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Seasonal habitat use indicates depth may mediate the potential for invasive round goby impacts in inland lakes

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ABSTRACT

1. The round goby (Neogobius melanostomus) is among the fastest-spreading introduced aquatic species in North America and is radiating inland from the Great Lakes into freshwater ecosystems across the landscape. Predicting and managing the impacts of round gobies requires information on the factors influencing their distribution in habitats along the invasion front, yet this information is not available for many recently-invaded ecosystems. We evaluated the seasonal habitat use and biomass of round gobies in an inland temperate lake to define the spatiotemporal scope of biological interactions at the leading edge of the round goby invasion.

2. Using novel statistical approaches, we combine hierarchical models that control for imperfect species detection with flexible smooth terms to describe nonlinear relationships between round goby abundance and environmental gradients. Subsequently, we generate accurate detection-corrected estimates of the standing stock biomass of round gobies.

3. Our results show seasonally differentiated habitat niches, where suitable round goby habitat in summer months is restricted to shallow depths (<18.4 m) with a mixture of vegetative and mussel cover. We found high round goby biomass of 122 kg ha^{-1} in occupied habitats during the summer, with a total lake-wide biomass of 766,000 kg. In winter, gobies migrate to deep offshore habitats and disperse, dramatically altering their scope for biological interactions with resident aquatic species across summer and winter seasons.

4. The results of this study indicate that the scope of biological interactions in inland lakes may be seasonally variable, with potential for high round goby biomass in shallow lakes or at the periphery of deep lakes in the summer months. Such shallow-water habitats may therefore present higher risk of ecological impacts from round gobies in invaded lentic ecosystems. As round gobies expand inland, consideration of seasonal habitat use will be an important factor in predicting the impacts of this pervasive invader.

INTRODUCTION

As exotic species spread to new ecosystems, abiotic conditions define the physical limits under which they can survive and reproduce, while the abundance of invading populations and biotic interactions define the scope for trophic impacts within ecological communities (Parker et al., 1999). Thus, information on the invasive species' ecological niches is central to forecasting ecosystem impacts from invasions and identifying appropriate management actions to resist establishment or contain further expansion (Peterson, 2003; Simberloff et al., 2013). Yet, data on recently invaded systems are typically scarce. In lieu of primary information from invaded locations, inferring species' niches from within their native range is often used as a de facto model to inform the ecology of invasive species in new systems. This approach relies on the assumption that species' realized niches are consistent across ecosystems (Pearman, Guisan, Broennimann, & Randin, 2008; Wiens & Graham, 2005); however, invaded habitats and ecological communities are often different from those in exotic species' native ranges (Broennimann et al., 2007; Fitzpatrick, Weltzin, Sanders, & Dunn, 2007; Rödder & Lötters, 2009). This mismatch between native and invaded habitats can lead to inaccurate forecasting about the spread and establishment of invading species and hamper resource managers' ability to mitigate the economic and ecological costs associated with species invasions. Instead, efforts to characterize invasive species' ecological niches within invaded habitats may better predict their potential distribution and provide relevant information to identify high risk habitats and inform ecosystem susceptibility along the invasion path (Loo, Mac Nally, & Lake, 2007).

The round goby (Neogobius melanostomus, Gobiiformes: Gobiidae) is a benthic fish native to the Ponto-Caspian region (Black, Caspian and Azov Seas) that has invaded aquatic systems in Asia, Europe, and North America (Charlebois et al., 1997; Corkum, Sapota, & Skora

2004; N'Guyen et al., 2018). The species was first introduced to North America in 1990 in the St. Clair River (Michigan, USA) through ballast water from transoceanic vessels, and has subsequently rapidly spread throughout the Laurentian Great Lakes region with an east–west range expansion of approximately 55 km year^{-1} and north–south range expansion of 40 km year^{-1} (Charlebois et al., 1997; Fuller et al., 2018; Jude, Reider, and Smith, 1992). Round gobies appear to quickly establish once introduced, and as novel community members they serve roles as predators, competitors, and prey. For instance, many populations within the Great Lakes basin have reached high abundances, and increased resource competition and predation by round gobies have been linked to population declines of native fish and invertebrates (Janssen & Jude, 2001; Krakowiak & Pennuto, 2008; Lauer, Allen, & McComish, 2004). Round gobies are also one of few fish species in North America that consume zebra mussels (Dreissena polymorpha) and quagga mussels (Dreissena rostriformis bugensis), another group of Ponto-Caspian invaders that profoundly impact North American freshwater ecosystems and likely facilitated round goby invasions (Ray & Corkum, 1997; Ricciardi & MacIsaac, 2000; Vanderploeg et al., 2002). As an abundant food source, round gobies may facilitate the transfer of energy, nutrients, and contaminants from the benthos up food webs with variable consequences for predator species (Hogan, Marschall, Folt, & Stein, 2007; Johnson, Bunnell, & Knight, 2005; King, Ray, and Stanford, 2006; Somers, Lozer, Kjoss, & Quinn, 2003).

