons, 2006). See Appendix A for additional details on otolith processing.

Total lengths back-calculated to annulus formation were used to assess round goby length at age. This method accounts for differences in size resulting from sampling tributary (April; July) and lake sites (August) at different times of year, as annulus formation likely occurs at a similar time at all sites (Gümüs & Kurt, 2009; MacInnis & Corkum, 2000a). Capture lengths of tributary fish from April were also included in the length-at-age analysis, as these fish were interpreted to be in the early stages of annulus formation (Appendix A). This is consistent with studies showing that annulus formation in round gobies occurs between April and late May/early June (Gümüs & Kurt, 2009; Kostyuchenko, 1961; MacInnis & Corkum, 2000a). Length at age was back-calculated using the relationship between fish total length and otolith area, determined through linear regression (e.g. equation 2 in Morita & Matsuishi, 2001; see Appendix B for regression results). A polygon tool (ImagePro Plus) was used to assess area at the otolith edge and each annulus. We established different otolith area/fish length relationships for lake and tributary sites because such relationships are growth dependent (Appendix B). R^2 was ≥.96 for both otolith area/fish length regressions, substantiating our assumption of that fish and otolith growth were proportional. Sagittal otoliths from recently hatched round gobies (Sunset Bay, Lake Ontario) were used to help estimate the intercepts of both otolith area/fish length relationships.

Analysis of covariance (ANCOVA, Proc GLM Procedure, SAS version 9.2.) was used to assess differences in back-calculated length at age between lake and tributary sites. The ANCOVA was interpreted using type I sum of squares because we were testing for the effect of a predictor (system, i.e. lake or tributary) beyond the effects of a known covariate (age). We also included a site-nested-in-system term to assess whether back-calculated length at age varied within tributary sites (i.e. Kewaunee River and West Twin River). Although male round gobies generally have greater length at age than females (Kornis et al., 2012), site-specific ANCOVA models treating sex as a grouping factor and age as a covariate found no significant effect of sex on length at age (p ranged from .26–.58). We therefore pooled male and female gobies together for this analysis, but plotted gobies by sex for consistency with prior studies. Von Bertalanffy growth functions were not fit to length-at-age data because length was linearly related to age for round gobies from both systems.

2.3 | Fecundity and maturity analyses

As round gobies spawn multiple times a year (Charlebois et al., 1997), all sites used in the fecundity analysis were sampled during early spring to precede the first spawning event. Sampling just prior to spawning also minimised the potential for counting eggs that might later be reabsorbed. Round gobies were collected from the two tributary sites and the two Lake Michigan break wall sites during 18–19 April 2010, and from the Bailey's Harbor Lake Michigan site on 11 May 2011. All collected mature females were analysed for fecundity. As a result, fish used in the fecundity analysis typically had a larger mean length than that of the overall population (Table 1), because the overall population included immature fish of smaller length.

Female round goby gonadosomatic index (GSI) did not differ between April 2010 and May 2011 in an ANCOVA model in which total length was a covariate ($F_{1,72} = .13$, $p = .72$ for the month term). Therefore, lake and tributary round gobies used in the fecundity analysis were in comparable prespawn condition. We followed the methods of MacInnis and Corkum (2000a) by placing ovaries from female round gobies in modified Gilson's fluid (Kelso & Rutherford, 1996), an egg fixative that hardens oocytes, for a minimum of 1 week with daily agitation to facilitate breakdown of the ovarian tissue. Oocytes were then rinsed in distilled water, and all ripe oocytes were enumerated. The fixative only hardens eggs that have begun to accumulate yolk (MacInnis & Corkum, 2000a), facilitating the ability to identify ripe oocytes. An ANCOVA was used to assess differences in fecundity between mature lake and tributary round gobies, with system (lake vs. tributary) as the grouping factor and total length as the covariate. The interaction between system and total length was also included to determine whether slopes were significantly different. As with the length-at-age analysis, we also included a site-nested-in-system term to assess whether round goby fecundity varied within tributary sites (i.e. Kewaunee River and West Twin River) and Lake Michigan sites (i.e. Bailey's Harbor, Kewaunee break wall and Two Rivers break wall). As above, the ANCOVA was interpreted using type I sum of squares to determine whether system had an effect on fecundity beyond the effect of length.

Age was not estimated from otoliths for many of the fish included in the fecundity analysis. However, we were able to estimate the age of fish included in the fecundity analysis using the system-specific length-at-age regressions described in the results. This allowed us to examine fecundity at age for lake and tributary round gobies. Maturity-at-age analysis was also possible because a small number of immature fish were collected from each system during the sampling events of 18–19 April 2010 (n = 8 and 7 from Lake Michigan and the tributaries, respectively; Table 1). We included both immature females (small ovaries containing no ripe oocytes) and immature round gobies of unknown sex (fish so young that gonads could not be identified as male or female). Sigmoidal functions were used to model the probability of maturity against estimated age, and to estimate the age at which 50% of females were mature, following methods used by several others (e.g. Madenjian, DeSorcie, & Stedman, 1998; Neuheimer & Grønkjær, 2012).

