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ORIGINAL PAPER

Twenty years in the making: long term population dynamics of an invasive fish in a contaminated ecosystem

Adrienne McLean · Sina Zarini · Erin S. McCallum · Julie R. Marentette · Marten A. Koops · Benjamin M. Bolker · Sigal Balshine

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Abstract Invasive species are a global problem with large ecological and economic costs. A better understanding of how invasive species populations change over time, how these species become integrated into ecosystems, and how their population demographics vary across different environments could help inform management priorities and shape control strategies. For 20 years (2002–2022), we have monitored round goby (*Neogobius melanostomus*) in Hamilton Harbour, Canada, an industrial harbour and an Area of Concern with high levels of contaminants. We sampled round goby across six sites that vary in contamination levels. We first quantified changes in round goby population demographics and morphology over a twenty-year period and second, we compared how abundance and other life history trajectories differ between sites of high and low contamination. Round goby abundance and body length both decreased over the study period. In contrast, body condition, gonadosomatic index (GSI), and the proportion of guarding parental males in the population increased over time. Over the many years of monitoring, there was no clear difference in round goby abundance between sites of high and low contamination, but individuals from sites of high contamination were smaller, had larger gonad investment, and higher hepatosomatic index compared to round goby from sites of low contamination. We also found there were fewer guarding parental males at sites of high contamination. Our results are valuable because they provide insights into how invasive species interact with different invaded habitats over the long-term. This information can help researchers and managers understand the effects of invasive species and develop strategies to predict, prevent, and manage them.

Keywords Area of Concern · Round goby · Invasive species · Hamilton Harbour · Morphology

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A. McLean (✉) · S. Zarini · E. S. McCallum · J. R. Marentette · S. Balshine
Department of Psychology, Neuroscience & Behaviour, McMaster University, 1280 Main Street West, Hamilton, ON L8S 4K1, Canada
e-mail: adrianne.mclean5@gmail.com

E. S. McCallum
Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Skogsmarkgränd 1, 906 42, Umeå, Sweden

M. A. Koops
Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada, 867 Lakeshore Road, Burlington, ON L7S 1A1, Canada

B. M. Bolker
Department of Mathematics and Statistics, McMaster University, 1280 Main Street West, Hamilton, ON L8S 4K1, Canada

B. M. Bolker
Department of Biology, McMaster University, 1280 Main Street West, Hamilton, ON L8S 4K1, Canada

Introduction

Invasive species are non-native species that enter, spread, and degrade ecosystem function (Alpert et al. 2000; Palmer et al. 2004), often inflicting large economic costs (Pimentel et al. 2005; Haubrock et al. 2021). These costs have motivated scientists and resource managers to develop more effective strategies for invasive species management. Given the difficulties associated with full eradication once an invasive species has been introduced, control measures intended to reduce abundance and restrict movement of an invasive species after it establishes are commonly used as invasive species management tools (Pyšek and Richardson 2010; Pyšek et al. 2020).

Both the effectiveness of control measures and our knowledge of the invasion process could be improved by better understanding the invasion trajectory (Flores-Moreno et al. 2015). Knowing how invasive species populations change over time and across environments can provide information critical to understanding how environmental conditions affect the persistence, integration, and long-term impacts of these species. Such information can be used to identify high risk species or environments or develop strategies to manage them. Understanding how environmental or habitat differences shape population dynamics of an established invasive species can be essential to effectively managing these species, especially when environmental conditions influence the likelihood or speed of spread and establishment (Dupuis-Desormeaux et al. 2022). Furthermore, many ecosystems are rapidly changing because of human activities (Palmer et al. 2004; Havel et al. 2015); anthropogenic effects, such as habitat destruction, overharvesting, or pollution, can affect invasive species success and management options (Hauser and McCarthy 2009; Lamb et al. 2022). Importantly, invasive species may benefit from human-modification of habitats and climate change (Didham et al. 2005; Smith et al. 2012).

There are at least three reasons why invasive species are commonly found in degraded or disturbed environments (Havel et al. 2015; Dupuis-Desormeaux et al. 2022). First, invasive species are often more tolerant of anthropogenic impacts and a wider range of habitat quality compared to native species or non-native species that fail to establish (Karatayev et al. 2009), and this tolerance has been hypothesized to contribute to the success of invasive species (Ricciardi and Rasmussen 1998). Second, heavily degraded environments often contain fewer native species (D'Antonio et al. 1999). Existing evidence suggests that species-poor environments often have fewer competitors and predators that could limit invader success (Leppäkoski and Olenin 2000). Third, because humans often serve as the vector of transport or introduction of species to new environments, species are more likely to successfully invade areas where human activity and impacts are greatest (Hulme 2009; Murray et al. 2014). Despite the value of having long-term (over decades) studies on invasive species trajectories across different environments that vary in anthropogenic degradation, such studies are exceedingly rare.

In this study, we aimed to address these knowledge gaps by: (1) assessing the long-term changes in population demographics, health, and reproductive traits of a widespread invasive species, the round goby (*Neogobius melanostomus*), within its invaded range, and (2) quantifying how these characteristics differed across environments that varied in their degree of anthropogenic degradation in a highly degraded ecosystem, Hamilton Harbour (Canada). The round goby is a widespread invasive fish that feeds voraciously on the eggs and young of native and desirable non-native fish species (Steinhart et al. 2004; Lutz et al. 2020). The round goby invaded the Laurentian Great Lakes and parts of Europe in 1990 likely through the unintentional transfer of ship ballast water from the Black Sea (Jude et al. 1992). The round goby now plays multiple roles within Great Lakes food webs, providing a food source to important native avian and fish predators such as double-crested cormorants (*Phalacrocorax auratus*) (Johnson et al. 2015), burbot (*Lota lota*), smallmouth bass (*Micropterus dolomieu*), lake trout (*Salvelinus namaycush*), and lake whitefish (*Coregonus clupeaformis*) (Kornis et al. 2012), but round goby also consumes the eggs of piscivorous fish (Steinhart et al. 2004). The round goby has been shown to outcompete native fish species occupying similar niches such as the Johnny darter (*Etheostoma nigrum*) and several species of sculpin (Dubs and Corkum 1996; Carman et al. 2006; Bergstrom and Mensinger 2009). Round goby consume invasive dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*) that can contain high contaminant loads (Kwan et al. 2003), while few native fish species prey on these non-native mussels (Johnson et al. 2005). Because round goby are a food source for many fish, mammals, birds, and reptiles in the Great Lakes (Kornis et al. 2012), the consumption of dreissenid mussels by round goby can facilitate contaminant transfer up the food chain, although this facilitation is influenced by existing environmental conditions (Charette 2024). The round goby is tolerant to a wide variety of ecological conditions and survives well in poor water quality (Marentette et al. 2010; Kornis et al. 2012), which may contribute to its widespread invasion success (Clapp et al. 2001).