Round gobies are radiating southward out of the Great Lakes basin via river and tributary systems and establishing populations in lentic and lotic environments that are dissimilar from both their native range and from the sites of primary invasion (Abbett, Waldt, Johnson, McKenna Jr., & Dittman, 2013; Kornis & Vander Zanden, 2010). However, although existing studies have documented the abundance, habitat preferences, and ecological impact of round gobies in the Great Lakes and their tributaries (Cooper, Ruetz III, Uzarski, & Shafer, 2009; Kornis, Mercado-Silva, & Vander Zanden, 2012; Kornis, Sharma, & Vander Zanden, 2013; Ray & Corkum, 2001; Taraborelli, Fox, Johnson, & Schaner, 2010), less is known about their recent expansion into inland lakes (but see Jackson et al. 2019). Given the high potential for ecological impacts from round gobies, there is a need to understand the habitat use of this invader and to assess the biomass of established round goby populations in systems along the rapidly expanding invasion front (Charlebois, Corkum, Jude, & Knight, 2001). Here, we assess the round goby population in Cayuga Lake, NY, at the southern extent of their current range. This lake harbors both deep and shallow habitats, as well as eutrophic and mesotrophic regions, providing an important reference ecosystem for a wide range of lentic habitats facing round goby along the inland invasion path. Using benthic videography and hierarchical statistical models to control for imperfect species detection, we characterize round goby habitat use across both summer and winter seasons and provide an unbiased assessment of the standing stock biomass of the population. Together, these analyses provide insight into the ecological niche of round gobies through a full annual seasonal cycle and advance understanding of the potential strength and scope of ecological interactions of round gobies in invaded inland lakes in North America.

METHODS

Our assessment of round goby habitat use and biomass involved a number of related analyses. We assessed round goby habitat use by fitting species distribution models to video quadrat data to explore the association between goby counts and habitat variables. Because the behavior and coloration of round goby can render them difficult to observe, we implemented hierarchical species distribution models that separate detection error from underlying distribution patterns. We complemented species distribution analyses with a repeated snorkel survey at an index location to assess round goby onshore/offshore migration phenology. We also coupled detection-corrected goby densities with size-to-weight relationships to estimate lake-wide biomass of the standing stock of round goby. Because the northernmost portion of the study lake is heavily vegetated, videography was not feasible and we therefore implemented a snorkel-based survey to assess round goby density in this area. In the sections below, we describe the Cayuga Lake study system, the videography sampling and species distribution modeling to asses round goby habitat use, and our approach to translate goby densities into an estimate of lake-wide biomass.

Study Area

Cayuga Lake (NY, USA) is the longest of New York's Finger Lakes (61 km) with an average width of 2.7 km (total area = 172 km^2; Figure 1). The main portion of the lake is mesotrophic and deep (maximum depth = 133 m), with a narrow nearshore shelf and steep drop-offs. The northern end of the lake is eutrophic and dominated by shallow, heavily vegetated habitat. The mixing regime in the lake is complex, but the main portion of the lake is typically monomictic with summer stratification (Oglesby, 1978). Cayuga Lake contains a diverse fish community encompassing both warm-water (e.g. bass and perch) and cold-water species (e.g. trout and salmon; www.dec.ny.gov). Invasive dreissenid mussels (predominately Dreissena rostriformis bugensis) have been established in the lake for approximately 25 years, and round gobies were first documented in 2011 (Fuller et al., 2018).

Habitat Use

Summer and winter round goby distributions were assessed with benthic video quadrats using a Seadrop 6000HD underwater camera (SeaViewer Cameras Inc., Tampa, FL) mounted on a PVC cage with a nominal sampling area of 0.65 m^2 (Figure S1). Sites were randomized along 16 fixed transects spanning the width of the lake during the summer survey season (Figure 1). Winter sampling was limited by weather conditions and targeted every other transect. Video was recorded for ≥ 6 minutes at 82 sites in summer (24 July 2017–1 August 2017) and 27 sites in winter (18 January 2018–3 February 2018), with depths ranging from 1.3–121 m in summer and 3.0–104 m in winter.