2.4 | Water temperature

Water temperature was recorded in both tributaries and in Lake Michigan to help interpret the results. Water temperature at the tributary sites (Kewaunee and West Twin Rivers) was recorded every two hours from 24 May through 28 October 2010 using Onset Optic StowAway temperature loggers (two per site). Mean difference between the two loggers at each site was 0.09°C, demonstrating low intrasite variability in water temperature. Temperature loggers deployed at the lake sites could not be located. Thus, we instead approximated water temperature at our lake sites using data from the Wisconsin Department of Natural Resources' Kewaunee continuous water quality monitoring station. This temperature probe is approximately 2-km offshore and 0.5 m off the bottom in 8.5 m of water and recorded data from 19 April through 29 September 2010 using a YSI 6600 thermistor. Although we did not sample this far offshore, round gobies are commonly found near bottom at this water depth and were sampled from 3–8-m water depth at our primary Lake Michigan site (Bailey's Harbor). Moreover, water at the Kewaunee monitoring station generally does not stratify and is considered part of the coastal zone (personal communication, Steven Greb, Wisconsin DNR) and thus should reasonably approximate water temperatures experienced by round gobies in our study.

3 | RESULTS

Round gobies from the two tributaries grew much faster than Lake Michigan gobies. A significant effect of system ($F_{1,100} = 97.2$, $p < .0001$) indicated greater length at age in tributaries, while a significant system × age interaction ($F_{1,100} = 23.7$, $p < .0001$) indicated different regression slopes (35.2 vs. 24.6 for tributary vs. lake sites, respectively; Fig. 2). Back-calculated length at age did not differ within the tributary sites (site-nested-in-system term, $F_{1,100} = .5$, $p = .47$). Back-calculated length was comparable for tributary gobies at age 2 (85.2 ± 11.9 mm [s.d.]) and lake gobies at age 3 (86.9 ± 9.7 mm). Tributary round gobies also showed rapid growth during their second year, with age 2 + gobies captured during July having an average capture length of 122.3 ± 9.7 mm, nearly double the capture length of age 2 + gobies taken from Lake Michigan in August (65.7 ± 9.3 mm) and comparable to the average capture length of age 4 + Lake Michigan gobies (124.4 ± 12.8 mm). Mean back-calculated length at age 2 for the July tributary fish (85.3 ± 10.2 mm) was comparable to mean capture length of age 2 tributary fish sampled in April (84.3 ± 14.9 mm), indicating the July fish were representative of growth between April and July for age 2 tributary round gobies.

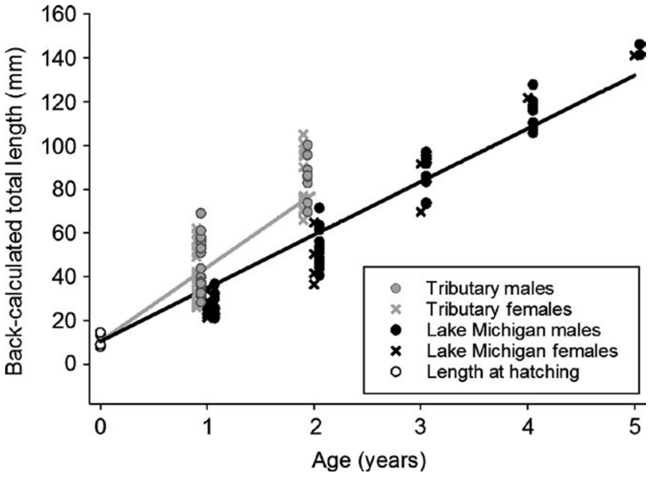

FIGURE 2 Round goby back-calculated total length at age for Lake Michigan (black symbols) and two tributaries (grey symbols). Round gobies were collected from tributaries (Kewaunee and West Twin Rivers; pooled in figure) on 18–19 April and 14 July 2010, and from Lake Michigan (Bailey's Harbor) on 26 August 2010. Males (circles) and females (*x*'s) are plotted separately, but sexes were pooled for analysis as sex did not have a significant effect on growth. All ages are in whole years (e.g. age 1, age 2), but data points are staggered by system and sex to show differences in areas of overlap. Length at capture was included for river fish captured on 18–19 April, as these fish were interpreted to be in the early stages of annulus formation. Both lines were fitted to a *y*-intercept of 10.6 mm based on the average length of five recently hatched round gobies collected from a Lake Ontario plankton tow on 13 July 2010 (open circles). $R^2 = .76$ and slope = 35.2 for the tributary regression, and $R^2 = .92$ and slope = 24.6 for the Lake Michigan regression

Despite differences in round goby growth, length distributions were comparable between lake and tributary sites (Fig. 3). Bailey's Harbor round gobies had a slightly wider length distribution (i.e. more fish at both small and large extremes), but overall, the length distributions were comparable for all three populations during summer 2010 (Fig. 3; note that collection dates were 6 weeks apart). With the exception of one Lake Michigan fish measuring 175-mm total length, all fish captured at both sites were ≤143 mm.

