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Swimming capacity and behaviour of juvenile round goby (*Neogobius melanostomus*)

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Abstract

The round goby (*Neogobius melanostomus*) is an example of an invasive species where the adults are unimpressive swimmers and yet via human activities, they have managed to rapidly invade the Laurentian Great Lakes, the Baltic Sea and many rivers in Western Europe. The secondary spread from human-impacted sites has been attributed to adult life stages, despite their poor swimming capacity. However, the swimming capacity of early life stages of round goby has not been considered before. We therefore quantified critical swimming performance (U_{crit}), sprint swimming performance (U_{sprint}), burst swimming speeds and swimming behaviours in early juvenile round goby that ranged between 10 and 25 mm in body length. The average U_{crit}, U_{sprint} and burst speeds of these fish were an impressive 0.22, 0.34 and 0.67 m/s respectively, with the capacity of these early juveniles ranging between 41 and 79% of what has been documented for adults. Notably, fish spent more time actively swimming as current speed increased, while station holding decreased. Taken together, our findings highlight that despite their small size, early juvenile round goby are not simply passively moved by currents but have movement capacities that approach that of the much larger adults. Our study emphasizes the need to consider the swimming capacity of *all* life stages as this information will better predict dispersal and range expansion and will help to design mitigation efforts to potentially prevent the spread of this and other invasive species.

KEYWORDS
burst speed, critical swimming performance U_{crit}, invasive species, juvenile life stages, sprint swimming performance U_{sprint}, swimming behaviour

1 | INTRODUCTION

The swimming performance or movement capacity of a species affects not only their prey–predator interactions, but also their dispersal ability, reproduction and ultimately their fitness (Cano-Barbacil et al., 2020; Plaut, 2001). Dispersal is the movement of an individual from its natal habitat to a new location where it will likely settle and reproduce (Croteau, 2010), a phenomenon that can occur at various life stages. Whereas dispersal of adult fish is usually considered to be an active process, dispersal in early life stages (i.e. larvae or juveniles) has traditionally in fishes been considered more passive and a result of water movements (Hayden & Miner, 2009; Zens et al., 2017).

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Given this traditional view and the additional difficulty of studying dispersal in small-sized individuals, the movement of early life stages of fishes are often overlooked. However, emerging studies in this research area have shown that even very small, young fish can exhibit clear active behaviours that can modify or enhance their ability to disperse (Failletaz et al., 2018; Zens et al., 2017).

Invasive species serve as an excellent model to study the mechanisms that underlie movement and dispersal because the invasion of new environments is often facilitated by their ability to move. While the initial introduction of many invasive species to new environments has historically been a result of anthropogenic activities, the subsequent secondary spread of many invasive species is usually a result of their own natural dispersal tendencies (Alford et al., 2009; Fraser et al., 2015). The high success of many invasive fish species can be attributed to their strong dispersal abilities (Rehage & Sih, 2004).

Round goby (*Neogobius melanostomus*) are benthic, euryhaline fish native to the Black and Caspian Seas and an invasive species in parts of North America and Europe. In North America, they were first detected in the St. Clair River (Jude et al., 1992), but have since spread to all five Laurentian Great Lakes and some other inland watersheds (Charlebois et al., 2001; Johansson et al., 2018). Round goby were introduced to this region as well as to the Baltic Sea, Rhine and Danube Rivers in the 1990s, presumably through the uptake of young via the ballast water of transatlantic ships (Charlebois et al., 2001; Jude et al., 1992; Kornis et al., 2012). The young emerge from eggs fully developed resembling the adults, therefore are considered to lack a true larval stage (Marsden et al., 1996) and are referred to as 'early juveniles' (Hayden & Miner, 2009). These fish, which hatch from eggs about 5 mm (TL) in size (Leslie & Timmins, 2004) typically reach maturity at sizes greater than 60 mm (Gutowsky & Fox, 2012). Their aggressive behaviour, diverse diet, short spawning cycles and high pollution tolerance are all thought to have contributed to their success as an invader (Charlebois et al., 2001; McCallum et al., 2014). The greatest concern with the round goby lies in the threat they place on biodiversity, as they proliferate quickly, outcompete native species for resources (Kornis et al., 2012) and are thought to be a vector for contaminant and disease transfer (McCallum et al., 2014). Knowledge of the movement patterns of round goby is crucial to inform conservation and management efforts focused on controlling their spread.

Previous studies on adult round goby have assessed their swimming capacity using critical swimming speed (U_{crit}) and sprint speed (U_{sprint}) tests in a swim tunnel (Egger et al., 2020; Tierney et al., 2011). While U_{crit} measures prolonged swimming ability, U_{sprint} assesses sprint speed over shorter time intervals. Similar to many other benthic species, round goby utilize a 'burst- and-hold' swimming mode, adhering closely to the substrate with their fused pelvic fins. Consequently, as argued by others, U_{crit} tests likely reflect their station holding ability, whereas U_{sprint} tests provide a better measure of swimming ability due to shorter speed increment intervals (Egger et al., 2020; Tierney et al., 2011).

U_{crit} and U_{sprint} experiments have often been criticized for their lack of ecological relevance, as fish rarely encounter conditions in natural environments where current speeds increase in set increments like those in swim tunnels (Plaut, 2001). However, swim tunnel experiments are useful in illuminating ecologically relevant traits like how routine activity and body size might influence swimming abilities (Plaut, 2001). Another measure of swimming capacity that is often tested alongside the other metrics is known as burst swimming capacity, which is the fastest speed an individual can achieve in a single burst of motion while in still water. Previous studies based on these methods have demonstrated the upstream capabilities of adult round goby. For example, Egger et al. (2020) showed that adult round goby can achieve U_{crit} speeds of 0.54 ± 0.10 m/s, which is comparable to the native European bullhead (*Cottus gobio*), another benthic species that similarly demonstrates a 'burst-and-hold' swimming pattern. These authors also showed that round goby in fact have a higher capability to disperse upstream than bullheads (Egger et al., 2020). This may be in part due to their swimming behaviour, which in adults mainly composed of holding onto the substrate (Gilbert et al., 2016).

To date, there have been no studies solely focused on the swimming capacity of juvenile round goby. Adult round goby may have a higher swimming capacity compared to juveniles because they have a much greater body mass that is capable of supporting higher metabolic rates and energy usage (Rubio-Gracia et al., 2020). Alternatively, adults could have a lower swimming capacity or motivation compared to juveniles because they often enter a more sedentary phase of life during reproduction. Juvenile Atlantic salmon 'smolts', for example, were found to have a higher swimming capacity than post-spawning adult 'kelts' (Booth et al., 1997). Comparisons of swimming capacity between juveniles and adults could reveal possible changes in swimming behaviour across ontogeny, as dispersal and active movement may be particularly concentrated during a particular life stage for round goby.