We have monitored round goby in Hamilton Harbour, Canada for 20 years (2002–2022) starting our monitoring shortly after the round goby was first detected in the harbour in 1999. Hamilton Harbour is a degraded area with heterogeneous contamination in the sediments, such as heavy metals, polycyclic aromatic hydrocarbons, and polychlorinated biphenyls. Some areas of the harbour are highly polluted as a result of historical industrial steel production, surrounding land-use, urban run-off, and sewage overflows, while other areas have received less anthropogenic impact or have received substantial remediation efforts (Hamilton Harbour Remedial Action Plan, 1992, 2002, 2018). Consequently, this long-term study of round goby across the harbour provides an opportunity to compare how trajectories of round goby populations might vary between sites of high and low contamination.

The dynamics of round goby populations should vary over time and across sites that differ in contamination levels. First, we predicted that overall abundance should decline post-establishment following the boom-bust pattern often observed for invasive species where a population initially grows very large, or booms, exceeding the carrying capacity of the ecosystem, followed by a decline, or bust, in population size over the long term as the species becomes integrated into the ecosystem (Strayer et al. 2017). Second, we predicted that round goby body size, body condition, and reproductive investment would all decrease over time as the population reached its habitat-specific carrying capacity, resulting in increased conspecific competition for resources (Reznik et al. 2002; Bøhn et al. 2004; Marchetti et al. 2004; Azour et al. 2015). In addition, because predation intensity and parasite loads are expected to increase over time since the initial invasion (Gendron et al. 2012; Kołodziej-Sobocińska et al. 2018), these processes too could lead to an energy allocation trade-off where individuals grow less and reproduce faster over time (Schultz et al. 2006), two traits often associated with *r*-selection (Reznick et al.2002). Third, since male round goby exhibit alternative reproductive tactics (ARTs; Marentette et al. 2009), we predicted that the proportion of care giving, courting guarder males would decrease over time, as the habitat carrying capacity is approached and competition for nesting resources and females presumably increases, leading to an increase in the success of sneaker males (Mills and Reynolds 2003). Fourth, we predicted that round goby populations from sites with higher contamination would decline more slowly over time, because round goby are tolerant to contaminants (Marentette et al. 2010; McCallum et al. 2017; Mehdi et al. 2021) and highly disturbed sites tend to have fewer native competitors, predators, and parasites – all extrinsic factors that may influence population growth rates and declines (Vila-Gispert et al. 2005). Finally, we predicted that round goby from sites of higher contamination would display a "live fast, die young" pace of life history as a consequence of living in a contaminated environment that could include smaller body size, lower body condition, a higher reproductive investment, and a higher proportion of sneaker males compared to the fish from sites of lower contamination (Couture and Pyle 2008; Bélanger-Deschênes et al. 2013).

Methods

Description of the study sites

The data for this study extend the collections described in both Young et al. (2010) and McCallum et al. (2014). From 2002–2022, we sampled round goby across six sites in Hamilton Harbour, Ontario, Canada, twice per month from May through October, except 2003, when sampling occurred only once per month. The six sites sampled included four sites with relatively low sediment contamination, La Salle Park (latitude 43.30, longitude −79.84), Grindstone Creek (43.29, −79.88), Desjardins Canal (43.27, −79.89), and Fisherman's Pier (43.29, −79.80) and two sites with high contamination, Pier 27 (43.28, −79.79)

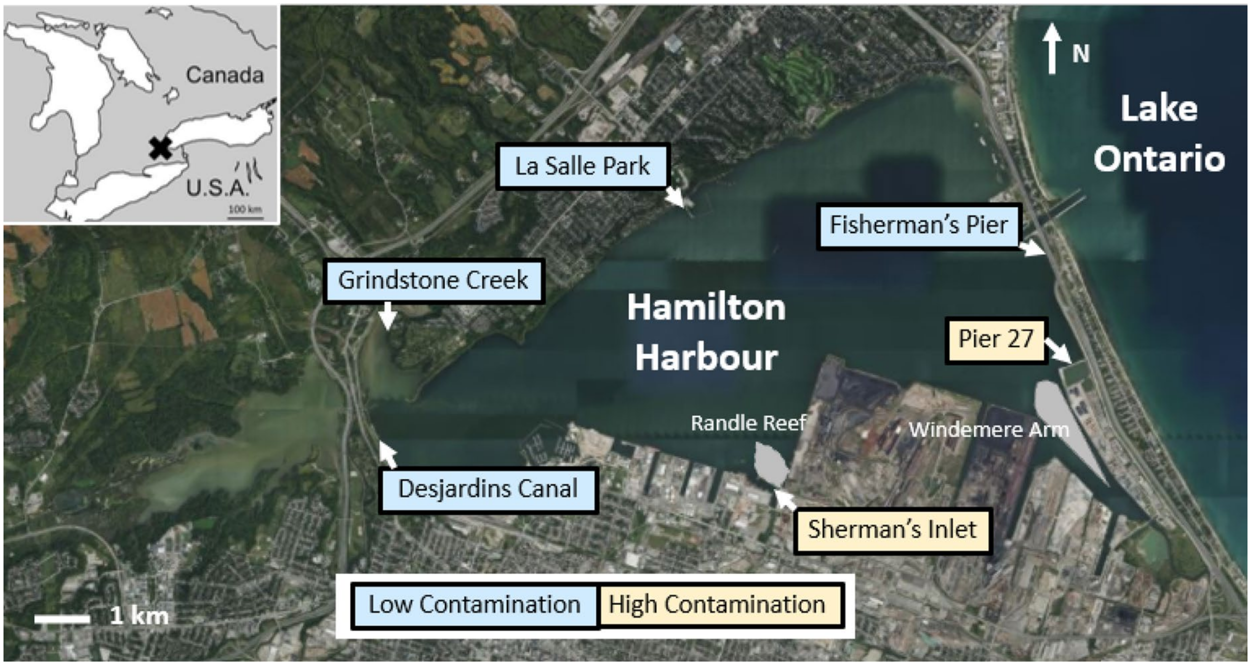

Fig. 1 A map (Bing Maps, Microsoft®) of Hamilton Harbour, ON, Canada (43°N, 79°W), the western-most embayment of Lake Ontario with sampling sites and areas of high contamination undergoing remediation (grey areas marked Randle Reef and Windemere Arm; RAP 1992, 2002), adapted from McCallum et al. 2014. Sites of higher contamination are yellow and sites with lower contamination are blue

