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Environmental patterns of establishment and early-stage impacts from invasive round gobies in an aquatic biodiversity hotspot

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ABSTRACT

Quantifying the establishment, spread, and impacts of invasive species requires an accurate understanding of ecosystem structure and function before and after introductions. In 2014, the round goby (*Neogobius melanostomus*) invaded the LeBoeuf Creek subwatershed of French Creek, a tributary to the Allegheny River, PA, USA. We report on a decade of stream monitoring within the immediate invasion front by describing the environmental conditions associated with round goby populations and the potential impacts and resource overlap with native fish communities. First, we found no evidence of a round goby population increase since invasion, and that round goby population densities were higher during early summer and in closer proximity to Lake LeBoeuf. Second, the presence of round gobies overlapped substantially with environments of low-oxygen conditions, low native fish richness, and macroinvertebrate communities dominated by non-insect taxa, all of which are representative of lentic environments. In contrast, greater aquatic insect diversity corresponded to higher native benthic fish diversity of uninvaded reaches. Finally, there was no evidence that round gobies have induced any changes to the native fish communities within the invasion front during the past decade. While our results have indicated a relatively localized invasion from round gobies with minimal impacts to the stream habitats of French Creek, the greatest impacts are likely to be in lentic habitats near Lake LeBoeuf, where round goby populations are most established.

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Introduction

Round gobies (*Neogobius melanostomus*) are benthic fish native to the Ponto-Caspian region of Eurasia and were first introduced in the Laurentian Great Lakes of North America in 1990 (Jude et al. 1992; MacInnis and Corkum 2000). Round gobies invaded all five of the Great Lakes within a decade (Clapp et al. 2001), potentially because of their high adaptability to new environments (Masson et al. 2018; Poslednik et al. 2023). As a result, round gobies have become a dominant fish species in the Laurentian Great Lakes, often displacing native benthic fishes due to their aggressive behaviors. Indeed, round gobies have been implicated in the decline of many native benthic fishes since their introduction (Dubs and Corkum 1996; Jansen and Jude 2000; Balshine et al. 2005; Firth et al. 2021), and consequently, round gobies alter the top-down and bottom-up forces acting on ecosystem function and food webs (Mikl et al. 2017; Henseler et al. 2021).

Round gobies are no longer confined to watersheds of the Laurentian Great Lakes and have exhibited range expansions in recent decades. For example, recent North American expansions have occurred eastward into the Hudson River and southward into the Mississippi River (George et al. 2021; Harris et al. 2024). These novel, emerging invasions have occurred in lentic and lotic environments that are markedly different from the large lentic habitats that invaded round gobies that have been most historically studied (Stauffer et al. 2016 A). These emerging invasions provide important opportunities for comparative

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research given the environmental differences between novel ecosystems compared with the Laurentian Great Lakes. For example, Masson et al. (2018) found similar life history shifts for round gobies across similar stages of invasion gradients on different continents. One recent and novel expansion of round gobies occurred into French Creek, which is a tributary of the Allegheny River in Northwest Pennsylvania, USA. The round goby introduction likely resulted from a bait bucket transfer from Lake Erie into Lake LeBoeuf, a natural glacial lake of the French Creek watershed (Mueller et al. 2017).

The French Creek watershed has a regionally renowned diversity with 27 species of native freshwater mussels (family Unionidae) and over 90 species of native freshwater fishes, especially with respect to benthic darters (family Percidae) and madtoms (family Ictaluridae) (e.g. 19 different *Etheostoma, Percina, Ammocrypta, Noturus spp.*; Smith and Crabtree 2010; Stauffer et al. 2016B). French Creek's high biodiversity could be attributed to a history of few human disturbances, such as landscape-level changes, because many native fishes have not experienced range declines through the 20th century (Kirk and Wissinger 2020). Round gobies have emerged as a new threat to French Creek's biodiversity, especially to the native mussel assemblages, which are predated by the invasive round goby (Bradshaw-Wilson et al. 2019, Clark et al. 2021, 2022). Aside from round gobies utilizing predominantly juvenile drift as a means for range expansion (Hemmelgarn et al. 2025), very little is known about the patterns of establishment, spread and impacts from the invasion thus far.

It has been over a decade since the round goby introduction in 2014, and a synthesis of the invasion in French Creek was warranted. Our study had three objectives. The first objective was to describe any spatial or temporal changes in population size, structure and distribution of round goby at the invasion front between years at the start of the invasion (2013–2017) compared to a decade later (2024–2025). The second objective was to document the environmental conditions, macroinvertebrate composition, and fish communities of reaches invaded by round gobies relative to those of reaches uninvaded by round gobies. The third objective was to determine whether native fish communities have changed in response to round goby invasion.

Methods

Study reaches and data collection

Our monitoring of the round goby invasion front consisted of 12 study reaches, most of which were in the immediate vicinity of the original invasion source of Lake LeBoeuf (i.e. within 15 river kilometers [rkm]; Figure 1). Stream surveys were grouped into four main reach categories based on gradients of environmental differences and invasion threat (i.e. listed from highest threat to lowest threat). The first set of reaches were stream surveys located within the invaded sub-watershed of LeBoeuf Creek and consequently under the highest invasion threat (three 'LeBoeuf' locations within ~7.0 rkm of the invasion source). The second set of reaches included surveys on French Creek downstream of the confluence with LeBoeuf Creek, thus at risk of downstream juvenile dispersal (three 'Threatened' locations ranging from 4.4 to 9.2 rkm away from the invasion source; Hemmelgarn et al. 2025). The third set of stream reaches was located on French Creek upstream of the mouth of LeBoeuf Creek, and thus round gobies must swim upstream to these locations (four 'Upper' locations ranging from 5.4 to 12.1 rkm away from the invasion source). Finally, two stream reaches are located far downstream of the immediate invasion front, which serve as 'Reference' reaches (28.2–39.3 rkm downstream of Lake LeBoeuf).