In this study, we aimed to fill the knowledge gap about swimming capacity of the earliest life stages. To do so, we examined the movement capacity of early juvenile round goby smaller than 25 mm (SL) using three different measures: U_{crit}, U_{sprint} and burst speed. Additionally, we scored the behaviour of each fish in the swim tunnels as they swam against different current speeds. While critical swimming speed (U_{crit}), sprint speed (U_{sprint}) and burst speed can all provide valuable insights into an organism's locomotive abilities and endurance, the success of dispersal is also intricately linked to a variety of behavioural decisions and motivation. Rapid dispersal in motile animals depends on shifts in locomotor performance (speed and endurance) and dispersal behaviour (Llewelyn et al., 2010), with factors such as rates of movement attempts and the duration of swimming efforts playing crucial roles in determining dispersal success (Castro-Santos, 2006; Silva et al., 2018). Hence, we extended our investigation of the dispersal capacity of early juvenile round goby beyond mere swimming performance to include swimming tendencies. Quantifying these behavioural aspects associated with movement propensity can serve as a proxy for understanding the motivation and capacity of a fish species to disperse (Goerig & Castro-Santos, 2017). We predicted that larger juveniles would have higher U_{crit}, U_{sprint} and burst speeds than smaller juveniles because larger individuals have greater muscle mass to power swimming. For the same reasons, we also predicted that larger juveniles would be more active, perform more forward movements and that individual fish that were faster on one measure of swimming performance would also be faster on another.

2 | METHODS

2.1 | Fish collection and maintenance

Early juvenile round goby were collected using a seine net (6m long × 1.5m high, with a 3mm mesh size) from La Salle Marina in Burlington, Ontario between June 2022 and October 2022. The fish were transported to the Aquatic Behavioural Ecology Laboratory (ABEL) at McMaster University in Hamilton, Ontario in aerated marine coolers (90cm long × 40cm wide × 40cm high). The early juveniles used in this study had a standard length ranging from 10 to 25mm and a total mass ranging from 0.01 to 0.33g. In the laboratory, the juveniles were kept in 20-gallon aquariums (60cm long × 46cm wide × 30cm high) housing a maximum of 20 individuals. Fish were kept on a 16:8h light:dark schedule, at water temperatures of 20–21°C and were fed frozen cyclopods and ground up fish flakes twice a day.

2.2 | Experimental overview

Endurance trials and sprint trials were conducted consecutively on the same fish in a swim tunnel (5L Loligo® swim tunnel) where fish swam against a current that increased in speed increments of 0.03m/s until exhaustion (Figure 1a). The current was produced by a motor (SEW-EURODRIVE) that spun a propeller, and the speed of the current was modulated by a voltage controller that regulated the electrical voltage powering the motor. A flowmeter was used to measure the various flow speed levels; the time between the increasing speed intervals were 5min for the endurance trials and 10s for the sprint trials. Essentially, endurance trials measured swimming capacity over the long term, whereas sprint trials measured swimming capacity over the short term. Endurance trials measured an individual's critical swimming speed (U_{crit}) while the sprint speed trials measured sprint speed (U_{sprint}). A video camera (Sony FDR-AX53) positioned above the swim tunnel recorded the entire length of each trial, and a mirror was positioned in the frame of the camera so the swim tunnel chamber could be simultaneously observed from both a top view and a side view.

Burst trials were conducted in still water in troughs (70cm long × 10cm wide × 10cm high) where fish were chased by a glass probe until exhaustion (Figure 1b). These burst swim trials measured the highest speed an individual could attain in a single swimming 'burst' in the absence of a current. A video camera (Sony FDR-AX53)

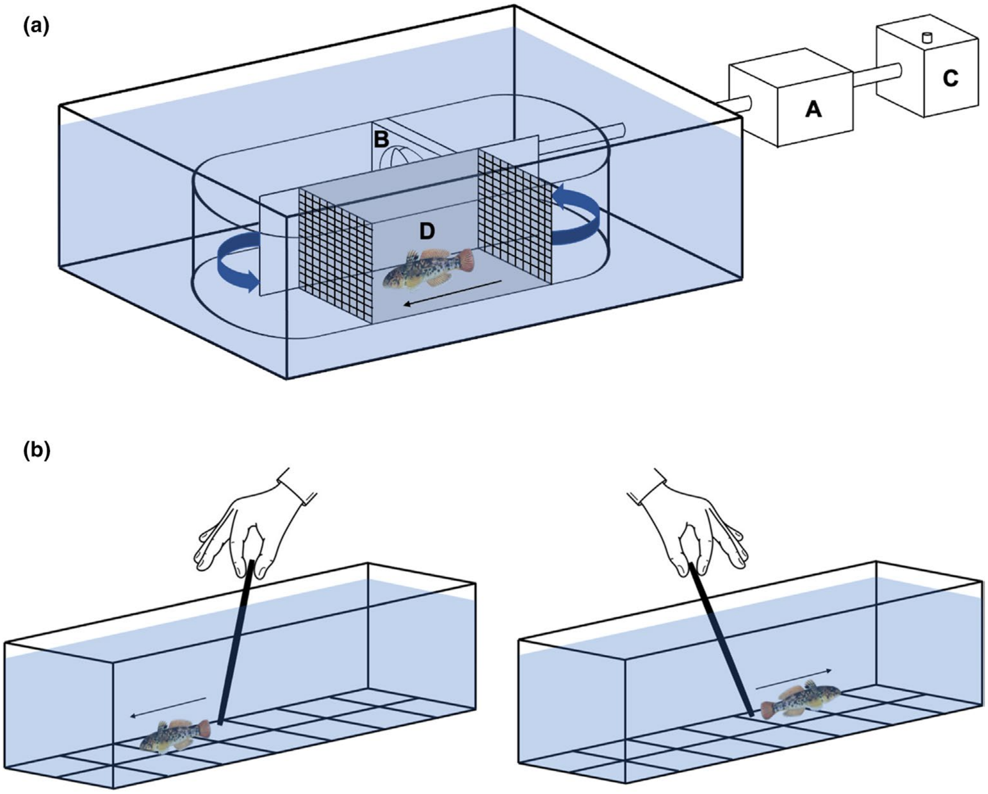

FIGURE 1 (a) Experimental set-up of swim tunnel trials. A motor (A) powered a propeller (B) that generated the current and a voltage controller (C) modulated the voltage entering the motor. Individuals were placed in a confined testing chamber (D) where they swam against the current. Arrows represent the direction of the current in the swim tunnel. (b) Experimental set-up of still water burst trials. Fish were chased with a rod in a standardized fashion in a narrow trough until they reached exhaustion.

positioned above the troughs recorded the entire length of each trial, and again, a mirror was positioned in the frame of the camera so the troughs could be simultaneously observed from both a top view and a side view. Water temperature was maintained at 20–21°C in all trials and experiments. The same individual was tested in both endurance and sprint trials, whereas still water burst trials were performed using a different set of individuals than those used in the endurance and sprint trials. At the end of the trials, we measured each fish's total mass (g) on an electronic scale (Mettler Toledo AB204-S) to the nearest 0.001 g, and total length (mm) and standard length (mm) using digital callipers to the nearest 0.01 mm. The mean standard length ± standard deviation (SD) of the fish used for the U_{crit} and U_{sprint} trials (Experiments 1 and 2) was 18.04 ± 4.11 mm ($n = 63$), while the mean standard length ± SD for the fish used in the burst speed trials (Experiment 3) was 18.28 ± 3.69 mm ($n = 74$).