and Sherman's Inlet (43.27, −79.83) (Fig. 1). The sites of lower contamination were sampled for the duration of the 2002–2022 sampling period, while the two sites of higher contamination were sampled from 2006–2008 and 2010–2022. Because of the nature and degree of environmental degradation, Hamilton Harbour was designated an International Joint Commission Area of Concern. This designation is in part because of the presence and concentrations of contaminants in the sediments, such as heavy metals, polycyclic aromatic hydrocarbons, and polychlorinated biphenyls (International Joint Commission 1999). The concentrations of these contaminants of concern vary by location and two of our sampling sites are found at the locations with the highest concentrations, known as Randle Reef and Windermere Arm (Burniston et al. 2016; Milani et al. 2017). We thus categorized our two sampling sites at Randle Reef and Windermere arm as higher contamination, and our remaining four sites as lower contamination (see Fig. 1) (Milani et al. 2017).

Round goby collection and measurements

We sampled round goby using black vinyl coated metal minnow traps (e.g., Eagle Claw Fishing Tackle Co.) placed at least 10 m apart at a depth of approximately 1 m and approximately 5 m from shore. Traps were placed at this depth and these locations for two reasons: first, sampling can be done safely by students without using a boat and second, round goby densities are found to be high at shallow sites along shorelines in the Laurentian Great Lakes watersheds (Taraborelli et al. 2009). Traps were set for a duration of 24 h. From 2002–2004, two minnow traps baited with approximately 25 g of frozen corn kernels were set at each site. From 2005–2022, the number of baited traps was increased to four for each site. Also in addition to the original four traps, two unbaited black traps were added from 2012–2022 and six silver traps (Gee's Fishing Gear) were added from 2018–2019 for a separate study (Synyshyn et al. 2023). Fish captured from both the unbaited traps and the silver traps were excluded from the analyses of this study. We also excluded any traps that were found broken, washed up on shore, tampered with, or opened. We accounted for such occurrences by examining the number of fish per trap.

Water temperature, dissolved oxygen (Lamonte tracer probe), pH, and salinity (YSI 550A & a multiparameter 35 probe) (Fig. 2) were measured at each sampling site during each sampling event when traps were collected from 2004 to 2022, with the exception of salinity which was only measured from 2017–2022 and temperature, where values were not recorded in 2011 and 2012. We counted and sexed all fish captured per trap before euthanizing them in a solution of benzocaine and transporting them on ice to the Aquatic Behavioural Ecology Laboratory at McMaster University, Hamilton, Ontario, Canada for dissection. Fish were sexed in the field by examining the urogenital papilla and any small fish (under 4.0 cm) that could not be identified as male or female were recorded as juveniles.

In the laboratory, we measured standard length and head width to the nearest 0.1 cm using calipers, and measured body, liver, and gonad mass to the nearest 0.001 g using a digital scale (Acculab Vicon Digital Scale), with the exception that gonad mass was not regularly measured, and liver mass was not measured at all in 2002 and 2003. For males, both seminal vesicles and testes contributed to total gonad mass. We measured the seminal vesicles and the testes separately when measuring gonad mass in males starting in 2006 to inform assignment of reproductive tactic (see below). For each fish, we calculated a gonadosomatic index (GSI; gonad mass/body mass) as a measure of reproductive investment (Schreck and Moyle 1990) and a hepatosomatic index (HSI; liver mass/body mass) as a measure of energy stores (Ighwela et al. 2014). Male ARTs were assigned based on morphology using a linear discriminant analysis (LDA) trained on a subsample of fish captured from 2007 to 2010, similar to McCallum et al. (2014) and McCallum et al. (2019). ARTs were only assigned to males considered to be reproductive with a GSI greater than 1% (Marentette and Corkum 2008). Four measures were used to assign a tactic to each reproductive male: (i) standard length, (ii) testes mass as a percentage of total body mass, (iii) seminal vesicle mass to testes mass ratio, and (iv) head width to standard length ratio. As seminal vesicle and testes mass are important for assigning male ARTs in round goby (Marentette et al 2009; McCallum et al. 2019) and they were not weighed separately until 2006, we focused on males collected from 2006–2022 for the LDA. Male colouration was not used in the assessment of ARTs because it was not consistently reported throughout the duration of the study. The LDA agreed with the ART assignments of the

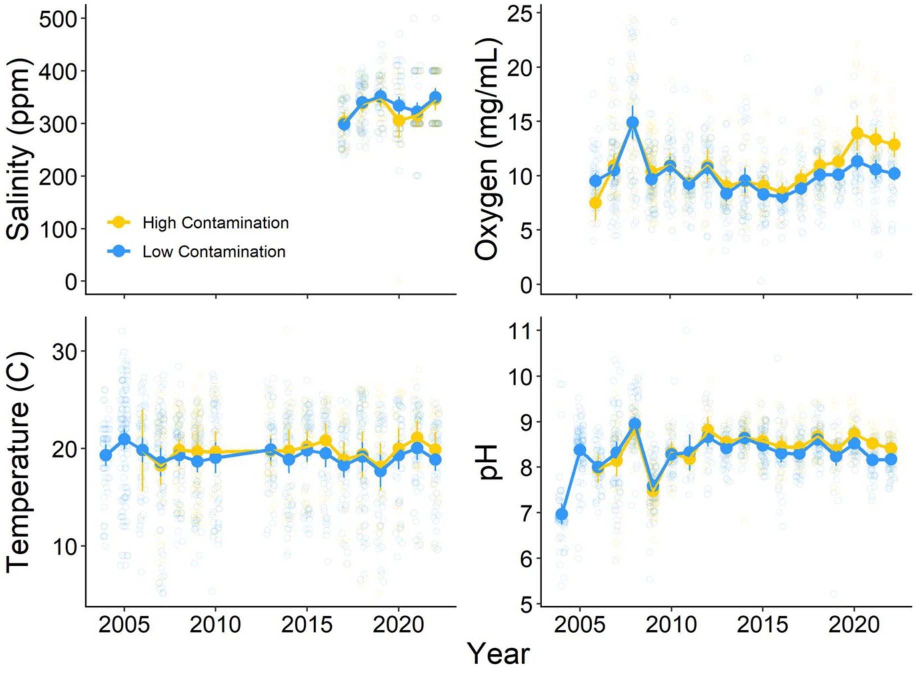

Fig. 2 Salinity in parts per million (top left), dissolved oxygen in mg/mL (top right), temperature in degrees Celsius (bottom left) and pH (bottom right) at sites of high (yellow) and low (blue) contamination. Opaque circles with error bars show the average value for each site type in each year, error bars denote standard error, and the open circles reflect data for each individual sampling site for each month of sampling. Dissolved oxygen values from 2004 to 2005 were excluded from the graph as they contained known errors

training dataset 86% of the time. Males that could not be assigned a tactic with 80% or greater confidence were labelled as unknown; the LDA assigned a tactic to 88% of reproductive males in the full dataset.