Round gobies are well camouflaged, and imperfect detection could lead to spurious inference about habitat use if left unaddressed (MacKenzie et al., 2002). We therefore employed multiple video observers to provide replicate fish counts suitable for hierarchical species distribution models that can control for imperfect round goby detection. Three independent observers counted round gobies in images extracted at one second intervals from video quadrat footage. The Seadrop videos indicated that gobies were attracted to the PVC cage from a wider area, with counts peaking at six minutes (Figure S2). Thus, we recorded the maximum count through minute six at each site for species distribution modeling (i.e. maximum count in 360 images; see below for details on additional processing to correct for attraction area for subsequent biomass estimation). Benthic habitat in video quadrats was characterized with categorical percent cover scores (‘zero’ = absent, ‘low’ = 1–50%, ‘high’ = 51–100%) for vegetation, mussels, and open habitat (combined rock, cobble, and silt; Figure S3). The presence of other fish species was recorded. Depth and water temperature profiles at sites were recorded with a CastAway CTD (YSI Inc., San Diego, CA), however these variables were highly correlated (Pearson’s $r = -0.78$, $P < 0.001$). We therefore retained depth over water temperature for habitat use modeling as temperature was relatively homogenous above and below a thermocline during summer and varied little during winter.

To accurately assess round goby habitat use, we implemented N-mixture hierarchical species distribution models that relate imperfectly observed video counts to the true underlying (i.e. ‘latent’) distribution patterns (Kéry & Royle, 2016; Royle, 2004). N-mixture models jointly estimate linked model components specifying abundance and observation processes:

$$y_i \sim Poisson(\mu_i) \tag{1}$$

$$x_{ij} | y_i \sim Binomial(p_i, y_i) \tag{2}$$

where y_i is the latent abundance (count) at video quadrat site i; μ_i is the expected count at site i; x_{ij} is the observed count at site i by replicate observer j; and p_i is the probability of detecting a given individual at site i. Estimating the probability of detection for a given observation technique requires replicate observations at sampling points, which in our case were generated using three observers to process video quadrat footage. To assess the influence of habitat or biological factors on species abundance or detection, N-mixture models relate explanatory variables to these processes through link functions (e.g. Kéry & Royle, 2016; Royle & Dorzio, 2008). We used a log-link to model expected counts, μ_i, as functions of explanatory variables and a logit-link to model probability of detection, p_i, as a function of explanatory variables.

Field sampling indicated potential for a strong depth threshold in both summer and winter goby distributions. We therefore implemented a novel N-mixture model structure which included depth as a smooth function (thin plate spline) in order to accommodate a potentially non-linear relationship between round goby abundance and depth. We programmed our N-mixture model with the depth smooth term for the JAGS statistical environment using the jagam function in the mgcv R package (Plummer, 2017; Wood, 2011; Wood, 2016; Text S1).

We ran separate N-mixture species distribution models for the summer and winter survey. The abundance model for the summer survey included categories of mussels, vegetation, open habitat, the presence of other fish, and depth as covariates. The sparser winter dataset exhibited statistical separability issues in which some values of explanatory variables were associated only with round goby absence, resulting in a lack of information to estimate covariate parameter values and model convergence problems. Thus, the winter abundance model contained only the depth smooth term and open habitat as covariates. Similarly, the use of multiple explanatory variables in the detection process caused model fitting problems due to a lack of sufficient data to estimate a larger number of model parameters. Therefore, we parameterized a simple detection model for summer data containing only vegetation as a key covariate potentially impacting video counts, and an intercept-only model for the winter data set.

Models were fit in a Bayesian framework with MCMC sampling in JAGS using the jagsUI package in the R statistical computing environment (Kellner, 2015, R Core Team, 2019). Each model was run with 8 parallel chains commencing with a 20,000 iteration burn-in followed by 10,000,000 iterations at a thinning interval of 100 for a total of 800,000 posterior samples. Chains were well mixed and achieved Gelman–Brooks–Rubin $\hat{R}$ convergence statistics of < 1.1 for all fitted parameters (Brooks & Gelman, 1998). We measured the relative importance of covariates using a posterior inclusion probability (PIP) for each variable, taking PIP > 0.50 as sufficient evidence of variable importance in both models (Kuo & Mallick, 1998).