2.3 | Experiment 1: U_{crit} (critical swimming speed) trials

U_{crit} trials were modified following a protocol used by Tierney et al. (2011) for adult round goby. Prior to the start of the experiment, juvenile fish were allowed to acclimate to the swim tunnel for 30 min. Once the acclimation period was over, the trial began with the current set to a speed of 0.04 m/s. Thereafter, the speed was increased by stepwise increments of 0.03 m/s every 5 min. During the trials, if a fish remained near the screen at the back of the chamber and refused to swim forward, it was stimulated to move by gently touching its tail once with a long glass rod. The trial continued if the fish swam in response to the stimulation, but if after three attempts to stimulate the fish to move, the fish did not respond, it was considered to have reached exhaustion, that speed was recorded, and the trial was consequently terminated by turning off the motor. U_{crit} was determined according to Brett's methodology (1964): $U_{crit} = V_f + V_i \times (t_{fi} \,/\, t_i)$, where U_{crit} represents the critical swimming speed, V_f is the speed of the last fully completed step (m/s), V_i denotes the speed increment of each step (0.03 m/s), t_{fi} represents the time completed on the last step and t_i stands for the duration of each step (5 min).

2.4 | Experiment 2: U_{sprint} (sprint swimming speed) trials

When a U_{crit} trial ended, each individual fish was given 30 min to recover in the swim tunnel chamber before beginning the U_{sprint} trials. U_{sprint} trials followed a protocol used by Starrs et al. (2011). The protocol was identical to that of the endurance trials, except that stepwise increases of 0.03 m/s in current speed occurred every 10 s rather than every 5 min. The highest swimming speed that the fish attained was recorded, as well as the trial start and end time, and the duration of each trial. U_{sprint} was calculated similar to U_{crit} as $U_{sprint} = V_f + V_i \times (t_{fi}/t_i)$, where V_f is the speed of the last fully completed step (m/s), V_i denotes the speed increment of each step (0.03 m/s), t_{fi} represents the time completed on the last step and t_i stands for the duration of each step (10 s).

2.5 | Experiment 3: Still water burst trials

Prior to the start of the trial, fish were introduced into a small enclosure at one end of the trough to acclimate for 30 min (Figure 1b). Eight individuals were run consecutively in separate troughs, with the start time staggered 2 min apart. Once the acclimation period was over, the enclosure was opened and then removed, allowing the individual to access the entire length of the trough. Fish were chased down the length of the trough by moving a probe in a standardized manner along the trough's bottom behind them. A ~ 5 cm distance was maintained between the probe and the fish's tail. When the fish no longer responded to the moving probe, the individual was deemed to have reached exhaustion and the trial was terminated. The trial start time and end time, and the duration were recorded. As explained above, the burst speed trials were recorded using two adjacent video cameras, both of which captured a top view of the experimental arena produced by a mirror positioned above the trough. One camera filmed the entire length of the trial in real time while a second slow-motion camera filmed only the fish's first burst in each trial and was used to measure their burst speed. Recordings on the slow-motion camera were controlled through the Edge Imaging smartphone application.

2.6 | Video behavioural analyses

Slow-motion recordings of still water burst trials were used to measure the fastest burst speed (m/s). Video recordings of endurance and sprint trials (U_{crit} and U_{sprint}) were uploaded to Behavioural Observation Research Interactive Software (BORIS version 7.9.1) and were scored for three separate movement behaviours: (1) active swimming (a combination of swimming forward: when the fish used all fins to move towards the front of the tank against the current, and any upward swimming: when the fish moved towards the water's surface), (2) sliding back (when the fish moved with the current towards the back of the tank) and (3) station holding (when the fish stayed in place by actively gripping the bottom of the tank with its fused pelvic fin). Using the analysis tool in BORIS, the time intervals of each speed step were inputted to calculate the length of time spent performing each behaviour and were converted to percentage of the trial time based on the length of the trial. Behavioural analysis was conducted on the endurance and sprint trial videos for 45 juvenile round goby trials of the 63 fish trials run (18 trials were excluded due to the lack of sufficient clarity in recorded videos for detailed behavioural measures). Following Gilbert et al. (2016), the critical substrate holding velocity (U_{hold}) was calculated as the last flow speed that fish spent more than 50% of time station holding during the U_{crit} trials.

2.7 | Statistical analyses

All statistical analyses were performed using R (version 4.3.2, R Core Team, 2024). Prior to conducting any statistical analysis, the data were visually assessed for normality and homogeneity of variance using histograms and quantile–quantile graphs. Additionally, Shapiro–Wilk and Bartlett tests were performed to formally test for normality and homogeneity of variances, respectively. The swimming speed data (U_{crit}, U_{sprint}, U_{hold}, burst speed) and behavioural observations (swimming, station holding, sliding) were analysed using generalised additive models (GAMs) with a Gaussian distribution. GAMs were individually applied to explore the relationships between each individual swimming metric (e.g. sprint, endurance, and burst capacities) and behaviour, with body size (standard length) as the predictor variable. The choice of using GAMs was motivated because by employing smooth functions they are well suited to capture complex non-linear relationships and account for potential non-linearity in the data (Swartzman et al., 1995). These models were assessed for goodness of fit through diagnostic checks, including evaluating residual normality and employing AIC (Akaike Information Criterion) for model comparison. The percentage of time that individuals performed each behaviour was compared across different water velocities using linear mixed-effects models, with water velocity as a fixed effect and fish ID as a random effect to account for the repeated measures. Only the first five velocities were used in this analysis since some fish did not reach higher velocities. Model fitting and interpretation were conducted using the 'mgcv' package in R (version 4.3.2). R-squared (R^2) values were used to assess the direction and strength of relationships between variables, while a significance level of $\alpha = .05$ was set to determine significant correlations. The difference between U_{hold} and U_{crit} was assessed using a paired *t*-test.