Twenty-five individuals were removed from the dataset due to suspected errors. These included 15 individuals where the GSI or HSI were greater than 0.30 ($n=7$ and $n=8$, respectively) as it is biologically unlikely that either the gonad or liver consisted of more than 30% of the total body mass for an individual fish. Three individuals were removed because their reported standard length was greater than the total length. One individual was removed because the reported standard length was less than 1 cm, as such individuals would not be trappable with the equipment used in this study. And finally, six individuals were removed because their recorded body mass was biologically unfeasible relative to their standard length, indicating a likely error.

Data analyses

Statistical analyses were performed using R version 4.2.2 (R Core Team 2022) and figures were created using ggplot2 (Wickham 2016). We calculated the average number of round goby captured per trap over each month of each year as a proxy for population abundance to account for differences in the number of traps set and collected because of trap loss. In all cases, model assumptions were checked graphically using standard plots implemented in base R.

To analyze how the average number of round goby captured in traps differed, and how their standard length, body condition, GSI, and HSI changed over time and across sites that vary in their degree of contamination, we used linear mixed effects models using the glmmTMB package, which allowed us to also test for and include temporal autocorrelation structures in our models (Brooks et al. 2017). Catch per trap and GSI were log base 10 transformed and HSI was square root transformed to meet assumptions of normality. For each model, site type (high or low contamination), and year (continuous) were included as fixed effects. In the catch per trap model, a quadratic effect of year was also included and year was scaled to start from zero. A quadratic effect of year was included to assess if the rate of catch changes over time, because we expect the relationship between catch and time may not be linear (e.g., may plateau). To assess differences in body condition over time and across sites, log base 10 transformed body mass was included as the response variable and standard length, and an interaction term between standard length and sex, were included as covariates. For each model, month (May–October) was included as a fixed effect to account for seasonal variation and sampling site was included as a random intercept to account for among-site differences. We also included a fixed effect of sex (male or female) for models analyzing changes in morphology and phenotype (standard length, body condition, GSI, and HSI), as round goby show sexual dimorphism (McCallum et al. 2014). We used AIC model selection to distinguish if seasonal (monthly) or yearly autocorrelation was present in our data by comparing a model without a temporal autocorrelation structure to models with monthly autocorrelation and yearly autocorrelation. The best-fit model for catch per trap included a yearly autocorrelation structure and the best-fit model for all phenotypic trait analyses included a seasonal autocorrelation structure. In each case, the best-fit models dominated the alternatives ($\Delta\text{AIC} > 10$). Thus, these autocorrelation structures were used in the respective analyses.

Juveniles and hermaphrodites were not included in any of the models, except for the analysis of catch per trap, because sex cannot be assigned to juvenile fish and because we had few records of hermaphroditic fish or fish displaying visual evidence of intersex (fish with evidence of both male and female gonadal tissue; $n=29$ out of 16,020 fish). Determination of hermaphrodism or intersex was based on visual inspection alone. Histological and microscope confirmation was not performed (but see Marentette et al. 2010 for a detailed histology from intersex fish from the contaminated sites in 2007 and 2008). Only data from 2004 to 2022 were used in the models for HSI and GSI because liver mass was not measured at all in the first 2 years of the study and male gonad mass was not measured consistently in the early years of the study. Also, the number of GSI observations for 2002 and 2003 were low ($n=155$ and 41, respectively) compared to the remainder of the study ($\text{mean} \pm \text{SE} = 692 \pm 73$). Liver mass values of zero in the dataset ($n=81$) were assigned a value of 0.001 g.

To analyze if the proportion of guarder males (out of the total number of reproductive males captured in a particular sample) decreased over time and if sites of higher contamination had a higher proportion of guarder males, we used a generalized linear mixed-effects model assuming a beta-binomial error distribution to capture overdispersion using the "glmmTMB" package (Brooks et al. 2017). The response variable was the proportion of guarder males relative to the total number of reproductive males; year, site type (low or high contamination), and an interaction term between year and site type were included as fixed predictor variables. Site (a factor with six levels, one for each site that was sampled) was included as a random intercept to account for unknown among-site differences.

Results

Over the 20 years of sampling, 9,639 males (60%), 5,941 females (37%), and 440 juveniles (~ 3%) were collected for this study for a total of 16,020 round goby. On average, the number of round goby caught per trap decreased over the twenty-year study period (Table 1, Fig. 3). The rate of decline in the number of goby caught per trap slowed over time (i.e., a positive quadratic term for time) (Table 1, Fig. 3). Round goby standard length decreased over time (Table 1, Fig. 4). Males were longer on average compared to females (Table 1, Fig. 4). Body condition and GSI increased for round goby while there was no clear difference in round goby HSI over the study period (Table 1, Fig. 5). Males had higher body condition, higher HSI, and lower GSI than females, on average (Table 1, Fig. 5). The proportion of guarder males increased over time (Table 1, Fig. 3).

We did not find a clear difference in the average number of round goby caught per trap over the twenty year study between sites of low and high contamination (Table 1, Fig. 3). However, round goby from sites of low contamination were longer compared to those from high contamination sites (Table 1, Fig. 4). Round goby from sites of low contamination had lower GSI than those from sites of high contamination and higher HSI (Table 1, Fig. 5). The effect of site contamination on body condition was statistically unclear (Table 1). The proportion of guarder males was lower on average at sites of high contamination (Table 1, Fig. 3).