Round goby populations and native fish assemblages in French Creek were sampled with a combination of seining (3 m by 1 m of varying mesh size [0.64–0.93 cm]) and direct current (DC) electrofishing using standardized methods employed by university and state agency researchers (see Kirk et al. 2017; Kirk and Wissinger 2020). All the surveys were performed during low- flow conditions (May–September). Due to the large nature of our study reaches (mean [range] stream widths = 23.9 m [8–42 m]; watershed areas = 581.8 km^2 [50–1,550 km^2]; Table 1), electrofishing surveys often employed multiple anodes, multiple passes, and extended sampling reaches to ensure representative sampling (e.g. 2–3 anode towbarge, multiple single anode backpacks). Hence, the survey effort varied greatly depending upon the stream size (mean [range] = 4.6 person hours [2.0–6.2]). Whereas electrofishing followed a progressive and systematic enumeration of all fish from all habitat types in a defined sampling reach, seining was more targeted to specific areas of defined sampling (e.g. sections of riffles and runs).

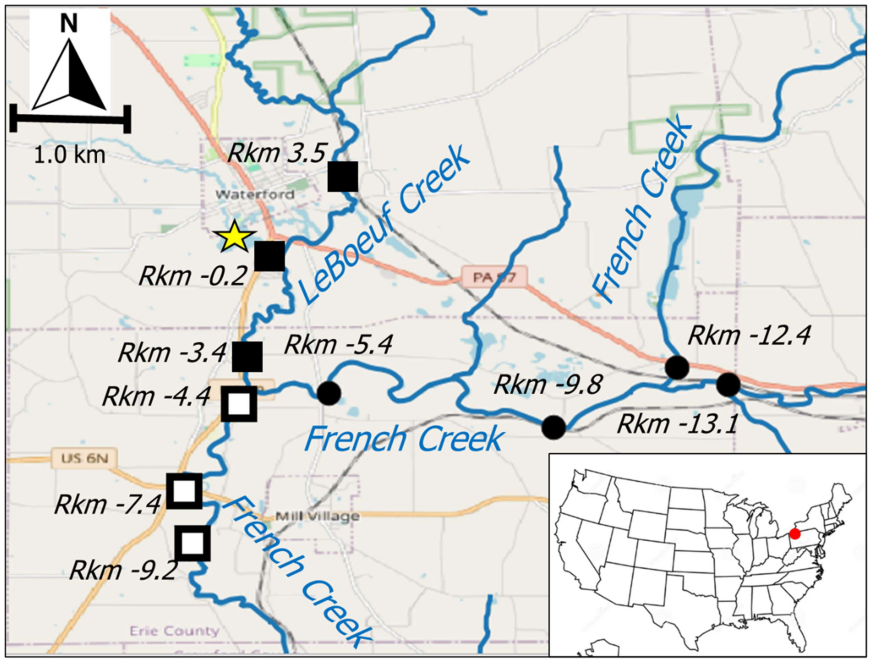

Figure 1. Map of the 12 study monitoring locations surrounding the French Creek and Lake LeBoeuf (yellow star) invasion front of round gobies. The numbers next to each location correspond to the river kilometer (rkm) of the site based on the distance from Lake LeBoeuf (negative values = distance downstream from the lake; positive values = distance upstream from the lake). The black circles represent French Creek upper sites, the black squares represent LeBoeuf Creek sites, and the white squares represent French Creek Threatened sites. The two reference locations are not shown in the main map and are located ~29–35 rkm away from the immediate invasion zone. The inset map shows our study area of Northwest Pennsylvania relative to the USA.

Table 1. Mean environmental and biological response variables of interest across the four different reach types of the round goby invasion front in French Creek.

Type	Variable	Reference	Upper	LeBoeuf	Threatened
Environment	Watershed area (km^2; range)	1,300–1,550	220–700	50–125	850–910
	Wetted widths (m; range)	34–41	17–26	7–18	32–35
	Temperature (°C)	24.0	22.5	24.2	23.5
	Dissolved oxygen (mg/L)	10.4	9.4	6.7	8.4
	Total dissolved solids (ppm)	143.0	168.8	146.5	163.3
Invertebrate	Family richness	19.7	17.0	15.8	19.3
	BIBI score (%)	55.2	48.7	35.9	53.3
	EPT (%)	8.8	15.7	2.3	23.0
	Family Chironomidae (%)	22.0	16.0	19.0	17.0
	Molluscs/Crustaceans (%)	1.8	1.2	3.6	0.4
Fish	Native species richness	24.8	26.6	21.0	28.3
	Native darter richness	9.8	10.3	5.8	10.3
	Native minnow richness	7.0	7.3	8.0	9.0
	Native madtom richness	2.6	1.7	1.0	3.0

Note: All means are based on standardized electrofishing surveys from the most recent contemporary periods (2024–2025). Macroinvertebrates were collected, identified and scored using a Benthic Index of Biotic Integrity (BIBI). EPT refers to the percentage of individuals belonging to the insect orders of Ephemeroptera, Plecoptera and Trichoptera.

There was a bias towards sampling in earlier periods with seining, while later years exclusively employed electroshocking methods. Seining methods tended to underestimate total species richness at French Creek sites, especially for minnow communities (Table S1 in Appendix I). While certain fish like bass (*Ambloplites, Micropterus* spp.), madtom (*Noturus* spp.) and minnows (Family Leuciscidae) all had lower detection rates with seining, there was no systematic bias in capturing round gobies with either approach (Table S2 in Appendix I). To avoid these concerns of detection, we imposed several other limitations for data inclusion to ensure accurate representations across periods. First, no seining data were considered without explicit data corresponding to effort (e.g. haul number, reach length and stream width) for estimating round goby population densities based on survey area (e.g. catch-per-unit-effort [CPUE]).