3 | RESULTS

Early juvenile round goby had an average U_{crit} of 0.22 ± 0.06 m/s (10.2 ± 2.6 body lengths (BL)/s), a mean U_{sprint} of 0.34 ± 0.08 m/s (16.3 ± 4.6 BL/s) and a mean burst speed of 0.66 ± 0.02 m/s (30.7 ± 1 BL/s). U_{crit} values ranged from 0.11 to 0.39 m/s (5.2 to 15.8 BL/s), U_{sprint} ranged from 0.19 to 0.60 m/s (9.3 to 29.9 BL/s) and burst speed ranged from 0.22 to 1.13 m/s (10.1 to 43.8 BL/s). Body size measured as standard length was positively correlated with U_{crit}, U_{sprint} and burst speed, meaning that larger fish moved faster (Figure 2a–c). However, albeit significant, U_{crit} and burst speed only demonstrated a modest relationship with standard length (GAMs, U_{crit} $R^2 = 0.17$, $p < .01$; burst speed $R^2 = 0.29$, $p < .001$) and U_{sprint} demonstrated a fairly weak relationship with standard length ($R^2 = 0.08$, $p = .03$).

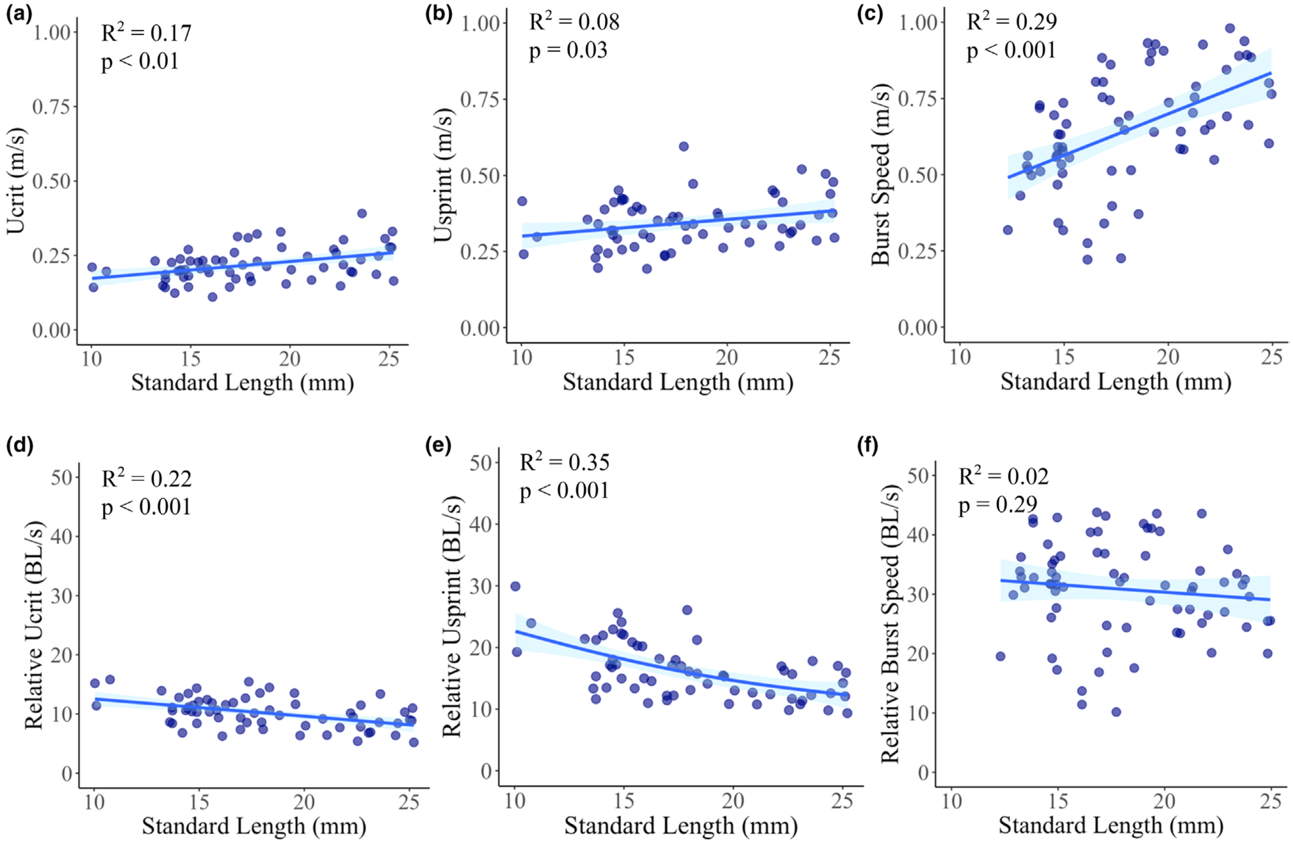

FIGURE 2 (a) U_{crit} (m/s), (b) U_{sprint} (m/s), (c) burst speed (m/s), (d) relative U_{crit} (BL/s = Body Lengths per second), (e) relative U_{sprint} (BL/s) and (f) relative burst speed (BL/s) as a function of standard length (mm). The blue lines represent generalized additive model (GAM) smoother fitted to the data, with a shaded blue area denoting the 95% confidence interval. Points represent individual data observations.

When body length was controlled for, we found that juveniles' relative U_{crit} and U_{sprint} were negatively correlated with their standard length (Figure 2d,e), suggesting that smaller fish actually had a higher relative swimming capacity given their overall smaller body sizes. The strength of this negative correlation was moderate (GAMs, U_{crit}, $R^2=0.22$, $p<.001$, Figure 2d; U_{sprint} $R^2=0.35$, $p<.001$, Figure 2e) and there was no clear negative correlation between burst speed and standard length once body mass was controlled ($R^2=0.02$, $p=.29$, Figure 2f). Absolute U_{crit} and U_{sprint} were strongly, positively correlated with each other ($R^2=0.73$, $p<.001$; Figure 3), so juvenile round goby with a high U_{crit} tended to also have a high U_{sprint}.

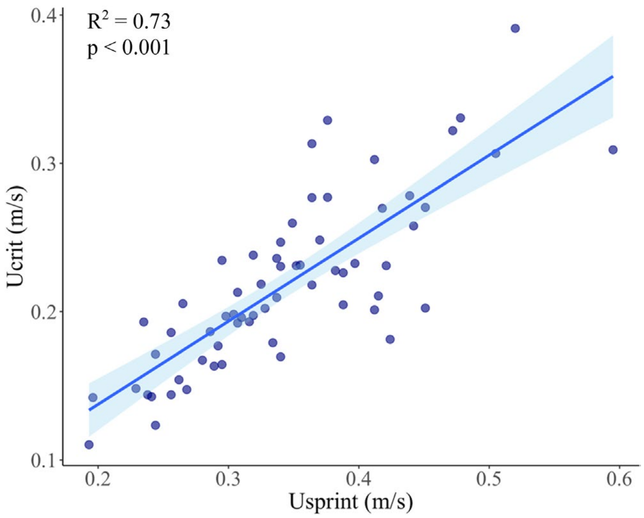

FIGURE 3 Scatter plot illustrating the correlation between U_{crit} (m/s) and U_{sprint} (m/s). The blue lines represent generalized additive model (GAM) smoother fitted to the data, with a shaded blue area denoting the 95% confidence interval. Points represent individual data observations.