Discussion

Our study had three central findings. First, the average number of round goby captured declined over the twenty year study period, decreasing from an average of 7 individuals per trap across study sites in the first year to only 3 individuals per trap in the final year. This decrease is consistent with our predictions of a declining (or bust) population, although there are other mechanisms that could produce a decline in catch at our study sites over time, such as changes in fish catchability or changes in round goby distribution in Hamilton Harbour. Similar results were revealed by two earlier studies; in Young et al. (2010) when the researchers only had 6 years of the data (from 2002–2008) and in McCallum et al. (2014) that analyzed 10 years of the data (2002–2012). The decline from the beginning of the study until 2012 was not statistically significant in these earlier studies, likely due to the large fluctuations in catch across years. Also, the initially steeper population decline has slowed in recent years, suggesting the population may be stabilising as the round goby becomes more integrated into the Hamilton Harbour ecosystem and the food web equilibrates. Declines in round goby abundance have also been reported for other Great Lakes locations (Johnson et al. 2005; Roseman and Riley 2009). These declines have been documented over much shorter time periods than the long term monitoring reported in this study (Johnson et al. 2005; Roseman and Riley 2009). Based on 7 years of data, Johnson et al. (2005) documented a 50% decline in round goby catches in Lake Erie following a peak observed in 1999. Round goby were first found in Lake Erie in 1994. Based on 13 years of data in Lake Huron, Roseman and Riley (2009) also reported a decline in round goby density of approximately 50% in 2006 after observing a peak in 2003, but the declines of other demersal forage fishes in their study were even more dramatic. In contrast to our biweekly sampling based on minnow traps, these two studies relied on trawls for their sampling of round goby and sampled the respective lakes between only 1–4 times per year, while we sampled ~ 12 times per year. Declines in abundance a few years after establishment have also been observed in other invasive species across a wide range of taxa as, including plants, invertebrates, amphibians, mammals, birds, and fish (Simberloff and Gibbons 2004). For example, the

Table 1 Regression coefficients (β), standard error (SE), z values and p values estimated for the variables included in the linear mixed-effects models predicting the average number of round goby captured in traps, standard length, body mass, body condition, gonadosomatic index, hepatosomatic index, and the generalized linear mixed-effects model predicting the proportion of guarder males

Variable	β	SE	z value	p value
Average number of round goby captured in traps (log_{10}-transformed)				
Year	−0.07	0.02	−4.37	0.003
Year^2	0.002	0.0007	3.03	< 0.0001
Site type (Low contamination)	−0.13	0.27	−0.48	0.63
Month (June)	0.17	0.05	3.25	0.001
Month (July)	0.20	0.05	4.00	< 0.0001
Month (August)	0.16	0.05	3.06	0.002
Month (September)	0.11	0.05	2.11	0.04
Month (October)	0.11	0.05	2.22	0.03
Standard length				
Year	−0.05	0.006	−9.35	< 0.0001
Site type (Low contamination)	0.60	0.16	3.62	0.0003
Sex (Male)	0.96	0.02	42.48	< 0.0001
Month (June)	−0.18	0.07	−2.71	0.007
Month (July)	−0.17	0.07	−2.29	0.02
Month (August)	−0.04	0.08	−0.47	0.64
Month (September)	0.15	0.08	1.83	0.07
Month (October)	0.14	0.09	1.64	0.10
Body condition (log_{10}-transformed body mass)				
Year	0.003	0.0004	9.23	< 0.0001
Site type (Low contamination)	0.01	0.007	1.51	0.13
Standard Length	0.22	0.0008	256.91	< 0.0001
Sex (Male)	0.16	0.006	26.78	< 0.0001
Standard Length:Sex	−0.03	0.0009	−27.74	< 0.0001
Month (June)	−0.004	0.004	−1.02	0.31
Month (July)	−0.005	0.004	−1.13	0.26
Month (August)	−0.01	0.004	−2.33	0.02
Month (September)	−0.01	0.005	−0.21	0.84
Month (October)	0.005	0.005	2.71	0.007
Gonadosomatic index (log_{10}-transformed)				
Year	0.01	0.002	5.82	< 0.0001
Site type (Low contamination)	−0.29	0.04	−6.51	< 0.0001
Sex (Male)	−0.76	0.01	−67.51	< 0.0001
Month (June)	−0.17	0.03	−4.99	< 0.0001
Month (July)	−0.28	0.04	−7.52	< 0.0001
Month (August)	−0.77	0.04	−20.23	< 0.0001
Month (September)	−1.04	0.04	−26.69	< 0.0001
Month (October)	−0.86	0.04	−21.48	< 0.0001
Hepatosomatic index (square-root transformed)				
Year	0.0002	0.0002	0.81	0.42
Site type (Low contamination)	0.01	0.005	2.57	0.01
Sex (Male)	0.002	0.0007	3.56	0.0004
Month (June)	0.01	0.002	6.16	< 0.0001
Month (July)	0.01	0.002	4.67	< 0.0001
Month (August)	0.02	0.003	6.98	< 0.0001
Month (September)	0.03	0.003	12.47	< 0.0001
Month (October)	0.04	0.003	14.901	< 0.0001

Table 1 (continued)

Variable	*β*	SE	*z* value	*p* value
Proportion of Guarder Males				
Year	0.05	0.01	3.39	0.0007
Site Type (Low Contamination)	99.05	46.99	2.11	0.04
Year x Site Type	−0.05	0.02	−2.10	0.04