Second, native fish assemblage data were considered representative from seining if the fish abundance had a minimum of 50 individuals from the minnow family and the darter family, which is a similar criterion for accurately estimating assemblage composition based on electrofishing data (Kirk et al. 2017). Finally, seining data were incorporated if collected alongside backpack electrofishing data to ensure accurate assemblage representation. A greater emphasis is placed on standardizing our methods for electrofishing because of long-term standardization monitoring for regional fish populations (Kirk and Wissinger 2020).

During fish surveys, data were also collected on stream environment conditions pertaining to water quality, habitat quality, and macroinvertebrate composition. Water quality data were collected with a YSI probe or Oakton handheld meters, and included water temperature (°C), dissolved oxygen (mg/L), pH (range of acidic to basic: 0–14), and total dissolved solids (TDS; ppm). Macroinvertebrates were collected at all survey reaches from riffle habitats with a D-frame net following protocols established by the Pennsylvania Department of Environmental Protection (DEP 2023). Finally, we performed instream and riparian assessments at all survey locations using standardized habitat assessments. Both assessments quantify instream and riparian habitat quality for explaining empirical differences in stream environment across sites (Peterson 1992; DEP 2009; see Tables S3 and S4 in Appendix II). For example, when using these forms, riparian scores distinguish well-forested, mature forested canopies with stable banks (high values) from clearcut canopies with unstable banks (low scores). Instream habitat scores distinguish habitats with diversely sized gravel-cobble substrates and heterogeneous flows (high values) from habitats dominated by fine sediments and homogeneous low flows (low values).

Data analysis

We performed an analysis of covariance (ANCOVA) with our round goby population density data from the long-term monitoring locations where round gobies are routinely encountered ($n = 15$ surveys; Table 2). Across the 12 study locations (Figure 1), round gobies were only documented at three of these monitoring locations (Table 2), which were pooled for the ANCOVA. The three variables modeled in the ANCOVA were river kilometer (rkm; spatial variation), day-of-year (DOY; intra-annual variation), and time period (2014–2016 vs. 2024–2025; annual variation). Round goby population densities were standardized based on survey length and stream width (number per m^2). Given that all round gobies were euthanized for complementary trophic niche studies (e.g. Bradshaw-Wilson et al. 2019), we also used a three-way analysis of variance (ANOVA) to test for spatial differences in spatial location based on lake proximity (Table 2), seasonal differences in early summer (May–July) vs. late summer (August–September), and time period differences (early vs. late invasion) in round goby total length (Table 2).

Data on environmental conditions, macroinvertebrate composition and fish assemblages were analyzed using unconstrained ordination methods. Differences in water quality (temperature, DO, pH and TDS) and habitat characteristics (width [m], riparian corridor score and instream habitat score) were summarized across the twelve study reaches using a Principal Components Analysis (PCA; R version 4.4.2). Axes were considered important when the eigenvalues were > 1.0 and explained > 10% of the cumulative variance. Individual variables were considered to be significantly associated with a PCA axis if the Pearson correlation coefficients (r) were > 0.4 (Gotelli and Ellison 2004).

Table 2. Round goby population demographics at the three invaded locations of the LeBoeuf Creek (LC) and French Creek (FC) invasion front.

Location	LC (Lake Outlet)	LC (Moore Road)	FC (FC Road)
rkm LeBouf Lake	−0.2	−3.4	−4.4
Mean Density (CPUE)	0.022	0.011	0.0002
Density Standard Error	0.012	0.003	0.0002
Sample size (*n*)	156	246	3
Mean TL (mm)*	78.7	57.8	66.3
TL Standard Error	1.37	1.26	2.91
Median TL (mm)	76.3	57.0	67.0
Range TL (mm)	45–125	25–115	61–71

Note: A – rkm value indicates the distance downstream from Lake LeBoeuf.
*indicates significant differences in mean total length (TL) for the two LeBoeuf Creek locations, with round gobies ~20 mm smaller at the downstream location at LeBoeuf Creek.

We analyzed differences in macroinvertebrate composition based on the benthic index of biotic integrity (BIBI) developed by the Pennsylvania Department of Environmental Protection. The BIBI includes six different metrics incorporating various aspects of taxonomic diversity and pollution, with higher values indicative of diverse assemblages with environmentally sensitive taxa. Additionally, we analyzed differences in three taxonomic metrics that are important contributors to the BIBI and benthic fish populations. The first is the percentage of total individuals as Ephemeroptera, Plecoptera and Trichoptera larvae (EPT), which are the quintessential pollution sensitive taxa. The second is percentage of Chironomids, which are the dominant dipteran taxa and dominant food item of benthic darters (van Snik et al. 1997). The third is the percentage of total individuals as molluscans and crustaceans, which are frequently documented as round goby prey items and contribute to lower BIBI scores. Differences in these macroinvertebrate taxonomic categories across spatial locations were analyzed using ANOVA.

We also summarized differences in macroinvertebrate and fish assemblages using non-metric multi-dimensional scaling (NMDS). NMDS is a form of unconstrained ordination that visualizes taxonomic groups and sampling sites in multi-dimensional space based on rank order distances. The NMDS was calculated based on Bray-Curtis similarity using proportional relative abundance data, with stress reported as a measure of fit. We performed three separate NMDS using our contemporary data: one based on family-level macroinvertebrate taxa; one based on species-level fish data of the family Percidae (e.g. darters), and one based on species-level fish data of the family Leuciscidae (e.g. minnows like chub, dace and shiner). Forty two macroinvertebrate families were included which were observed in at least 10% of sampling reaches. Across all locations, these 42 macroinvertebrate families accounted for 95.4% of the total abundance across reaches (range: 77%–100%). We focused on these two fish families because they comprised 92% of the total abundance of fish species captured during our surveys (range: 84.8%–98.9%) and 70% of the total richness. Twelve of 14 observed darter species and 11 of 15 observed minnow species met the criteria for statistical inclusion (observed at > 10% of samples). Differences in the richness of these two taxonomic groups were also analyzed across the different reach types using an ANOVA.