Longevity appeared to differ between lake and tributary sites, with sampled round gobies reaching age 5 in Lake Michigan but only age 2 in tributaries (Fig. 2). Tributary round gobies also had higher variability in back-calculated length at both age 1 (range of 26–62 mm) and age 2 (66–105 mm) than lake round gobies (21–37 mm and 37–71 mm). This difference could be related to the multiple spawning behaviour of round gobies if, for example, spawning in tributaries occurs over a longer period of time than in Lake Michigan, or if there are lake/tributary differences in survival of round gobies across different spawning dates.

Lake Michigan round gobies had higher fecundity at a given length compared to tributaries when comparing similar-sized fish (total length ≤110 mm; Fig. 4a). Slopes were approximately parallel for lake and tributary gobies ($F_{1,59} = .05$, $p = .83$ for total length × system interaction term testing for difference in slope). Intercepts were significantly different ($F_{1,59} = 4.3$, $p = .04$), indicating greater fecundity at length in Lake Michigan round gobies prior to the first spawning event. There was no significant effect of site nested in system ($F_{3,59} = 2.1$, $p = .12$), although a larger sample size may have detected a site-specific fecundity effect.

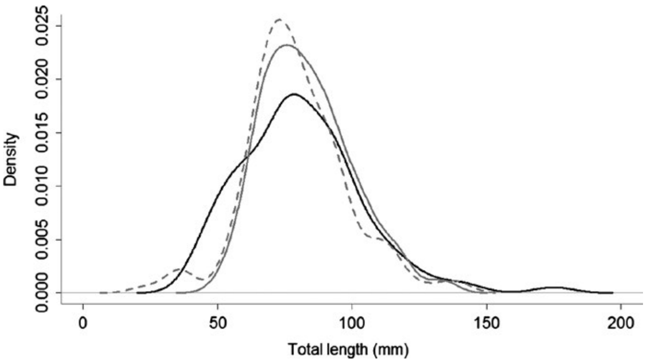

FIGURE 3 Probability density plots of round goby length distributions from Bailey's Harbor (solid black, *n* = 103), Kewaunee River (solid grey, *n* = 205) and West Twin River (dashed grey, *n* = 133). Round goby total length was measured on 14 July 2010 for the two river sites and 26 August 2010 from the Bailey's Harbor Lake Michigan sites. A subset of fish was retained for length-at-age analysis from these and other dates (Table 1). Fecundity analyses occurred on fish collected from these sites on other dates (Table 1). Kernel density estimation was used to plot probability densities of round goby length from each site

Although Lake Michigan round gobies had greater fecundity at length, tributary round gobies had higher fecundity at ages 1 and 2 (Fig. 4b), while Lake Michigan round gobies had greater maximum fecundity by virtue of greater longevity (i.e. fecundity of Lake Michigan females at ages 4 and above were greater than fecundity of even the oldest observed tributary female; Fig. 4b). Across all ages and sizes, the relationship between length and egg number appeared to be curvilinear for Lake Michigan round gobies (Fig. 4b; $R^2 = .83$ vs. .90 for linear and quadratic models, respectively). Female round gobies also matured at earlier ages in the tributaries (Fig. 4c). We estimated 50% of tributary females were mature at 1.6 years versus 2.4 years for Lake Michigan females (Fig. 4c).