The quadratic term for year is represented by Year^2

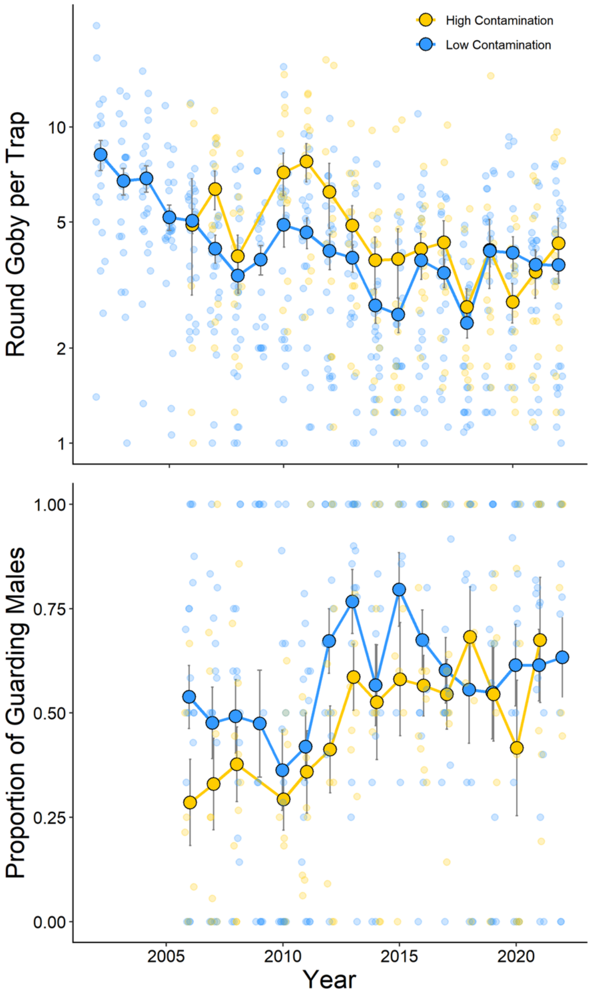

Fig. 3 Top: The number of round goby captured per trap at sites of high (yellow) and low (blue) contamination. Bottom: the proportion of guarder males relative to total reproductive males captured at sites of high (yellow) and low (blue) contamination. For both panels, large brightly coloured circles with error bars show the average value for each site type in each year, error bars denote standard error, and small lighter coloured circles show mean number of fish per trap (top) and proportion of guarder males (bottom) for each individual sampling site and for each month of sampling

invasive Indo-Pacific lionfish (*Pterois volitans/miles*) in the eastern Caribbean initially showed a rapid increase in catch per trap in the first few years post-invasion, but this was followed by a sharp decline in the later years of the nine-year study period (Debrot et al. 2023). Similarly, invasive cane toads (*Rhinella marina*) in Australia declined in abundance post-invasion over a 10 year period (Brown and Shine 2019). However, cane toad abundance increased again following this decline, demonstrating the importance of long-term data collection to inform population trajectories of invasive species post-establishment (Brown and Shine 2019).

The second core finding of our study is that round goby phenotypic traits changed in several, albeit small, ways over the study period, including a decrease in overall body size, an increase in body condition, reproductive investment, and in the proportion of guarding males. The reduction in body size is consistent with the findings of previous studies of round goby in invaded locations. Gutowsky and Fox (2012) found that 1 and 2 year old round goby from established population sites were smaller by an average of 1–15 mm compared to fish at sites where the population had more recently invaded. Brandner et al. (2018) also found that round goby at established sites were smaller compared to those at the invasion front, by as much as almost 5 cm. These results suggest average fish size decreased over time since invasion. Changes in body size have been observed in several other invasive species after establishment. For example, invasive sea lamprey (*Petromyzon marinus*) in the upper Great Lakes were found to be smaller on average than sea lamprey in their native range (Gambicki and Steinhart 2017). However, following extensive control efforts that decreased sea lamprey densities in the invaded range, female sea lamprey body size and fecundity increased (Gambicki and Steinhart 2017).

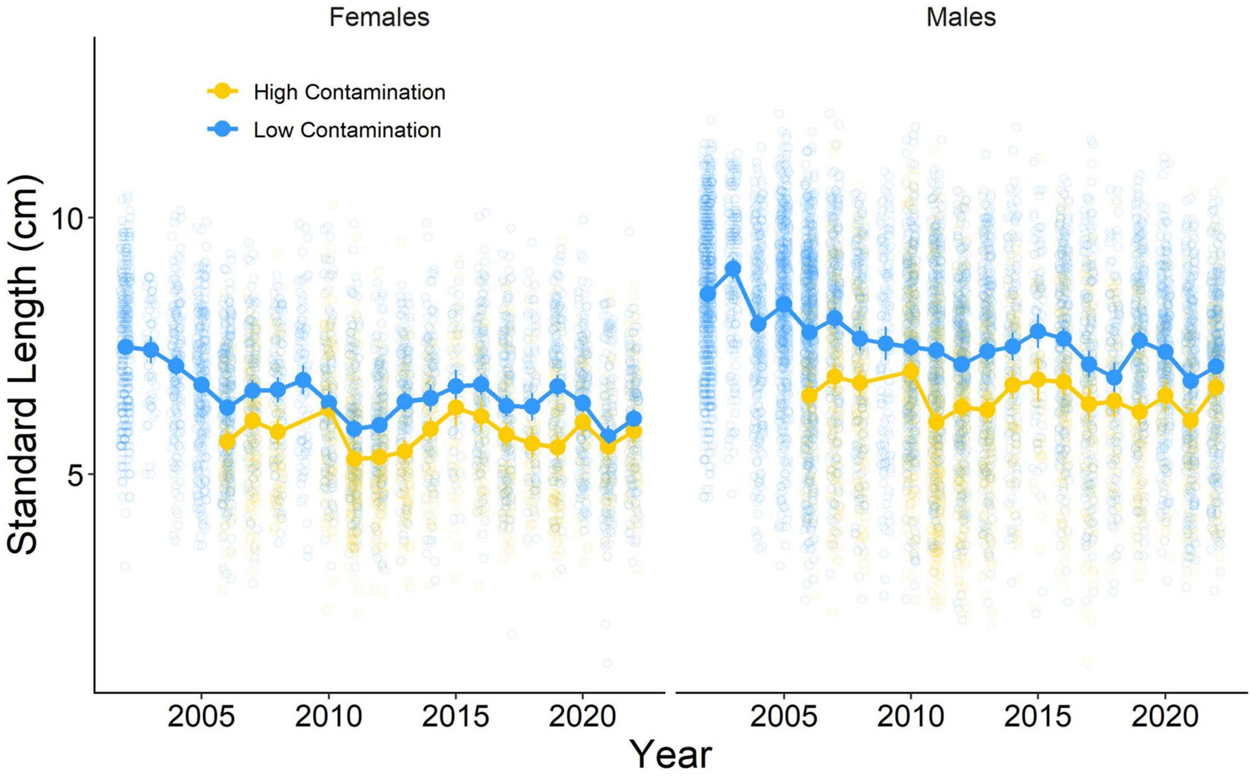

Fig. 4 The standard length of both females and males at sites of high (yellow) and low (blue) contamination. Opaque circles with error bars show the average value for each site type across years, error bars denote standard error, and the open circles reflect data for individual fish

Size of captured fish may have declined over time in Hamilton Harbour for two reasons that are not mutually exclusive. First, the mean age of the population may have decreased, so that younger fish are now being captured. Second, growth rates may have decreased, leading to smaller size-at-age. Previous studies have provided evidence that round goby growth rate decreases when population density is high (Kornis et al. 2014), that round goby reach a smaller size-at-age in habitats that had been invaded for 5 years compared to newly invaded habitats (Gutowsky and Fox 2012), and that round goby from invaded freshwater habitats matured at a smaller size compared to in their brackish native range (Gertzen et al. 2016). Freshwater possibly imposes physiological stress on round goby (which is believed to have invaded the Laurentian Great Lakes from the brackish Black Sea) compared to living in more saline environments (Puntila-Dodd et al. 2021). This idea is supported by observations that round goby living in brackish environments in their native range are larger than those of similar age living in freshwater environments (Velkov et al. 2014). In our study, we found body size to be decreasing concurrently with decreasing catches suggesting that declining growth rate may not be the cause of the smaller fish size. Aging, age-at-maturity, and size-at-maturity studies are now needed to test these alternative hypotheses.