Finally, in a separate field effort we assessed seasonal onshore/offshore migration behavior with periodic snorkel surveys at an index site known to harbor round goby at Long Point State Park, Aurora, NY (Figure 1). At each of eight sampling occasions between April 2017 and May 2018 (Figure 2b), a snorkeler surveyed a minimum of 6 transects randomly chosen over a 250m stretch of shoreline. Transects were approximately 30 m in length and 1 m in width perpendicular from shore to breath-hold depth limits of the sampler (10 m). The snorkeler recorded the shallowest depth at which round goby were observed at the site and a visual estimate of maximum round goby density (i.e. maximum goby count within a 1 x 1 m transect section), if present.

Biomass estimation

Lake-wide round goby biomass (B) was estimated using the summer data set. Accurate biomass estimation involved a number of processing steps including developing estimates of goby counts, converting these to biomass densities (fish biomass per area) through size-weight relationships, and scaling up biomass densities to habitable lake area to estimate lake-wide biomass. This approach required separate treatment for the weedy northern end of the lake (8.9% of total lake area; Figure 1) where video data could not be obtained. For the main portion of the lake, we generated round goby densities using video quadrat data. In order to produce the most accurate density estimates, we corrected quadrats counts for imperfect detection and adjusted effective quadrat sampling areas for the attraction of fish beyond video viewing areas. To do so, we inflated the mean raw count across all video quadrats ($\overline{X}$, average round goby counts among the three video observers) shallower than the maximum depth at which round gobies were observed during summer (18.4 m) using an estimate of overall probability of detection (δ). This detection probability was generated by fitting the full summer hierarchical habitat use model as outlined above with an intercept-only detection model. Next, because round gobies were attracted to the camera cage, we estimated the effective video quadrat sampling area by observing goby movement using an additional camera (Hero3+, GoPro, Inc.) pointing outward from the quadrat frame. We calculated the effective quadrat sampling area ($R_{\overline{M}}$, units in m^2) as the nominal area plus a buffer attraction zone with width equal to the mean distance round gobies traveled to reach the video quadrat perimeter ($\overline{M}$; n = 54 movements; Figure S1). We then converted round goby counts to weights using a head width-to-weight regression fit to a separate sample of 150 specimens collected from Cayuga Lake. Head widths from video quadrat images containing the maximum number of round gobies per site were measured by a single observer using ImageJ (v1.8) and mean width ($\overline{H}$) was translated to a predicted mean weight ($W_{\overline{H}}$, units in g per fish). Finally, correcting for species detection and specimen attraction, we calculated goby biomass per unit area and expanded this to total suitable habitat area in the main portion of the lake (91.1% of total lake area) during the summer season, A_{Main}, which was defined as the lake bottom area above the maximum depth at which round gobies were observed:

$$B_{Main} = A_{Main} * \left(\frac{\overline{X}/_{\delta}}{R_{\overline{M}}} * \ W_{\overline{H}} \right) \tag{3}$$

In the northern end of the lake where heavy vegetation precluded videography (A_{North}), we obtained a round goby density estimate from a snorkel survey conducted at seven locations positioned at the north end of the lake on August 11, 2018 (Figure 1). At each survey location, two snorkelers surveyed separate 25 m linear transects 1 m wide with starting locations at least 50 m apart. Snorkelers repeatedly dove to the lake bottom (depth range 1–3 m) and visually counted round gobies, using their hands and dive lights to explore vegetation stands when necessary. Subsequently, we combined the mean round goby density across snorkel surveys (fish m^{-2}, $\overline{D}$) to calculate biomass in this region as:

$$B_{North} = A_{North} * \left(\overline{D} * \ W_{\overline{H}} \right) \tag{4}$$

where we converted fish densities to biomass density using the predicted mean weight of round gobies as in Equation 3. Total biomass was estimated as the sum of the two region-specific estimates: $B = B_{Main} + B_{North}$.

To propagate uncertainty in the total biomass estimate, we generated 10,000 parametric bootstrap estimates of B, treating round goby count from video quadrats, goby attraction distance, snorkel density, and predicted weight at mean head width as Normal random variables ($\overline{X}, \overline{M}, \overline{D}$: mean = sample mean, standard deviation = sample mean standard error; $W_{\overline{H}}$: mean = model-predicted weight, standard deviation = prediction standard error). Overall detection probability (δ) was also treated as a random variable with bootstrap draws taken directly from the posterior distribution generated from the Bayesian hierarchical distribution model.