Early juvenile round goby spent the majority of their U_{crit} and U_{sprint} trials in a stationary position (44% and 38% of the trial time respectively), holding on to the substrate with their fused pelvic fins. Average critical station holding speed (U_{hold}) was 0.14 ± 0.01 m/s and it was not correlated with fish body size (GAM, $R^2=0.11$, $p=.67$). U_{hold} was clearly lower than U_{crit} (−36%; $t_{44}=6.72$, $p<.001$). Juveniles spent on average 28% of the U_{crit} trials and 36% of U_{sprint} trials actively swimming, while spending less time sliding back (19% in both U_{crit} and U_{sprint} trials). Like the case for U_{crit}, U_{sprint} and burst speed, body size was also correlated to duration of swimming (Figure 4a–c). Larger fish spent more time actively swimming in the U_{crit} (GAM, $R^2=0.44$, $p=.003$) and U_{sprint} trials (GAM, $R^2=0.26$, $p<.001$). The time spent station holding significantly decreased with fish size in U_{crit} trials (GAM, $R^2=0.27$, $p=.04$), however this negative correlation was not statistically clear in the U_{sprint} trials (GAM, $R^2=0.08$, $p=.06$). Sliding did not show a clear correlation with body size during U_{crit} (GAM, $R^2=0.02$, $p=.38$) or U_{sprint} trials (GAM, $R^2=0.01$, $p=.47$).

The swimming behaviour of early juvenile round goby changed as water velocity increased. Station holding declined during the later faster current steps (linear mixed-effect model; U_{crit}: $F=12.99$, $p<.001$; U_{sprint}: $F=130.22$, $p<.001$), while active swimming and sliding both showed the opposite trend, each increasing in relation to water velocity (linear mixed-effect models; U_{crit}: $F=4.65$, $p=.03$; $F=59.71$, $p<.001$; U_{sprint}: $F=115.31$, $p<.001$; $F=11.99$, $p<.001$).

4 | DISCUSSION

Previous studies that have assessed the swimming capacity of round goby have mainly focused on adults and researchers have overlooked juvenile movement, which may be due to the assumption that juveniles simply move passively with currents (Janáč et al., 2013; Lechner et al., 2016). However, our study demonstrates that juveniles have a strong swimming capacity; not only can they

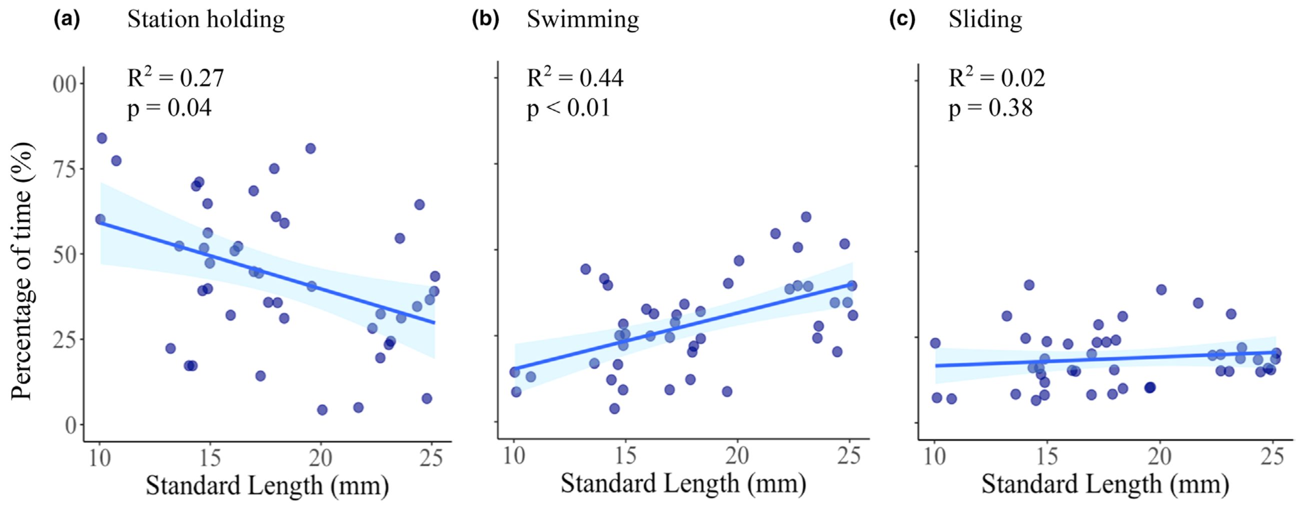

FIGURE 4 Scatter plots showing the relationships between the ratio of (a) holding, (b) swimming and (c) sliding behaviours relative to the length of fish during the endurance trials. The blue lines represent generalized additive model (GAM) smoother fitted to the data, with a shaded blue area denoting the 95% confidence interval. Points represent individual data observations.

swim and hold their position against considerable moving currents for extended periods of time, but some of the juveniles in this study achieved speeds close to the swim speeds that are typical of adults (Egger et al., 2020; Tierney et al., 2011).

As observed in other species, body size was a good predictor of swimming capacity in the juvenile round goby tested, with body length positively correlating with U_{crit}, U_{sprint} and burst speed (Hogan et al., 2007; Mateus et al., 2008; Ojanguren & Braña, 2003; Rubio-Gracia et al., 2020). Similar to what has been reported for adult round goby, juveniles showed a 'burst-and-hold' swimming style, with short periods of active swimming followed by attempts to station hold (Egger et al., 2020; Hoover et al., 2003; Tierney et al., 2011). Larger juvenile round goby actively swam for longer periods of time compared to smaller juveniles and the smallest juveniles spent more time station holding. In this study, early juvenile round goby spent the majority of the time (43%) station holding and performed this behaviour throughout the trials. Adult round goby in a study by Gilbert et al. (2016) also spent most of the trial time (66%) station holding. These results are in contrast with another study on adult round goby where holding behaviour occurred only 23% of the time and was limited to only the earlier, lower current speeds (Egger et al., 2020). This contrast between study results is most likely due to methodological differences since in the present study on juveniles and the one done by Gilbert et al. (2016) on adults, swimming was stimulated as soon as the fish touched the rear grid of swim tunnel, but Egger et al. (2020) instead allowed resting at the rear end of the swim tunnel during U_{crit} trials. As the current became stronger, juveniles began to swim more. Under particular environmental conditions, like fast flowing water, remaining in place by using their pelvic fin for suction may be an energy-saving strategy that is favoured over active swimming by small juveniles.