Contradicting our predictions, round goby gonad investment and body condition increased over our study period. Increases in gonad investment may explain, at least in part, the higher body condition observed and the decrease in body size over time, as increased energy allocation to reproduction should decrease somatic growth (Kozlowski 1996; Joanna et al. 2011). Previous studies also similarly reported increased reproductive investment of round goby over time since invasion (Raby et al. 2010; Brandner et al. 2013; Azour et al. 2015). Our findings of body condition increasing over time contrast with previous studies of invasive round goby in the Great Lakes watershed and in Europe that have found that

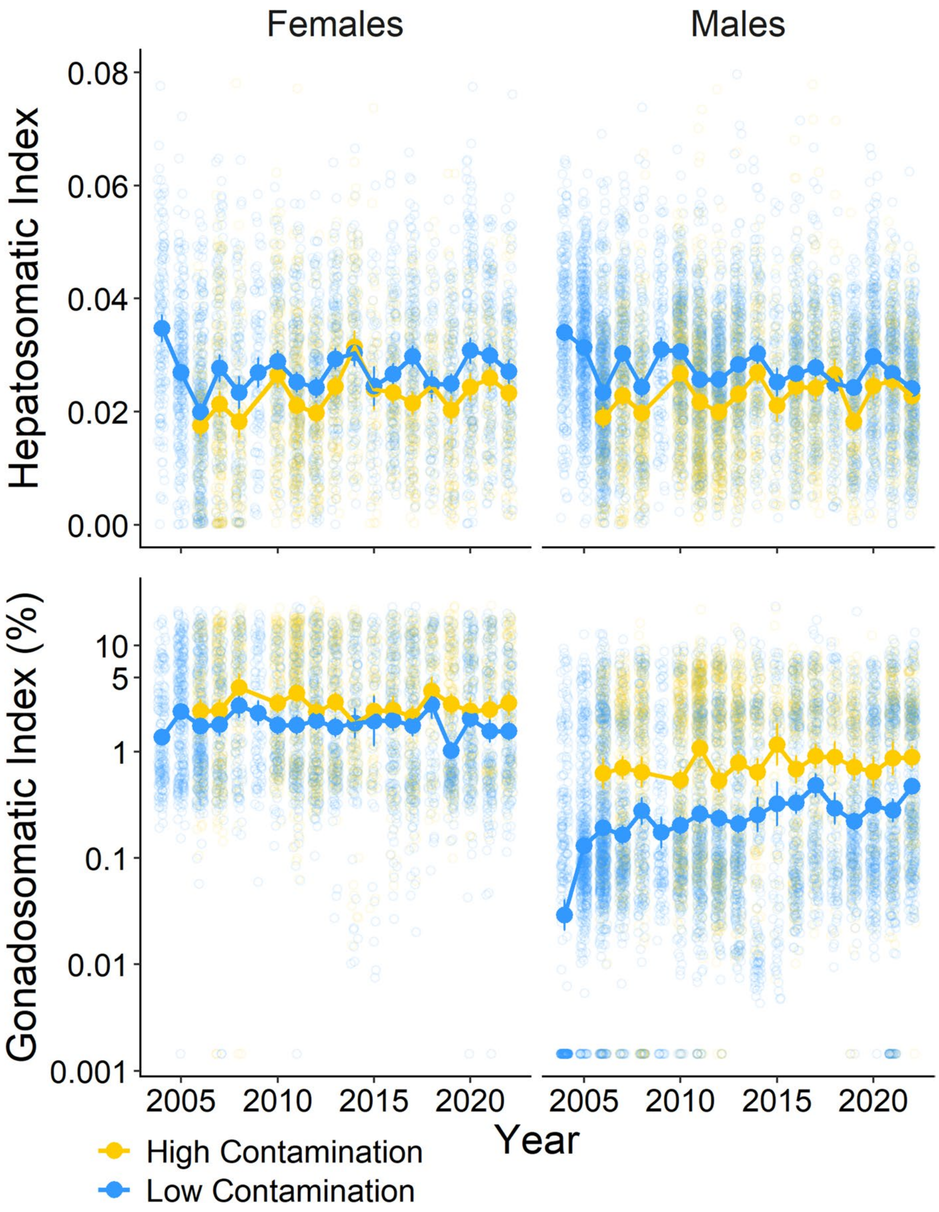

Fig. 5 The hepatosomatic index (top panel), and gonadosomatic index (bottom panel) shown as a percentage of both male and female round goby captured at sites of high (yellow) and low (blue) contamination. Opaque circles with error bars show the average value for each site type across years, error bars denote standard error, and the open circles reflect data for individual round goby

individuals from recently invaded sites typically have better body condition compared to round goby from sites that have been established for longer periods of time (Raby et al. 2010; Brandner et al. 2013; Azour et al. 2015; Masson et al. 2016). However, these population comparisons along invasion gradients suggest that condition decreased over time since the initial invasion but do not track this explicitly as we did in our study. These other studies occurred on much shorter sampling durations (1–2 years vs 20 years in our study). The increase in gonad investment and body condition we observed over the two-decade study period may be due to the observed decrease in population abundance, suggesting a density-dependent response on gonads. Similar responses have been observed in invasive mosquitofish (*Gambusia holbrooki*), where reproductive investment increased after population abundance was experimentally lowered through controlled removals from a small, isolated stream in south-eastern Spain (Ruiz-Navarro et al. 2013).