Temporal changes in fish assemblages were also evaluated using NMDS between the two periods to determine whether round goby invasion induced community-level changes. Unlike prior ordinations, this temporal analysis was based on presence–absence data rather than abundance data. Surveys were pooled into two temporal periods: an early invasion period (2013–2017) and a post-invasion period (2024–2025). The time period groupings ensured adequate sample sizes for each period based on the results of prior studies that found no long-term changes to the watershed through 2019 (Kirk and Wissinger 2020). Species needed to be detected at > 10% of sites in both time periods for inclusion, resulting in 37 fish species for inclusion.

Significant differences in fish and macroinvertebrate were determined using NMDS models and multivariate analysis of variance (MANOVA). The MANOVA for all models included the four different reach types within the immediate round goby invasion front (LeBoeuf Creek, French Creek Reference, French Creek Threatened and French Creek Upper; Figure 1) as a single predictor variable. The temporal NMDS included the two time periods as the main predictor variable, while the four reach types controlled for spatial differences. Multivariate pairwise comparisons were used to determine specifically which reach types differed. All the results from the univariate (ANOVA's and ANCOVA's) and multivariate parametric tests (MANOVA) met assumptions for normality and homoscedasticity (Zuur et al. 2009). Finally, effect sizes from the parametric tests were considered significant at $p < 0.05$ and marginally significant at $p < 0.10$ given the small sample sizes for certain analyses.

Results

LeBoeuf Creek sites had average round goby densities 39.0 × and 78.4 × higher than those of the French Creek Threatened site with occurrences (Table 2). No round gobies were detected upstream of Lake LeBoeuf nor in the French Creek Upper and Reference reaches (Figure 2). Round gobies constituted a small percentage of the total fish composition at the original long-term LeBoeuf Creek site (rkm −3.4) based on quantitative assemblage-wide estimates ($n = 4$; mean = 2.9% of total abundances). Length–frequency histograms from 446 round goby captures revealed a notable bimodal structure, with peaks occurring for juvenile fish and mature fish (Figure S1 in Appendix 3). While round goby size did not differ between the early summer and late summer periods ($F = 0.27$;

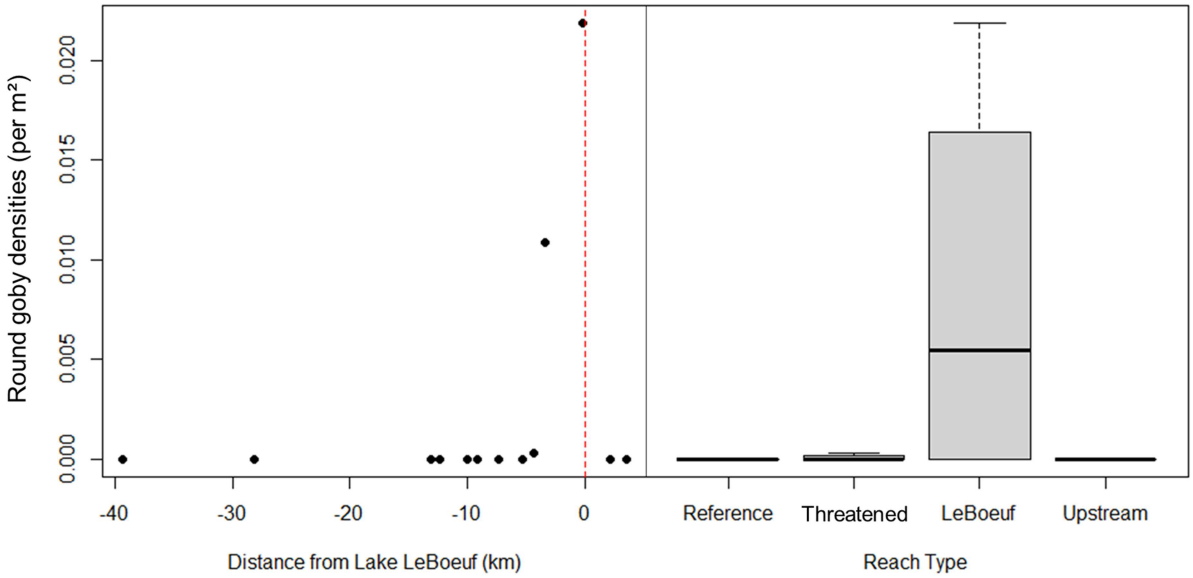

Figure 2. Round goby densities as a function of river kilometer from the original invasion source of Lake LeBoeuf (red dashed line; left panel) and as a function of the four reach types in the invasion zone of French Creek (right panel). Both graphs highlight the localized distribution of round gobies within LeBoeuf Creek.

$p = 0.604$), there was a significant difference in size between the two LeBoeuf Creek sites ($F = 64.57$; $p < 0.001$), with smaller sizes of round gobies detected at the downstream site (rkm −3.4) and larger sizes closer to the lake (rkm −0.2; Table 2). There was also a significant difference in size between the two invasion periods ($F = 42.88$; $p < 0.001$), with a bias to smaller individuals in the early invasion period versus late invasion period (56.3 vs. 75.8 mm, respectively).

Round goby population densities at the three invaded locations were explained more by intra-annual variation than inter-annual variation and spatial variation. All three variables jointly explained 35.3% of the variation in the ANCOVA ($n = 18$ population surveys; $R^2 = 0.35$; $p = 0.053$). After accounting for the non-significant effect of year (all pairwise $p > 0.733$) and distance from the lake ($\beta = -0.03$, $p = 0.151$), we found a nearly significant negative relationship between DOY and round goby densities ($\beta = -0.001$, $p = 0.061$), revealing higher round goby densities earlier in the sampling season (Figure 3).