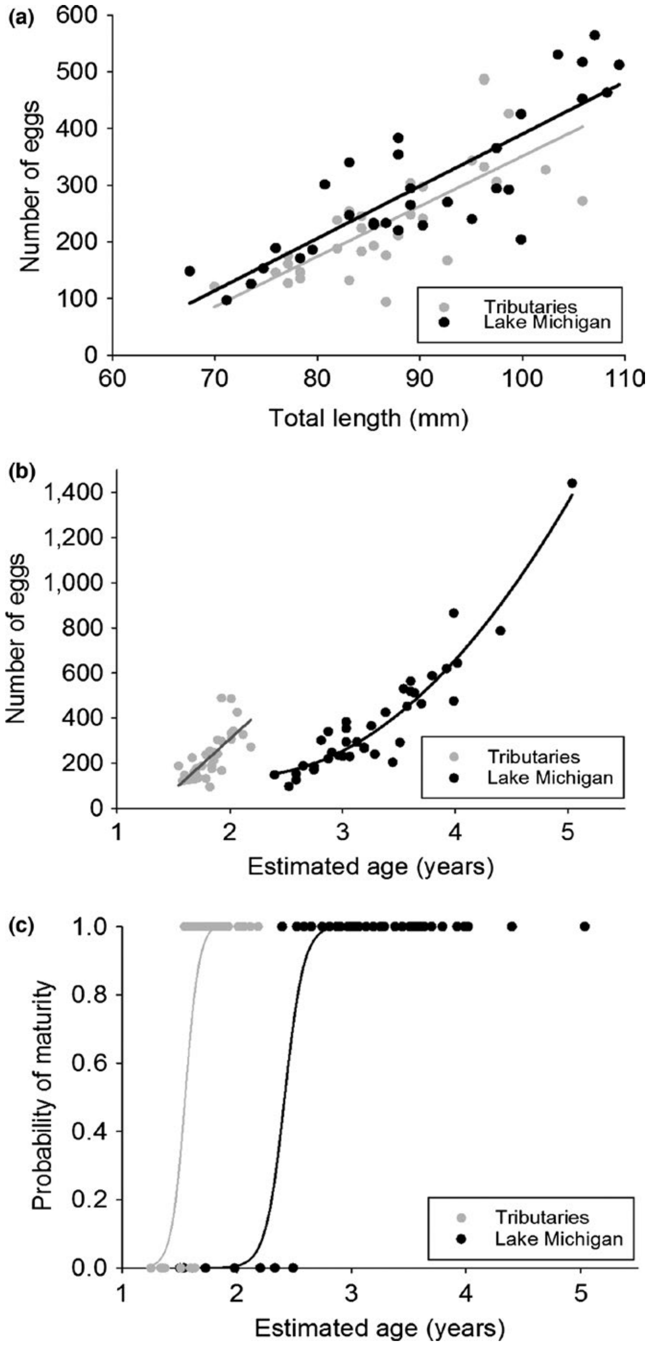

FIGURE 4 Relationships between (a) fecundity (number of eggs) and total length; (b) fecundity and estimated age; and (c) probability of maturity and estimated age for females from lake and tributary sites. Black circles/regression lines are from Lake Michigan (pooled from three sites) and grey circles/regression lines are from tributaries (pooled from two sites). Data are shown from mature female round gobies ≤110 mm in panel (a) to allow comparison between lake ($R^2 = .71$) and tributary ($R^2 = .57$) gobies within the size range of spawning females found in tributaries. In (a), intercepts are significantly different ($p = .046$), but slopes are not ($p = .84$). In (b), data are shown from mature female round gobies; tributary round gobies ($R^2 = .51$) clearly spawn at an early age than lake round gobies. Lake Michigan round gobies also appeared to have a curvilinear relationship between age and fecundity ($R^2 = .90$ for curvilinear relationship [shown] vs. .83 for linear relationship). In (c), the age at which 50% of female round gobies were mature was younger in tributaries (1.6) versus Lake Michigan (2.4); R^2 of the sigmoidal probability functions were .68 and .85 for tributary and Lake Michigan gobies, respectively. For panels (b) and (c), age was estimated from total length using the linear regressions described in Figure 2

Mean daily water temperature was notably higher in the two tributaries compared to Lake Michigan (Fig. 5). During the period of overlap (days of year 144–272), the median mean daily water temperature was 21.5°C, 20.4°C and 12.7°C in Kewaunee River, West Twin River and Lake Michigan, respectively. An interquartile range of 9.9–15.4°C was observed in Lake Michigan versus 16.3–21.7°C in West Twin River and 18.6–23.5°C in Kewaunee River.

4 | DISCUSSION

We describe noteworthy differences in invasive round goby life history in Lake Michigan and two of its tributaries. Round gobies from our tributary sites had greater length at age than from our Lake Michigan site. Tributary round gobies also appeared to have reduced longevity relative to Lake Michigan gobies, as fish ≥ age 3 were observed in Lake Michigan but not the tributaries. Older round gobies may have been present in deeper areas downstream of our sample sites, or migrated out to Lake Michigan. However, length distributions from the lake and tributary sites were comparable (Fig. 3), illustrating that earlier maturation and faster growth of stream round gobies were not related to an overall difference in length distribution, and that sampling methods were adequate to capture larger and presumably older fish up to 140 mm from all sites. We argue that an accelerated life history in tributaries is the most plausible explanation for comparable length distributions between systems but reduced maximum age in tributaries.

Observed length at age and longevity from both sites were within the range of values known from introduced round goby populations in North America and Eurasia. Lengths at age from the Lake Michigan site were similar to lengths at age from male round gobies taken from cold-water areas of Lake Huron (Hammond Bay and Harbor Beach, MI; French & Black, 2009). We observed smaller back-calculated

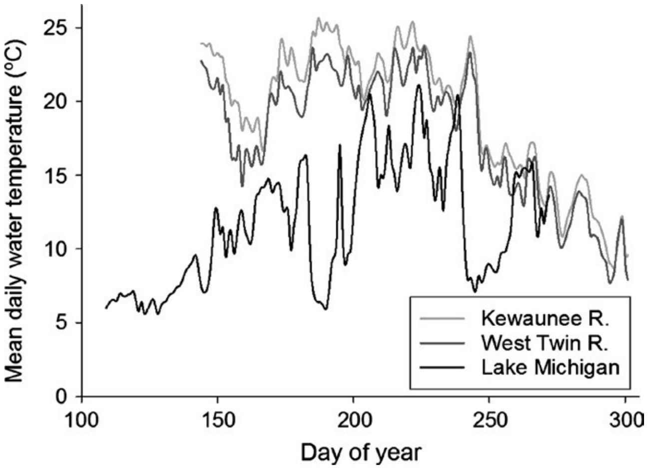

FIGURE 5 Mean daily water temperature (°C) during 2010 for Lake Michigan (black line), West Twin River (dark grey line) and Kewaunee River (light grey line) sites. During the period of overlap (days of year 144–272), the mean daily water temperature was 21.5°C, 20.4°C and 12.7°C in Kewaunee River, West Twin River and Lake Michigan, respectively. For reference, day of year 100 = April 10, 150 = May 30, 200 = July 19, 250 = September 7 and 300 = October 27