As mentioned above, some juveniles were capable of achieving speeds recorded for adult round goby by Tierney et al. (2011), who clocked average adult U_{crit} speeds at 0.35 ± 0.01 m/s, average U_{sprint} speeds at 0.65 ± 0.02 m/s, and average burst speeds at 0.97 ± 0.08 m/s. Our juveniles also matched the speeds recorded by Egger et al. (2020) for adult round goby averaging around 0.54 ± 0.10 m/s for U_{crit} and 0.43 ± 0.14 m/s for U_{sprint}. As with swimming behaviour, differences in methodology between the two previous adult-focused studies may explain the different U_{crit} and U_{sprint} values reported by Tierney et al. (2011) versus Egger et al. (2020). For example, there were differences in the stepwise flow speed increment used in U_{crit} and U_{sprint} trials (e.g. 0.10 m/s vs. 0.03 m/s for U_{crit} trials), the specific order that the experiments were run and the type and frequency of stimulation (physical contact with an object vs. an electrified grid) used to motivate fish to swim when they touched the rear grid of the testing chamber. Early juveniles in our study demonstrated similar movement patterns to those reported by Tierney et al. (2011) where burst speeds were the highest, followed by U_{sprint} speeds and then U_{crit} speeds. These similarities may be attributed to our experimental protocols and stepwise increments which were similar in magnitude to those used in Tierney et al. (2011). In addition, average U_{hold} for juveniles in the present study was much lower than U_{crit} compared to what has been reported by Gilbert et al. (2016) for adult round goby (−36% compared to −18%). This suggests that juveniles rely on behaviours other than station holding more than adults do to achieve U_{crit}. This difference between adults and juveniles appears to be more related to the increased sliding behaviour in juveniles (19% in this study compared to only 6% in adults), rather than differences in active swimming (28% for both juveniles and adults). This increased reliance on sliding behaviour may reflect juveniles' need to conserve energy while still maintaining their position in flowing waters. The similar rates of active swimming between juveniles and adults suggest that while both life stages employ this strategy, juveniles additionally use sliding to cope with their lower holding capacities.

Although larger juvenile round goby tended to achieve higher absolute swimming speeds, smaller juveniles achieved higher relative swimming speeds. We observed that once body length was accounted for, smaller juveniles in fact swam faster than larger juveniles. The inverse relationship between absolute and relative swimming speed is a common pattern among fishes (e.g. He et al., 2013; Mateus et al., 2008) and is a result of allometric growth. As body size increases, the relative values of surface area and muscle mass scale up so that absolute swimming speed increases but relative swimming speed decreases (Cai et al., 2020). Studies have also shown that swimming speed is limited by tail beat frequency and that smaller fish can achieve higher tail beat frequencies than larger fish (Bainbridge, 1958; Wardle, 1975).

The strong positive correlation between U_{crit} and U_{sprint} highlights the remarkable repeatability of individual swimming performance, suggesting that fish that excel in sustained swimming capacity likely exhibit strong sprinting performance as well. The high correlation between the two measures underscores the consistency and predictability of swimming abilities within individuals. U_{crit} and U_{sprint} tests have been argued to provide different measures of swimming capacity as U_{sprint} is thought to be a better suited measure for benthic species since it forces the individual to swim for more of the trial while U_{crit} trials best capture a fish's maximum sustained swimming speed (Egger et al., 2020; Tierney et al., 2011). In the context of fish dispersal and passage through instream structures, Starrs et al. (2011) argue that U_{sprint} provides the more relevant measure. The swimming mode that a fish exhibits while migrating through turbulent water is more similar to the speeds and times observed in sprint swimming than sustained swimming tests, particularly for small-bodied, benthic fishes (Egger et al., 2020). In contrast, Crawford et al. (2023) have recently argued that there are no real differences between the swimming speeds obtained from U_{crit} tests versus U_{sprint} tests, even for benthic species that demonstrate station holding behaviour like the round goby. However, our findings show that early juvenile round goby had much higher U_{sprint} than U_{crit} values which suggests that these measures may capture different aspects of swimming performance. To fully test the claim about the relevancy of U_{crit} versus U_{sprint} measures, more species need to be tested beyond the two used in the Crawford et al. (2023) study (the īnanga, *Galaxias maculatus* and the banded kokopu, *Galaxias fasciatus*).

4.1 | Implications for round goby dispersal and invasion potential

Studies that have assessed the upstream dispersal patterns of round goby have suggested a 'bigger is better' hypothesis; where round goby at the invasion front (i.e. newly established areas) are expected to typically be larger fish and be in better body condition than individuals in longer established areas. This bigger is better idea contradicts the theory that upstream movement is a result of weak or juvenile individuals being driven out of high-density areas due to high intraspecific competition (Brandner et al., 2013, 2018). However, a more recent study by Šlapansky et al. (2020) demonstrated a contrary result. Following a stimulated colonization event (after releasing a larger number of adult individuals from a single point), smaller, mostly male goby moved further and were often the first colonizers in uninvaded areas (Šlapansky et al., 2020). This concentrated release of individuals resulted in higher movement rates than are typically observed in established populations, where upstream movement dominates (Šlapansky et al., 2020). The surprisingly high capacity of early juveniles to attain swimming speeds typical of adults as demonstrated in our study suggests that juvenile round goby have the capacity to lead and contribute significantly to range expansion of this species and be present at the invasion fronts. Furthermore, the unexpectedly strong swimming abilities observed in early juvenile round goby may be linked to their unique life history strategies and behaviours. While adult round goby are typically benthic, closely associated with the substrate (Kornis et al., 2012), juvenile round goby have been shown to exhibit diel vertical migration, where they can move between different water depths (Hayden & Miner, 2009; Hensler and Jude, 2007). This behavioural flexibility may contribute to the development of robust swimming abilities in juvenile round goby, which in turn could give them the ability to navigate diverse aquatic environments.

4.2 | Implications for round goby management strategies

Not only do our findings expand what we know about the movement of juvenile round goby, but they can also inform strategies to manage the spread of round goby more effectively. The eradication of invasive species is not considered practical for species, such as the round goby, that have already spread so far and wide (Green & Grosholz, 2020). Exclusion barriers like dams, culverts, and fish passes have been used to restrict the spread of aquatic invasive species, but barriers can have unintended negative consequences for native species by fragmenting habitats and excluding native species (Cooney & Kwak, 2013; Jones et al., 2021). Current strategies focus on designing barriers that selectively block invasive species while providing passage to native species. A goal of management is to design barriers that restrict the upstream dispersal of round goby via flow rates while protecting native species (Egger et al., 2020; Tierney et al., 2011). Egger et al. (2020) demonstrated that round goby were incapable of passing a vertical slot fish pass with a hydraulic barrier but that two native European benthic species, the European bullhead (*Cottus gobio*) and the gudgeon (*Gobio gobio*), were able to pass such barriers. A related study using the same three species demonstrated that passage of round goby was prevented at flow speeds of 0.97–1.04 m/s but gudgeon and bullhead were able to pass the hydraulic barrier (Wiegleb et al., 2022). In areas that largely contain juvenile round goby, prevention for spread might include implementing barriers with flow rates that exceed the U_{crit} and/or U_{sprint} of juvenile round goby, but not the U_{crit} and/or U_{sprint} of native species. Future studies are needed that compare the swimming capacity of juvenile native species with the capacity of juvenile round goby and facilitate the effective design of these juvenile specific barriers.