Regarding environmental conditions ($n = 17$ observations), the first PCA axis explained 35.4% of the variation in environmental conditions and was strongly correlated with dissolved oxygen ($r = 0.54$) and instream habitat scores ($r = 0.57$; Figure 4). The MANOVA revealed significant differences for most of the different reach types ($F = 30.59$; $p < 0.001$). LeBoeuf Creek differed from all other stream reaches in having lower dissolved oxygen (DO) and lower instream habitat scores (all pairwise $p < 0.001$; Table 1). Hence, LeBoeuf Creek has relatively more homogenous habitats composed of uniformly fine substrates. The French Creek Threatened reaches also had lower DO and lower instream habitat compared to the French Creek Reference reaches ($p = 0.019$).

The second PCA axis explained 21.9% of the variation in environmental conditions and was strongly correlated with temperature ($r = -0.54$) and total dissolved solids ($r = -0.56$). While significant differences were observed across reach types ($F = 3.76$; $p = 0.041$), pairwise differences indicated that the only difference was between French Creek Reference reaches (warmer; lower TDS) and French Creek Upper reaches (cooler, higher TDS; $p = 0.031$). The third PCA axis explained 21.6% of the variation in environmental conditions and was strongly correlated with riparian habitat scores ($r = -0.70$) and loosely correlated with temperature ($r = 0.48$). No significant differences were observed for the different reach types with respect to this environmental gradient (all pairwise $p > 0.835$).

Two axes were considered important for the NMDS explaining the variation in the 42 family-level macroinvertebrates ($n = 36$ macroinvertebrate collections; stress = 0.19). Chironomidae was the most dominant insect taxa (19.5%), followed by Elmiidae (16.6%) and Hydropsychidae (11.0%). Oligochaete

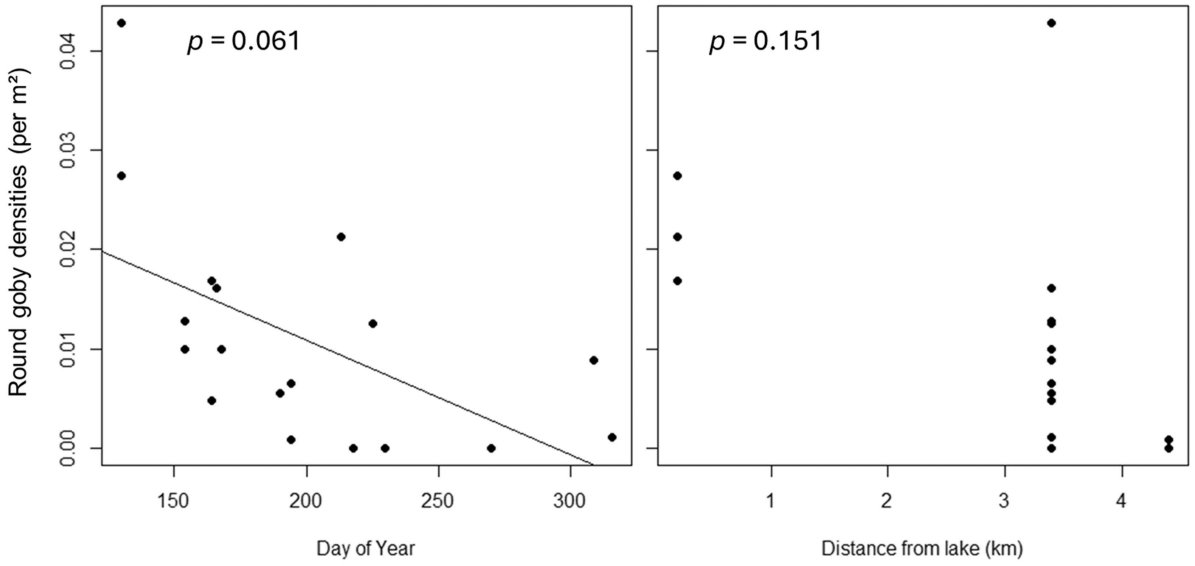

Figure 3. Intra-annual variation (left panel) and spatial variation (right panel) in round goby densities at three of the long-term monitoring locations where round gobies were detected (see Table 2).

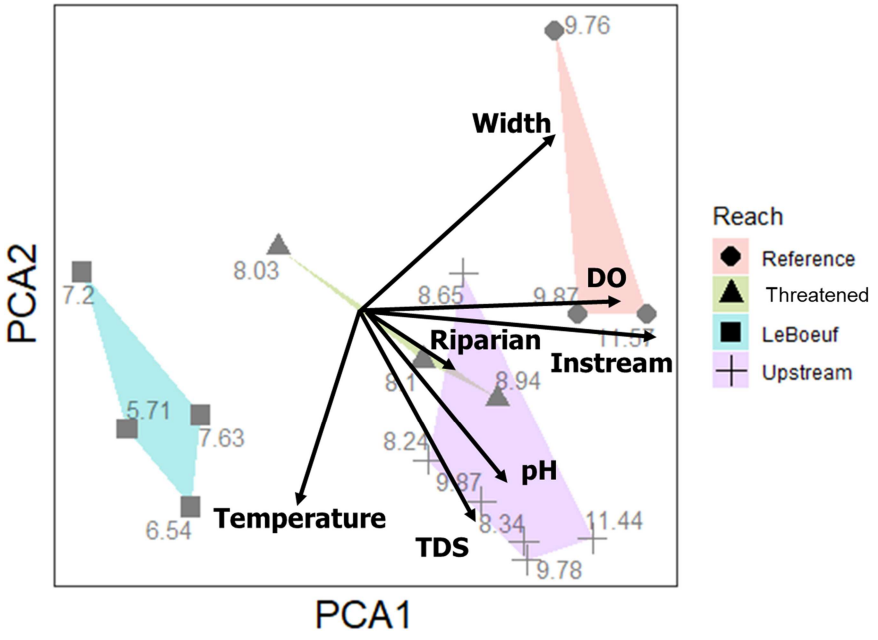

Figure 4. Principal component analysis displaying the variation in the environmental conditions of the four different reach types of the round goby invasion front. The environmental variables included dissolved oxygen (DO), total dissolved solids (TDS), and instream and riparian habitat score assessments. Dissolved oxygen values are shown on the graph to particularly highlight the lower oxygen levels in LeBoeuf Creek (see also Table 1).