lengths at younger ages (25.4 mm [this study] vs. 40.0–45.0 mm [French & Black, 2009] at age 1 and 52.4 mm vs. 61.4–72.1 mm at age 2) and larger back-calculated lengths at older ages (116.1 mm vs. 88.7–97.5 mm at age 4 and 142.8 mm vs. 97.4–105.4 mm at age 5). Back-calculated lengths at age from our Lake Michigan site were also nearly identical to those reported from three other sites in northwest, southwest and northeast Lake Michigan (Huo et al., 2014), suggesting our Lake Michigan site was representative of round goby growth elsewhere in Lake Michigan. Lengths at age from tributaries exceeded the fastest growth rates reported from the Great Lakes in a review paper (Kornis et al., 2012), specifically those from warm-water areas of the Upper Detroit River (MacInnis & Corkum, 2000b) and Central Basin Lake Erie (Johnson et al., 2005). Both of those studies reported capture lengths from mid-to-late summer, so it is most appropriate to compare the mean capture length of age 2 tributary gobies from July (122.3 mm) to the values from Central Basin Lake Erie (90.3 mm and 104.0 mm for age 2 females and males; Johnson et al., 2005) and the Upper Detroit River (77.8 mm and 91.4 mm for age 2 females and males; MacInnis & Corkum, 2000b). Even faster round goby growth has been reported from brackish waters of the Baltic Sea, and the back-calculated lengths at age from our tributary sites (40.6 mm and 85.2 mm at ages 1 and 2) were considerably less than back-calculated lengths from the Gulf of Gdansk (106.8 and 119 mm for males at ages 1 and 2; Sokołowska & Fey, 2011) and the Vistula Lagoon (81–87 mm at age 1 and 126–135 mm at age 2 for females and males, respectively; Pliszka, 2002). Interestingly, round goby lengths at age from the St. Louis River Estuary, a transition between tributary and Lake Superior habitat, were similar to our observations from tributaries (73.0–84.5 mm for age 1 + females and males and 94.0–103.0 mm for age 2 + female and males, respectively; fish captured in August; Leino, 2013). Another study from the St. Louis River Estuary focused on seasonal growth of round gobies, and found most growth occurred between April and September (Lynch & Mensinger, 2013), substantiating our finding of rapid growth between April and July for age 2 tributary round gobies.

Age at maturity and fecundity also appeared to differ between the two systems. Tributary females reached reproductive maturity about one year earlier than Lake Michigan females, although Lake Michigan round gobies appeared to have greater overall reproductive potential due to large egg clutches associated with ages 4 and 5 individuals. Our age-at-maturity analysis was limited by a need to estimate age from total length rather than from a calcified structure. Nonetheless, the contrast between tributary and Lake Michigan round gobies is substantial and, in our view, provides strong evidence of earlier maturation in the tributary sites. Tributary round gobies also had fewer ripe eggs prior to the first spawning event versus lake fish of the same body size. This may indicate reduced fecundity for tributary fish, but it is possible that tributary round gobies spawn more often during summer than lake round gobies given the differences in water temperature. Thus, it is not clear from our data whether annual fecundity at length differed between our lake and tributary sites. Nevertheless, our results are consistent with earlier findings that round gobies from the Upper Detroit River and other Great Lakes tributaries have earlier maturation (age 1), reduced fecundity and reduced longevity compared to the native range (MacInnis & Corkum, 2000a, b; Phillips, Washek, Hertel, & Niebel, 2003).

We were not able to determine the mechanisms behind the observed differences in lake/tributary round goby life history, but there are at least three possible explanations for our results: lake/tributary differences in water temperature, lake/tributary differences in forage and differences between established (lake) and invasion-front (tributary) populations. Warmer tributary water temperature was probably the strongest factor contributing to length-at-age differences. Mean daily water temperature at the tributary sites approached the round goby's energetic optimum (26°C; Lee & Johnson, 2005) during summer, but was much colder at our Lake Michigan site. Warmer tributary water temperatures could have also facilitated earlier maturation, which in turn could contribute to reduced longevity due to the stress of spawning, particularly on male round gobies (Charlebois et al., 1997). Reduced longevity is often linked with high reproductive effort and early maturation across a variety of taxa (Bertschy & Fox, 1999; Dunlop, Orendorff, Shuter, Rodd, & Ridgway, 2005; Gunderson, 1997; Sabat, 1994) including round gobies from the upper Bay of Quinte, Lake Ontario (Taraborelli, Fox, Johnson, & Schaner, 2010). However, cause and effect is difficult to establish because early maturation is also selected for in populations with high mortality, as individuals that mature earlier under these circumstances are more likely to contribute their genes to the next generation (Gunderson, 1997; Shine & Charnov, 1992).