AUTHOR CONTRIBUTIONS

S. Z. and S. B. developed the study. S. Z. conducted the statistical analyses, reviewed and helped write the manuscript, and oversaw and assisted in running all the experiments. E. C. performed the Ucrit and Usprint trials, wrote the first draft of the manuscript, and assisted with statistical analyses. O. C. analysed the behavioural videos, contributed to the statistical analyses, reviewed, and assisted with writing the manuscript. Q. C. conducted the burst speed trials, assisted with Ucrit and Usprint trials, and reviewed the manuscript. All authors contributed to the writing and revision of the final manuscript. S. Z. and S. B. provided supervision.

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CONFLICT OF INTEREST STATEMENT

We declare no financial or non-financial conflicts of interest.

DATA AVAILABILITY STATEMENT

All manuscript data and R code for analysis and figure generation will be archived with the McMaster University of Portal on MacSphere.

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REFERENCES

Alford, R. A., Brown, G. P., Schwarzkopf, L., Phillips, B. L., & Shine, R. (2009). Comparisons through time and space suggest rapid evolution of dispersal behaviour in an invasive species. *Wildlife Research*, *36*(1), 23–28. https://doi.org/10.1071/WR08021

Bainbridge, R. (1958). The speed of swimming of fish as related to size and to frequency and amplitude of the tail beat. *Journal of Experimental Biology*, *35*(1), 109–133. https://doi.org/10.1242/jeb.35.1.109

Booth, R. K., Bombardier, E. B., McKinley, R. S., Scruton, D. A., & Goosney, R. F. (1997). Swimming performance of post spawning adult (kelts) and juvenile (smolts) Atlantic salmon, Salmo salar. Canadian Manuscript Report of Fisheries and Aquatic Sciences. 2406.

Brandner, J., Cerwenka, A. F., Schliewen, U. K., & Geist, J. (2013). Bigger is better: Characteristics of round gobies forming an invasive front in the Danube River. *PLoS One*, *8*(9), e73036. https://doi.org/10.1371/journal.pone.0073036

Brandner, J., Cerwenka, A. F., Schliewen, U. K., & Geist, J. (2018). Invasion strategies in round goby (*Neogobius melanostomus*): Is bigger really better? *PLoS One*, *13*(1), e0190777. https://doi.org/10.1371/journal.pone.0190777

Cai, L., Chen, J., Johnson, D., Tu, Z., & Huang, Y. (2020). Effect of body length on swimming capability and vertical slot fishway design. *Global Ecology and Conservation*, *22*, e00990. https://doi.org/10.1016/j.gecco.2020.e00990

Cano-Barbacil, C., Radinger, J., Argudo, M., Rubio-Gracia, F., Vila-Gispert, A., & García-Berthou, E. (2020). Key factors explaining critical swimming speed in freshwater fish: A review and statistical analysis for Iberian species. *Scientific Reports*, *10*(1), 18947. https://doi.org/10.1038/s41598-020-75974-x

Castro-Santos, T. (2006). Modeling the effect of varying swim speeds on fish passage through velocity barriers. *Transactions of the American Fisheries Society*, *135*(5), 1230–1237.

Charlebois, P. M., Corkum, L. D., Jude, D. J., & Knight, C. (2001). The round goby (*Neogobius melanostomus*) invasion: Current research and future needs. *Journal of Great Lakes Research*, *27*(3), 263–266. https://doi.org/10.1016/S0380-1330(01)70641-7

Cooney, P., & Kwak, T. J. (2013). Spatial extent and dynamics of dam impacts on tropical Island freshwater fish assemblages. *Bioscience*, *63*(3), 176–190. https://doi.org/10.1525/bio.2013.63.3.6

Crawford, R., Gee, E., Dupont, D., Hicks, B., & Franklin, P. (2023). No difference between critical and sprint swimming speeds for two galaxiid species. *Journal of Fish Biology*, *102*, 1141–1148. https://doi.org/10.1111/jfb.15355

Croteau, E. K. (2010). Causes and consequences of dispersal in plants and animals. *Nature Education Knowledge*, *3*(10), 12.

Egger, B., Wiegleb, J., Seidel, F., Burkhardt-Holm, P., & Hirsch, P. E. (2020). Comparative swimming performance and behaviour of three benthic fish species: The invasive round goby (*Neogobius melanostomus*), the native bullhead (*Cottus gobio*), and the native gudgeon (*Gobio gobio*). *Ecology of Freshwater Fish*, *30*, 391–405. https://doi.org/10.1111/eff.12592

Faillettaz, R., Paris, C. B., & Irisson, J.-O. (2018). Larval fish swimming behaviour alters dispersal patterns from marine protected areas in the north-western Mediterranean Sea. *Frontiers in Marine Science*, *5*, 97. https://doi.org/10.3389/fmars.2018.00097

Fraser, E. J., Lambin, X., Travis, J. M. J., Harrington, L. A., Palmer, S. C. F., Bocedi, G., & Macdonald, D. W. (2015). Range expansion of an invasive species through a heterogenous landscape – The case of American mink in Scotland. *Diversity and Distributions*, *21*(8), 888–900. https://doi.org/10.1111/ddi.12303

Gilbert, M. J., Barbarich, J. M., Casselman, M., Kasurak, A. V., Higgs, D. M., & Tierney, K. B. (2016). The role of substrate holding in achieving critical swimming speeds: A case study using the invasive round goby (*Neogobius melanostomus*). *Environmental Biology of Fishes*, *99*, 793–799.

Goerig, E., & Castro-Santos, T. (2017). Is motivation important to brook trout passage through culverts? *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(6), 885–893.

Green, S. J., & Grosholz, E. D. (2020). Functional eradication as a framework for invasive species control. *Frontiers in Ecology and the Environment*, *19*(2), 98–107. https://doi.org/10.1002/fee.2277

Gutowsky, L. F. G., & Fox, M. G. (2012). Intra-population variability of life-history traits and growth during range expansion of the invasive round goby, Neogobius Melanostomus. *Fisheries Management and Ecology*, *19*(1), 78–88.

Hayden, T. A., & Miner, J. G. (2009). Rapid dispersal and establishment of a benthic Ponto-Caspian goby in Lake Erie: Diel vertical migration of early juvenile round goby. *Biological Invasions*, *11*, 1767–1776. https://doi.org/10.1007/s10530-008-9356-5

He, X., Lu, S., Liao, M., Zhu, X., Zhang, M., Li, S., You, X., & Chen, J. (2013). Effects of age and size on critical swimming speed of juvenile Chinese sturgeon *Acipenser sinensis* at seasonal temperatures. *Journal of Fish Biology*, *82*(3), 1047–1056. https://doi.org/10.1111/j.1095-8649.2012.12015.x

Hensler, S. R., & Jude, D. J. (2007). Diel vertical migration of round goby larvae in the Great Lakes. *Journal of Great Lakes Research*, *33*(2), 295–302.