annelids was the dominant non-insect taxa (9.6%). The taxa negatively associated with the first NMDS axis included Hydropsychidae ($r = -0.71$), Brachycentridae ($r = -0.42$), and Elmiidae ($r = -0.63$), while positively associated taxa included Perlidae ($r = 0.40$), Lymnaidae/Planorbidae gastropods ($r = 0.40$), and Oligochaete annelids ($r = 0.67$). The second NMDS axis was positively correlated with Heptaganiidae ($r = 0.54$), Psephenidae ($r = 0.43$), and Perlidae ($r = 57$), while the negatively associated taxa included only Chironomidae ($r = -0.81$). The MANOVA revealed significant differences in macroinvertebrate communities across reaches for the first axis ($F = 3.95$, $p = 0.017$). However, only one pairwise comparison was

significant ($p = 0.024$), indicating differences between French Creek Threatened (negative axis scores) and French Creek Reference reaches (positive axis scores). No differences were observed for the second NMDS axis (Figure 5).

Significant differences were also observed in macroinvertebrate communities based on DEP BIBI scores ($F = 3.04$, $p = 0.043$), with LeBoeuf Creek having significantly lower BIBI scores than French Creek Reference locations ($p = 0.033$; Table 1). The proportion of taxa belonging to the orders Ephemeroptera, Plecoptera, and Trichoptera (EPT) also varied among locations ($F = 4.05$, $p = 0.015$), with LeBoeuf Creek having significantly lower proportions of EPT than all French Creek reaches (all pairwise $p < 0.053$). There was only a marginally significant difference among the sampling reaches in the mollusc and crustacean taxa ($F = 2.35$; $p = 0.091$), with the highest proportions in LeBoeuf Creek (Table 1). No spatial variation was observed with respect to Chironomidae ($F = 0.36$; $p = 0.781$).

The MANOVA for the native darter NMDS ($n = 18$ quantitative fish surveys; stress = 0.11) revealed significant differences among the four reach types ($F = 3.29$; $p = 0.014$). The proportional abundance of variegate darters (*Etheostoma variatum*; $r = -0.87$), spotted darters (*Etheostoma maculatum*; $r = -0.67$), and tippecanoe darters (*Etheostoma tippecanoe*; $r = -0.56$) were all negatively correlated with the first NMDS axis, which was associated with French Creek Reference reaches. The proportional abundance of banded darters (*Etheostoma zonale*; $r = 0.85$) and bluebreast darters (*Etheostoma camurum*; $r = 0.40$) was positively associated with the first NMDS axis and had higher abundances in LeBoeuf Creek reaches (Figure 6). Pairwise comparisons revealed that the LeBoeuf Creek darter composition differed from that of all the other reach types (all $p < 0.018$), while all the French Creek reaches did not significantly differ (all $p > 0.604$). Darter richness was thus significantly lower in LeBoeuf Creek compared with all French Creek reaches ($F = 9.60$; $p < 0.001$; Table 1). In contrast, the MANOVA for the native minnow NMDS ($n = 18$ quantitative surveys; stress = 0.14) did not reveal significant differences among the four reach types ($F = 1.56$, $p = 0.196$). Minnow richness also did not differ among the reach types ($F = 2.38$; $p = 0.114$; Table 1).

Finally, the MANOVA for the native fish NMDS ($n = 39$ qualitative surveys; stress = 0.21) revealed no evidence for temporal changes between the early invasion period ($n = 17$; 2013–2017) and the recent invasion period ($n = 22$; 2024–2025; $F = 2.40$; $p = 0.103$). There were also no spatial differences in native

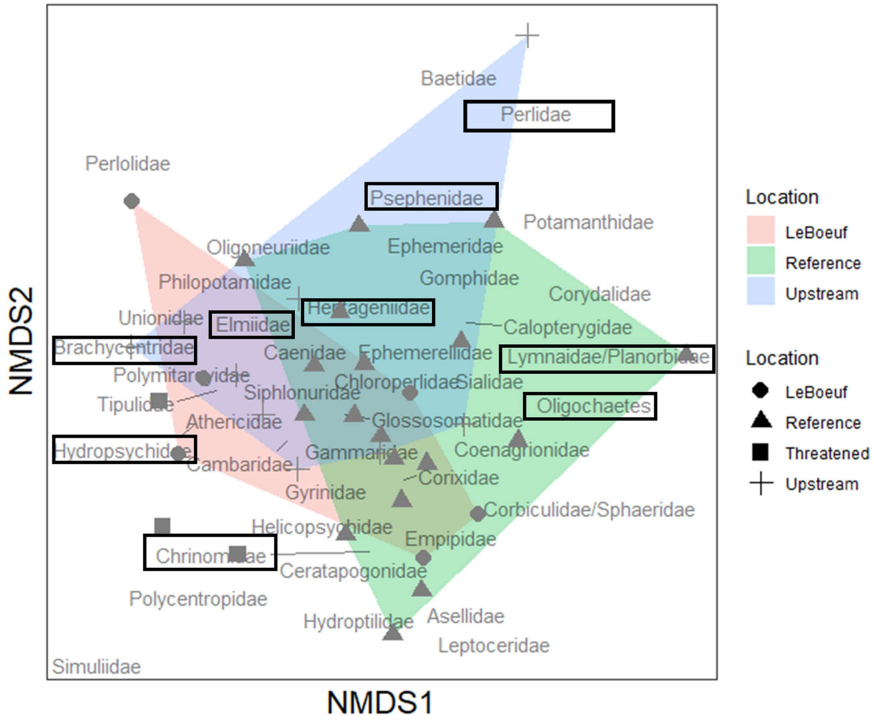

Figure 5. NMDS of quantitative surveys for 42 macroinvertebrate families. Black rectangles are placed around the taxa (insect, crustacean, and molluscan families plus oligochaetes) significantly correlated with each axis ($r > 0.40$).