Differences in forage between Lake Michigan and its tributaries may also affect round goby longevity. Although round goby diet was not assessed at our sample sites, round gobies primarily fed on benthic insects in neighbouring tributaries (Kornis et al., 2012) versus

Dreissenid mussels, amphipods and zooplankton in the Great Lakes, with increased *Dreissenid* mussel consumption at larger round goby lengths (Barton, Johnson, Campbell, Petruniak, & Patterson, 2005; Johnson et al., 2005; Ray & Corkum, 1997). If we assume round goby diets were similarly distinct at our lake and tributary study sites—this seems reasonable given that *Dreissenid* mussels were abundant at our Lake Michigan sites and absent from our tributary sites (authors' observation)—the difference in available prey may offer population-level advantages to Lake Michigan round gobies. *Dreissenid* mussels are a preferred prey item of adult round gobies in their native range (Jude, Janssen, & Crawford, 1995), and *Dreissenid* mussel abundance likely facilitated round goby's spread and success in the Great Lakes (Ray & Corkum, 1997; Ricciardi & MacIsaac, 2000). By contrast, round gobies compete with other native benthivorous fishes for benthic insects in Lake Michigan tributaries (Kornis, Carlson, Lehrer-Brey, & Vander Zanden, 2014) where *Dreissenid* mussels are often absent (Kornis & Vander Zanden, 2010). Differences in available forage likely only affect larger round gobies, as smaller round gobies are limited by gape size (Ghedotti et al. 1995; Ray & Corkum, 1997), resulting in limited consumption of *Dreissenids* at lengths ≤70 mm (Janssen & Jude, 2001; Johnson et al., 2005) and a more comparable diet between lake and tributary round gobies of this size. Differences in available forage for larger round gobies are also likely compounded by warmer temperatures that increase resting metabolic costs for tributary round gobies and necessitate greater consumption despite more limited prey options.

It should be noted that the observed differences between tributary and lake round gobies are also consistent with life-history theory predicting rapid growth, early maturation and high investment in reproduction during the early, density-independent stages of population establishment (Bøhn et al., 2004; Roff, 1992; Stearns, 1992). Several studies have described divergent life histories of round gobies at invasion fronts where the mechanistic ambiguities present in our study (e.g. water temperature difference between lake and tributary sites) were better controlled. For example, round gobies at the edge of invasion fronts in the Trent–Severn Waterway had increased fecundity and energy allocation towards reproduction (Masson et al., 2016) as well as younger age at maturity (Gutowsky & Fox, 2012; Masson et al., 2016) compared to more established populations in the same system. Houston, Rooke, Brownscombe, and Fox (2014) suggested increased energy allocation of round gobies at invasion fronts in the Trent–Sever Waterway may be due to elevated autumn lipid content. Increased length at age was also observed in invasion fronts from the same system by one study (Gutowsky & Fox, 2012) but not by another (Masson et al., 2016). These studies are generally consistent with our findings of earlier maturation and increased length at age in the tributary sites, but contrast our finding of larger fecundity at length in Lake Michigan round gobies. Notably, all of the Trent–Severn studies speculated that observed divergence in life history was likely due to density-independent conditions at the invasion front, while noting that additional processes (e.g. fluctuations in density and food availability) were also potential factors. In our study, round gobies in the tributary sites may or may not have been in the early stages of population establishment at the time of sampling. Round gobies were first reported from northwestern Lake Michigan in 1999 (U.S. Geological Survey, 2015), and thus, populations at our tributary sites were likely 3 to 8 years old based on observed presence in 2007 (Kornis & Vander Zanden, 2010) and on reported upstream migration rates (0.5–4 km·year^{-1} [Bronnenhuber, Dufour, Higgs, & Heath, 2011; Kornis et al., 2012] suggest a minimum of 2.5 years to reach sites about 10-km upstream of Lake Michigan). However, the wide range of estimated population age, combined with the absence of density estimates at our sample sites and the suggestion of density-dependent population effects in nearby tributaries (Kornis et al., 2014), make evidence for an invasion-front effect very weak in our study, especially as round goby life-history traits in invasion-front populations can change over fine temporal scales as brief as one year (Masson et al., 2016). We conclude our observations are more likely driven by environmental and forage differences between Lake Michigan and its tributaries.