Hogan, J. D., Fisher, R., & Nolan, C. (2007). Critical swimming speed of settlement-stage coral reef fishes from the Carribean: A methodological and geographical comparison. *Bulletin of Marine Science*, *80*(1), 219–231.

Hoover, J. J., Adams, S. R., & Killgore, K. J. (2003). *Can hydraulic barriers stop the spread of the round goby? Aquatic nuisance species program ERDC/TN ANSRP-0301*. Engineer Research and Development Center (U.S.).

Janáč, M., Šlapansky, L., Valová, Z., & Jurajda, P. (2013). Downstream drift of round goby (*Neogobius melanostomus*) and tubenose goby (*Proterorhinus semilunaris*) in their non-native area. *Ecology of Freshwater Fish*, *22*(3), 430–438. https://doi.org/10.1111/eff.12037

Johansson, M. L., Dufour, B. A., Wellband, K. W., Corkum, L. D., MacIsaac, H. J., & Heath, D. D. (2018). Human-mediated and natural dispersal of an invasive fish in the Great Lakes. *Heredity*, *120*(6), 533–546. 10.1038%2Fs41437-017-0038-x

Jones, P. E., Tummers, J. S., Galib, S. M., Woodford, D. J., Hume, J. B., Silva, L. G. M., Braga, R. R., Garcia de Leaniz, C., Vitule, J. R. S., Herder, J. E., & Lucas, M. C. (2021). The use of barriers to limit the spread of aquatic invasive animal species: A global review. *Frontiers in Ecology and Evolution*, *9*, 611631. https://doi.org/10.3389/fevo.2021.611631

Jude, D. J., Reider, R. H., & Smith, G. R. (1992). Establishment of *Gobiidae* in the Great Lakes Basin. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*(2), 416–421. https://doi.org/10.1139/f92-047

Kornis, M. S., Mercardo-Silva, N., & Vander Zanden, M. J. (2012). Twenty years of invasion: A review of round goby *Neogobius melanostomus* biology, spread and ecological implications. *Journal of Fish Biology*, *80*(2), 235–285. https://doi.org/10.1111/j.1095-8649.2011.03157.x

Lechner, A., Keckeis, H., & Humphries, P. (2016). Patterns and processes in the drift of early developmental stages of fish in rivers: A review. *Reviews in Fish Biology and Fisheries*, *26*, 471–489.

Leslie, J. K., & Timmins, C. A. (2004). Description of age-0 round goby, *Neogobius melanostomus Pallas* (Gobiidae), and ecotone utilisation in St. Clair lowland waters, Ontario. *The Canadian Field-Naturalist*, *118*(3), 318–325.

Llewelyn, J., Phillips, B. L., Alford, R. A., Schwarzkopf, L., & Shine, R. (2010). Locomotor performance in an invasive species: Cane toads from the invasion front have greater endurance, but not speed, compared to conspecifics from a long-colonised area. *Oecologia*, *162*, 343–348.

Marsden, J. E., Charlebois, P., Wolfe, K., Jude, D. J., & Rudnicka, S. (1996). *The round goby (Neogobius melanostomus): A review of European and north American literature*. Illinois Natural History Survey Technical Reports.

Mateus, C. S., Quintella, B. R., & Almeida, P. R. (2008). The critical speed of Iberian barbel *Barbus bocagei* in relation to size and sex. *Journal of Fish Biology*, *73*(7), 1783–1789. https://doi.org/10.1111/j.1095-8649.2008.02023.x

McCallum, E. S., Charney, R. E., Marenette, J. R., Young, J. A. M., Koops, M. A., Earn, D. J. D., Bolker, B. M., & Balshine, S. (2014). Persistence of an invasive fish (*Neogobius melanostomus*) in a contaminated ecosystem. *Biological Invasions*, *16*, 2449–2461. https://doi.org/10.1007/s10530-014-0677-2

Ojanguren, A. F., & Braña, F. (2003). Effects of size and morphology on swimming performance in juvenile brown trout (*Salmo trutta* L.). *Ecology of Freshwater Fish*, *12*(4), 241–246. https://doi.org/10.1046/j.1600-0633.2003.00016.x

Plaut, I. (2001). Critical swimming speed: Its ecological relevance. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *131*(1), 41–50. https://doi.org/10.1016/S1095-6433(01)00462-7

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Rehage, J. S., & Sih, A. (2004). Dispersal behavior, boldness, and the link to invasiveness: A comparison of four Gambusia species. *Biological Invasions*, *6*(3), 379–391.

Rubio-Gracia, F., García-Berthou, E., Guasch, H., Zamora, L., & Vila-Gispert, A. (2020). Size-related effects and the influence of metabolic traits and morphology on swimming performance in fish. *Current Zoology*, *66*(5), 493–503. https://doi.org/10.1093/cz/zoaa013

Silva, A. T., Lucas, M. C., Castro-Santos, T., Katopodis, C., Baumgartner, L. J., Thiem, J. D., … Cooke, S. J. (2018). The future of fish passage science, engineering, and practice. *Fish and Fisheries*, *19*(2), 340–362.

Šlapansky, L., Janáč, M., Roche, K., & Jurajda, P. (2020). Round goby movement in a non-navigable river. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(3), 475–483. https://doi.org/10.1139/cjfas-2018-0488

Starrs, D., Ebner, B. C., Lintermans, M., & Fulton, C. J. (2011). Using sprint swimming performance to predict upstream passage of the endangered Macquarie perch in a highly regulated river. *Fisheries Management and Ecology*, *18*(5), 360–374.

Swartzman, G., Silverman, E., & Williamson, N. (1995). Relating trends in walleye pollock (Theragra chalcogramma) abundance in the Bering Sea to environmental factors. *Canadian Journal of Fisheries and Aquatic Sciences*, *52*(2), 369–380.

Tierney, K. B., Kasurak, A. V., Zielinski, B. S., & Higgs, D. M. (2011). Swimming performance and invasion potential of the round goby. *Environmental Biology of Fishes*, *92*, 491–502. https://doi.org/10.1007/s10641-011-9867-2

Wardle, C. S. (1975). Limit of fish swimming speed. *Nature*, *255*, 725–727. https://doi.org/10.1038/255725a0

Wiegleb, J., Hirsch, P. E., Seidel, F., Rauter, G., & Burkhardt-Holm, P. (2022). Flow, force, behaviour: Assessment of a prototype hydraulic barrier for invasive fish. *Hydrobiologia*, *849*, 1001–1019. https://doi.org/10.1007/s10750-021-04762-z

Zens, B., Glas, M., Tritthart, M., Habersack, H., & Keckeis, H. (2017). Movement patterns and rheoreaction of larvae of a fluvial specialist (nase, *Chondrostoma nasus*): The role of active versus passive components of behaviour in dispersal. *Canadian Journal of Fisheries and Aqautic Sciences*, *75*(2), 193–200. https://doi.org/10.1139/cjfas-2016-0276

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