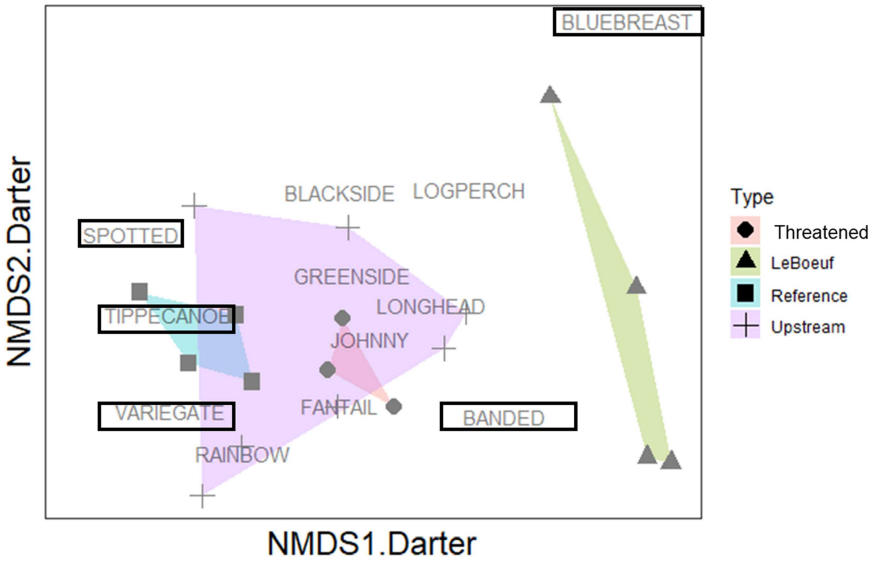

Figure 6. NMDS of quantitative surveys for 12 native darter species from 2024 to 2025. Black rectangles are placed around the species significantly correlated with each axis ($r > 0.40$).

fish composition among the four reach types for temporal NMDS ordination ($F = 1.01$; $p = 0.426$). After accounting for the previously acknowledged spatial differences in darter and minnow richness (see Table 1), there was still no evidence of a change in darter richness ($p = 0.312$) or minnow richness between time periods ($p = 0.097$).

Discussion

Our monitoring and assessment of the round goby invasion gradient in the French Creek watershed has revealed several interesting patterns, which have broader implications to other invaded ecosystems. First, there has been no upstream range expansion and weak downstream establishment of round gobies over the past decade, indicating that passive downstream movement and human-assisted dispersal have been the primary means of expansion for invaded watersheds outside the Laurentian Great Lakes (Harris et al. 2024; Hemmelgarn et al. 2025). Second, round goby population densities at the invasion front have also not increased over time, despite potential changes in size structure. When comparing these conclusions with prior studies from invaded Lake Erie tributaries using similar electrofishing methods for stream habitats (see Philips et al. 2003; Krakowiak and Pennuto 2008; Kornis et al. 2013), round gobies have lower population densities and lower proportions of assemblage composition at the long-term LeBoeuf Creek monitoring site (rkm −3.4; Table 2). Interestingly, round gobies were never detected at French Creek Reference reaches during our study despite detection with other methods in deeper reaches nearby (e.g. trawling, boat electrofishing, eDNA), revealing that range expansions are occurring for a very small subset of the population (Bradshaw-Wilson et al. *unpublished data*).

Third, spatiotemporal differences were observed in round goby body size, suggesting potential demographic patterns. Round goby populations have shown an increase in body size during later years of invasion, which could be affiliated with population booms during the initial invasion followed by subsequent declines as populations achieve equilibrium (Vélez-Espino et al. 2010). Round gobies have shown a consistent bias towards smaller sized individuals at the long-term monitoring site over the past decade (see also Mueller et al. 2017). Based on literature-derived estimates from Laurentian Great Lakes populations of invasive round gobies (Table S5 in Appendix III), our samples are strongly skewed to juvenile round gobies. Given that round goby body size also increases with proximity to Lake LeBoeuf (Table 2), we currently hypothesize that Lake LeBoeuf represents the core established population and that LeBoeuf Creek represents a downstream expansion corridor for dispersing juveniles and selecting adults (*sensu* Brownscombe and Fox 2012). Variation in size and growth could also be attributed to abiotic and

biotic differences in lake and tributary environments (Kornis et al. 2017), seasonal differences in reproduction and migration (Hemmelgarn et al. 2025), and/or founder effects (Rawlings et al. 2021).

These first three conclusions about population and demographic changes requires addressing assumptions of round goby detectability. While our combination of seining and electrofishing successfully detected invasive round gobies (Appendix I), round gobies have been traditionally sampled via a variety of methods, and debate remains regarding the most effective sampling technique (Kornis et al. 2013; Byington 2020; Harris et al. 2024). As benthic fish, round gobies are most often found in non-wadeable lentic systems, which are often difficult to sample (i.e. deep, slow-moving water; Bradner et al. 2013). Round gobies can also be difficult to effectively sample individuals for all size classes with a single method, including in wadable streams (Diana et al. 2006; Brownscombe and Fox 2012; Nett et al. 2012). Nonetheless, we are confident in our conclusion that the low round goby occurrence rates and low population densities are more related to the environmental conditions of the watershed versus discrepancies in sampling efficiency.