Caution is needed in extrapolating results from our study sites to Lake Michigan or the Great Lakes. Water temperature is likely a key driver of our findings, and numerous Great Lakes tributaries are classified as cold-water streams (<18°C mean summer water temperature; McKenna, Butryn, & McDonald, 2010). Nonetheless, a study of 73 Lake Michigan tributaries found round gobies were most likely to be present in large, low-gradient tributaries with warmer water temperature (Kornis & Vander Zanden, 2010). Large Great Lakes tributaries with low gradients tend to be characterised by warmer water (McKenna et al., 2010), and thus, water temperature differences similar to those observed between our tributary and lake sites may be prevalent throughout the round goby's range in the Great Lakes basin. Lake/tributary differences in forage base are also likely, as *Dreissenid* mussels cannot move upstream unassisted and are thus absent from many tributaries (Kornis & Vander Zanden, 2010). Therefore, divergent round goby life histories could be expected in other Great Lakes locations based on environmental traits, and as such, they have implications for management. Round gobies have invaded tributaries throughout the Great Lakes basin (Campbell & Tiegs, 2012; Kornis & Vander Zanden, 2010; Poos et al., 2010), raising concern due to their impact in the Great Lakes. Our results suggest divergent life histories between lake and tributary round gobies could affect their abundance and impact. The relationship between survival, fecundity and longevity has important implications for managing biological invasions because the abundances of short-lived invaders are more constrained by recruitment and propagule pressure than long-lived invaders (Marco, Páez, & Cannas, 2002) and are less resilient to variations in year class strength (Longhurst, 2002). Thus, the short longevity and early maturation we describe from our tributary sites may limit round goby density and overall impact on invertebrates and native benthic fish. Indeed, Kornis et al. (2013) found an average 10.8-fold increase in round goby abundance over a four-year period had no effect on the abundance of five native benthic fishes across 23 Lake Michigan tributaries, despite substantial declines in the population of three of these species (i.e. mottled sculpin [*Cottus bairdi*], Johnny darter [*Etheostoma nigrum*] and logperch [*Percina caprodes*]) following round goby invasion of the Great Lakes (Balshine, Verma, Chant, & Theysmeyer, 2005; Janssen & Jude, 2001; Lauer et al., 2004). Our results may have broad implications if the divergent round goby life histories observed in our study are typical elsewhere, but at a minimum, they underscore the potential for divergent life histories to affect invasive species management.

Divergent life histories may be more commonplace in aquatic invasive species, even in connected ecosystems, than previously recognised. Invasive species are frequently characterised by phenotypic plasticity and an ability to rapidly adapt to novel environmental conditions (Agrawal, 2001; Davidson et al., 2011; Sakai et al., 2001). It follows that such plasticity could lead to life-history changes (Alcaraz & García-Berthou, 2007; Daehler, 1998; Fox et al., 2007; Lockwood, 1999). One generalisation supported by both empirical and theoretical research is that life-history divergence is most likely when introduced species spread into suboptimal or increasingly novel habitats. Once an introduced species has overcome geographical barriers, it needs to survive and reproduce in the new environment to successfully establish an introduced population (Blackburn et al., 2011; Vander Zanden & Olden, 2008). The more an introduced species spreads, the more it will encounter environmental conditions different from the point of introduction, essentially exposing the species to multiple, sequential establishment events (Blackburn et al., 2011). Our case study is an example of this, as the environmental characteristics of Great Lakes tributaries are novel compared to the round goby's native and early invasive ranges (Kornis & Vander Zanden, 2010). Similar findings have been reported from introduced mosquitofish, which native in freshwater and have earlier maturation, higher reproductive investment and reduced density under saline conditions (Alcaraz & García-Berthou, 2007). If life-history divergence is a function of environmental novelty, then certain traits like decreased longevity and early maturation may be common along invasion fronts, as suggested by others (Bøhn et al., 2004; Fox et al., 2007).

We speculate that divergent life histories at the invasion front may be particularly prevalent in invasive species, like round goby, engaged in secondary invasions from large open systems into connected tributaries. The Great Lakes serve as a prime example, as they are a springboard for secondary invasions into inland waters (e.g. *Dreissenid* mussels, rainbow smelt, spiny water flea; Vander Zanden & Olden, 2008) and selection likely favours different traits in the Great Lakes (large, cold, oligotrophic systems) than in secondary invasion systems (i.e. inland lakes and streams). Given these differences in environmental conditions, it is probable that introduced species occurring in both ecosystems will have distinct life-history characteristics. In turn, divergent life histories may help explain some of the spatial variability in invasive species impacts, as postulated here for round gobies, providing useful information for invasive species management.

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APPENDIX A

Background and justification of whole sagittal otolith ageing methods.

Whole sagittal otoliths collected from round gobies were dried prior to mounting for at least 6 days, after which otolith weights were taken to the nearest 10,000th of a gram (0.0001) with a Mettler AE-160 balance. Whole sagittal otoliths were mounted using Cytoseal 60 low-viscosity mounting medium (Richard-Allan Scientific) and allowed to dry for at least 10 hr. Mounted otoliths were then photographed using an Olympus BX-40 microscope and a Q-Imaging Go-3 digital camera using reflected light (Fig. A1). Otolith photographs were manipulated using ImagePro Plus version 6.2.1.491: a high-Gaussian filter was used to clarify and sharpen images. Otoliths were aged by three independent readers without reference to fish length. A total of 80%