Also contrary to our initial predictions, the proportion of guarding males increased over the study duration. This increase may also have been a density-dependent response to the decreased population abundance and consequently reduced competition for nests and mating opportunities, consistent with theory of alternative reproductive tactics (Gross 1996). Our study contributes to growing evidence that the demographics of invasive species can still be changing long after introduction in their new range and that these changes can fluctuate significantly rather than a consistent or linear progression. While this may be expected given the fisheries literature has a long history of recognizing that population parameters fluctuate through time, studies of invasive populations post-establishment often assume linearity (Flores-Moreno et al. 2015). That invasive species populations are still changing many years after introduction, and in non-linear ways, suggests their long-term impacts and full potential as invaders are not fully realized by short term studies (Flores-Moreno et al. 2015).

Our third central finding was that there was no clear difference in the number of round goby captured at sites with high and low contamination, but the sites differed in the kinds of individuals captured, in terms of their life history traits. Round goby are short-lived fish (average age in the Great Lakes is estimated to be between 3–4 years and reproduction can begin after 1 year;MacInnis and Corkum 2000; Duan et al. 2016). The persistence of goby populations at highly contaminated sites for over two decades and at similar abundances to sites with lower contamination supports the notion that this species is pollution-tolerant (Marentette et al. 2010; McCallum et al. 2014). While no clear differences in body condition were observed between fish from sites of low and high contamination, round goby from more contaminated sites were smaller in size and had higher gonad investment, particularly so for males, when compared to those from sites of lower contamination. These findings were consistent with our predictions and with existing theory that posits that individuals in highly stressful impaired environments should display a "live-fast, die-young" pace-of-life suite of traits (Couture and Pyle 2008). Living in environments with high contamination can be metabolically costly (Adams et al. 1992; Du et al. 2019); one adaptation to living in these environments could be to prioritize energy allocation to reproduction over growth, especially in areas with few predators and lowered intraspecies competition for shelter and food (Bélanger-Deschênes et al. 2013). Live-fast die-young strategies have been observed in other fish populations living in high contamination environments. For example, English sole (*Pleuronectes vetulus*) at sites of higher contamination had higher fecundity compared to sole at sites of lower contamination (Johnson et al. 1997). Contaminated populations of redbreast sunfish (*Lepomis auritus*) had smaller age-specific sizes and larger proportions of smaller fish compared to less contaminated (Adams et al. 1992). That morphology varied in an invasive species across an environmental gradient with different degrees of anthropogenic degradation is interesting because understanding environmental variation in life history traits is essential for predicting the effects of climate change and other anthropogenic abiotic changes and interactions with biological invasions. However, this topic has rarely been studied (Carmona-Catot et al. 2011; Reidmiller et al. 2018). Freshwater ecosystems are particularly at risk, as they are among the most severely degraded habitats (Oberdorff et al. 2002) but also are hosts to an ever increasing number of non-native freshwater species (Marchetti et al. 2004).

Our study is one of the few studies to have compared traits of established populations at sites that vary in anthropogenic impacts on a small spatial or local scale. Our six study sites were no more than 10 km apart and all located in the same harbour, at the western tip of Lake Ontario. While we do not currently have information on the genetic differentiation between these sites, previous studies on round goby within the Laurentian Great Lakes have found this species shows high site fidelity and home ranges substantially less than the distance between our sites (Ray and Corkum 2001; Marentette et al. 2011). Also, studies of round goby in other invaded ranges have found genetic differentiation between three sites all located less than 10 km from one another (Green et al. 2023), suggesting our sites may be reflective of different populations. We found evidence that invasive species population trajectories can vary substantially over time by quantifying catch and collecting phenotypic data over a two-decade period. Without this extensive biweekly sampling, we may not have detected that the population decline has stabilised, which may signal that this population has finally reached equilibrium and integrated into the invaded ecosystem. The possible density-dependent compensatory mechanisms such as increasing body condition and increasing reproductive investment that we observed were not uncovered in earlier studies over shorter time periods (Young et al 2010; McCallum et al. 2014). Despite these strengths, our study cannot rule out the possibility that local environmental change (e.g., possible shoreline restoration has reduced the amount of rocky shoreline) is driving the observed abundance and phenotypic changes (Valladares et al. 2014). In fact, our study does provide evidence that local environmental differences do seem to result in different phenotypic changes observed over the study. Hamilton Harbour has undergone significant remediation over the study period (Costa et al. 2020), and the fish community has varied greatly over the past three decades (Maynard et al. 2022). This includes shifts from predominantly tolerant species and low piscivore abundance to higher piscivore abundance and the presence of many less tolerant species, although overall the fish community is still highly dominated by invasive and pollution-tolerant species (Boston et al. 2016). These shifts in community may also help explain the patterns we observed in round goby abundance and morphology over the study duration. Canada's largest contaminated sediment remediation project in the Laurentian Great Lakes started in 2015 at one of our study sites; this project has capped a large area contaminated with polycyclic aromatic hydrocarbons, tar, and heavy metals, and was completed in 2024 (Hartig et al. 2020). How remediation measures impact invasive and native species is a topic worth further investigation. Our study could serve as an important baseline to gauge change.

Managing aquatic resources in the face of both environmental change and invasive species can be challenging, in part because we know remarkably little about the long-term trajectories of invasive species post-establishment across environments that vary in their degree of anthropogenic impact. Studies like this one help to inform how a species can change over time since invasion, how these changes can be non-linear, and how differences in environments that vary in the degree of anthropogenic impact mediate these changes. Such information can ultimately be used to improve our understanding of the invasion process, possible responses and resiliency of invasive species to disturbed habitats, and aquatic resource management.

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Authors contribution Study conception and design was led by Sigal Balshine, with significant contributions from Julie Marentette, Erin McCallum, and Marten Koops. Data collection was performed by Adrienne McLean, Erin McCallum, Julie Marentette, Sina Zarini, and Sigal Balshine. Data analyses were performed by Adrienne McLean, with significant contributions from Erin McCallum, Julie Marentette, Sina Zarini, Benjamin Bolker, and Marten Koops. The first draft of the manuscript was written by Adrienne McLean. All authors contributed to manuscript revisions and approved the final manuscript.

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Data availability The data in CSV format and R code used in the analyses described in the manuscript are currently publicly available online through a public GitHub repository and can be accessed through this link.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

Ethical approval All methods for handling round goby were approved by McMaster University's Animal Research Ethics Board (Animal Utilization Protocols: 03–09-54, 06–10-61, 10–11-70, 13–12-51, 17–12-45, 22–04-11) and adhere to the standards of the Canadian Council on Animal Care.

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