Within the immediate invasion front, established round goby populations are localized in reaches of lower LeBoeuf Creek and are associated with environmental conditions of low dissolved oxygen and low instream habitat scores (i.e. homogenous run habitats dominated by fine substrates). The low gradient, deepwater, warmwater nature of LeBoeuf Creek matches predictions of the tributaries expected to be invaded by round gobies in the Laurentian Great Lakes (Kornis and Vander Zanden 2010; Kornis et al. 2013), including low dissolved oxygen (Krabbenhoft and Kashian 2022). Similarly, the invaded LeBoeuf Creek watershed had macroinvertebrate assemblages with notably higher proportions of crustaceans and molluscans than aquatic insects. French Creek Threatened reaches also differed in their NMDS macroinvertebrates, and were also found to have significantly higher mussel diversity than the other Reference and Upper reaches (see Clark et al. 2022). Molluscans have been documented as a dominant food resource of round gobies in their invaded ranges (Mikl et al. 2017; Bradshaw-Wilson et al. 2019; Poslednik et al. 2023). Taken together, we hypothesize that round gobies have higher performance in lentic environments than in lotic environments given that the Laurentian Great Lakes being their original invasion source (Stauffer et al. 2016B). For example, it only took round gobies two years to become the dominant fish species when they were introduced to Oneida Lake, New York (George et al. 2021). Hence, our results suggest that round goby invasions may be repressed when invaded habitats are suboptimal.

Round goby population densities can also be explained by seasonal changes in the environment (e.g. day-of-year) rather than early versus late stages of the invasion. Higher densities during early summer likely reflect spawning activity and juvenile dispersal (Byington 2020; Hemmelgarn et al. 2025). Patterns of early summer breeding invasions and emigrations of round gobies were also observed in the Laurentian Great Lake tributaries (MacInnis and Corkum 2000; Philips et al. 2003; Blair et al. 2019). Our demographic and seasonal patterns are confounded by the fact that round gobies have extended reproductive seasons, as observed in the LeBoeuf populations (Hemmelgarn et al. 2025; Figure S1 in Appendix III). Producing multiple broods in a single reproductive season is one trait contributing to the highly invasive nature of round gobies (MacInnis and Corkum 2000). Time-of-year may only be a proximate explanation of these patterns, as streamflow and temperature might be better predictors corresponding to the reproductive and juvenile dispersal periods.

Finally, no long-term changes have been induced to the native fish assemblages from the round goby invasion at our sampling reaches (i.e. same assemblages as Mueller et al. 2017), which is in stark contrast to the documentation of benthic fish declines in the Laurentian Great Lakes (Jansen and Jude 2000; Lauer et al. 2004). However, studies have also found evidence that round gobies preferentially invade high-diversity tributaries and have not caused long-term diversity changes in tributary habitats (Kornis et al. 2013). The invaded reaches of LeBoeuf Creek show lower species richness compared to the French Creek mainstem, primarily due to habitat and stream size effects. The two darter species (banded and bluebreast) most likely to co-occur with round gobies in LeBoeuf Creek have similar trophic ecologies (i.e. small dipteran specialists; Van Gray et al. 1997), with some moderate overlap in the diet of the round goby (Bradshaw-Wilson et al. 2019). Notably, common logperch also showed potential overlap in LeBoeuf Creek with round gobies, which are a species particularly susceptible to the antagonistic interactions of round gobies (Balshine et al. 2005).

Together, these results suggest two potential hypotheses for explaining the limited invasion success of round gobies in French Creek (see Enders et al. 2020). The first is the biotic resistance hypothesis, which posits that higher native diversity yields low non-native fitness (Beury et al. 2020). While the biotic resistance hypothesis has been well-tested in tropical ecosystems, French Creek represents a relatively novel, high diversity ecosystem for the invasive round goby. Tributaries of the Laurentian Great Lakes have lower native fish diversity than French Creek (Philips et al. 2003; Kornis et al. 2013), and higher native diversity can limit invasive species performance (Fitzgerald et al. 2016). The second hypothesis is the habitat filtering hypothesis because French Creek lacks optimal habitat for the round goby (i.e. habitat matching; Hayes and Barry 2008). LeBoeuf Creek, and Lake LeBoeuf specifically, provide environmental conditions that are well-suited to round gobies, closely resembling the lentic habitats of the Laurentian Great Lakes in terms of flow conditions and food resources. Alternatively, juvenile round gobies may not be as competitive in the French Creek environment because of their small body sizes in the stream environment.

Similarly, emerging round goby expansions also appear to be associated with environmental constraints on spread, establishment and biotic interactions. The spread of round gobies from Lake Michigan into the Illinois Waterway and Mississippi River has also occurred through downstream movement, whereby round gobies experience sharp declines in abundance farther from the original invasion source and have relatively low abundances (Harris et al. 2024). Round gobies have also spread eastward across New York through invasion of the New York State Canal System, which provides the homogenous and uniform habitat conditions that are likely tolerable for round gobies (George et al. 2021). While phenotypic plasticity likely plays an important role in round goby invasion performance (Masson et al. 2018; Rawlings et al. 2021), our results indicate that the spread of round gobies is heavily dependent upon the habitat and biodiversity of their invading ecosystem.

Despite the highly invasive nature of round gobies being well-documented, our conclusions suggest that the round goby invasion of French Creek has been relatively benign with no long-term population increases, limited spread, and no fish assemblage extirpations. However, demographic differences were also observed based on proximity to the original invasion source, which matches expectations of differences between core and expanding populations along invasion routes (Masson et al. 2018). Future environmental changes could lead to abrupt and rapid expansions of invasive fish that require management or conservation action (see Smith et al. 2021; Kirk et al. 2022). There is a lack of current management strategies for addressing round goby invasions, and future research is needed to understand the limits of round goby success in various environments (Masson et al. 2018). Within the United States, most information comes from invasion within watersheds of the Laurentian Great Lakes, and our study provides valuable comparative research into understanding the limits and constraints on round goby invasion success.

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Author contributions

CRediT: **Mark A. Kirk:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Visualization, Writing – original draft, Writing – review & editing; **Casey R. Bradshaw-Wilson:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing; **Kelly J. Pearce:** Conceptualization, Funding acquisition, Investigation, Project administration, Writing – original draft, Writing – review & editing.

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Data availability statement

The data and code associated with this manuscript is available at https://github.com/mkirk2118/JFE_Gobies_2026_2648202: Repository for data associated with the manuscript: 'Environmental patterns of establishment and early-stage impacts from invasive round gobies in an aquatic biodiversity hotspot'.

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