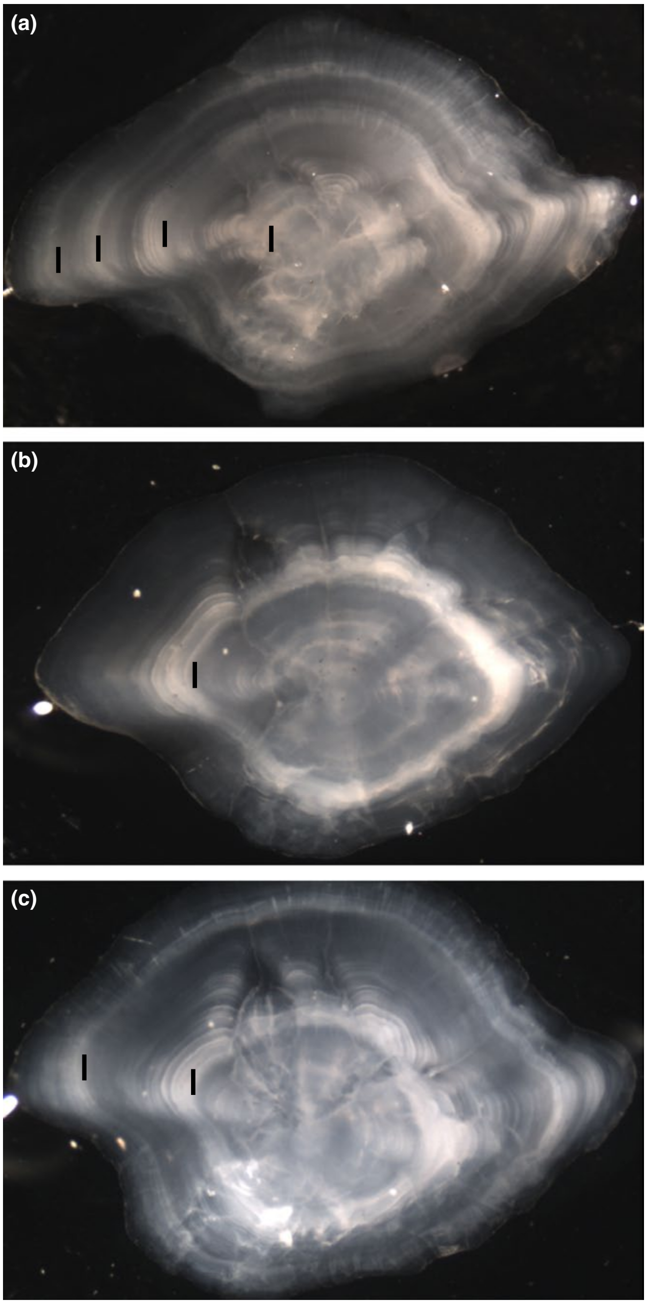

FIGURE A1 Photos of whole sagittal otoliths mounted and examined for age estimation. Thick black lines indicate the locations of interpreted annuli. (a) Age 4 round goby from Bailey's Harbor, Lake Michigan, demonstrates the clarity of the method on an older individual. (b) The wide translucent band at the edge of this otolith from a Kewaunee River round goby collected on 19 April 2010 suggests this fish is in the early stages of annulus formation. (c) An example age 2 round goby captured from the Kewaunee River on 14 July 2014 confirms annulus formation occurred for most individuals between late April and mid-July, and likely toward the earlier end of that range given the postannulus growth already evident at the otolith margin agreement was achieved after the first read and disagreements were discussed; if no agreement could be resolved, the otolith was removed from further analysis. We interpreted the transition from translucent to opaque zones as the annual growth mark (Fig. A1).

Conventional age-estimation techniques use polished, cross-sectioned otoliths rather than whole mounted otoliths. However, whole mounted sagittal otoliths have been previously used to estimate age from round gobies (Gümüs & Kurt, 2009) and are considered a reliable structure for age estimation on fish that have <6 visible annuli (Maceina & Sammons, 2006). Several studies have also found that whole mounted and sectioned sagittal otoliths produce comparable age estimates in younger individuals (Beckman 2002; Brouwer and Griffiths 2004). Thus, we have high confidence in the accuracy of our age estimation, as all round gobies in the analysis had 5 or fewer annuli.

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APPENDIX B

Relationships between otolith area and total fish length used for back-calculating round goby total length at annulus formation

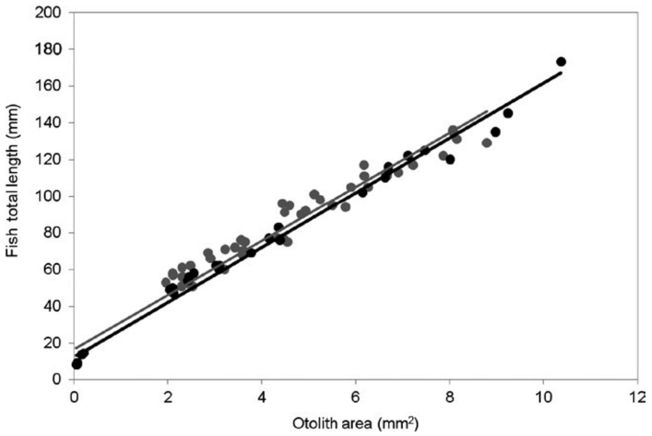

FIGURE B1 Relationships between sagittal otolith area and total length for round gobies from Lake Michigan (black circles/line) and two tributaries (gray circles/line). These relationships were used to back-calculate length at age from the area of otoliths at each annual check. TL = 14.8 × otolith area + 16.4 for streams (R^2 = 0.96) and =14.91 × otolith area + 12.439 for Lake Michigan (R^2 = 0.99). Round gobies from Lake Michigan were collected from Bailey's Harbor, while tributary gobies were collected from both Kewaunee River and West Twin River, Wisconsin. Both regression lines included recently hatched round gobies (TL = 8.5–14 mm) from Sunset Bay, Lake Ontario