RESULTS

Seasonal habitat use

Benthic videography demonstrates that suitable habitats for round gobies in Cayuga Lake vary by depth. Benthic environments in the narrow nearshore shelf (< 8 m) are characterized by high vegetation and little open habitat, while very deep environments (> 60 m) are almost exclusively open habitats. Dreissenid mussel cover peaks at around 15–30 m, forming dense 'pavement' just below the summer thermocline (8–17 m), although mussels were detected across the entire range of depths. The hierarchical species distribution modeling approach indicated that round goby detection from benthic videography was imperfect, with variable round goby counts among observers (Figure S2) and the lowest detectability probability in dense vegetation (0.49, Table 1).

Within the diverse environments of Cayuga Lake, we found strong seasonal differences in the habitat niche utilized by round gobies (Figure 2a). The summer hierarchical distribution model emphasized strong support for depth as influencing habitat use (PIP = 1.00; Table 2), with predicted maximum abundance at 8.5 m. During this season, gobies were restricted to a narrow band of shallow depths around the edge of the lake, with the lower edge of the occupied zone (18.4 m) coinciding with the lower limit of the lake thermocline (Figures 3–4a; Figure S4). The summer model also indicated support for the presence of mussels and vegetation, where predicted goby abundance in the summer was highest in habitats with low vegetation cover and either low or high mussel cover (Figure 3).

Repeated snorkel surveys at the index location revealed that gobies remained in nearshore 'summer' shallow habitats well into fall 2017 until migrating to deeper offshore habitats, coincident with nearshore water temperatures dropping below 12º C (Figure 2b). The last round goby observation in fall 2017 occurred on October 28, and gobies were not observed again until mid-May 2018, indicating a protracted 'winter' distribution period. While it is possible round gobies could have made temporary nearshore migrations to shallow habitats during the winter months not captured by our survey efforts, video quadrat sampling indicates that round gobies shifted to a much deeper distribution and were found at a broader range of depths (47.2–104.2 m; Figure 4b) in the winter compared to the shallow-water habitats occupied in the summer. Round goby densities also decrease in winter, as evidenced by lower mean densities from the videography data in winter (mean raw count in occupied habitats = 1.6 gobies per quadrat; 0.6 per m^2 when adjusted for effective video quadrat sampling area) than in summer (6.9 per quadrat; 2.7 per m^2). Similarly, maximum predicted abundance (Figure 3) was much smaller in the winter model (0.8 gobies per quadrat, 0.3 per m^2) than in the summer model (11.9 per quadrat; 4.6 per m^2).

The winter distribution model indicated support for open habitat (Table 2) and predicted highest round goby densities in low to high levels of open habitat (Figure 3). However, the winter model lacked support for a specific depth preference (Figure 4), indicating the round goby habitat niche is deeper and more diffuse in winter months compared to summer. Finally, after the winter season, round gobies returned to shallow nearshore habitats at the index snorkeling site by May 14, 2018, when water temperatures warmed to 12º C (Figure 2).

Biomass estimation

The overall estimated probability of detecting an individual specimen from the summer season hierarchical distribution model was 0.62 (95% highest posterior density interval = 0.50, 0.73). Supplementary video exploring attraction behavior to the camera cage indicated a mean round goby attraction distance of 41.7 cm (SE = 2.8 cm), yielding an estimated effective video quadrat sampling area of 2.56 m^2, considerably greater than the nominal quadrat area of 0.65 m^2.

The mean raw goby count from video quadrats in the main portion of the lake at depths shallower than 18.4 m (4748 ha) was 2.88 fish (SE = 0.70), leading to a mean density of 1.82 fish m^{-2} after adjusting for imperfect species detection and fish attraction. In the densely vegetated north end of the lake (1521 ha; Figure 1), gobies were present in all snorkel locations and density estimates were consistent across snorkelers (t-test, t = 0.82, d.f. = 12, p = 0.43), with a mean density across locations of 0.34 fish m^{-2} (SE = 0.09). The size-weight regression indicated a tight positive relationship between head width and weight ($F_{1,104} = 7408$, $P < 0.001$, $R^2 = 0.99$; Figure S5a), and the mean head width from summer videography (14.26 mm, SE =

0.72, range = 3.38–32.00 mm; Figure S5b) was associated with a predicted weight of 8.28 g (prediction SE = 1.01). Combining information on estimated round goby density, predicted weight, and suitable habitat lake areas, the total summer season standing stock biomass of round gobies was estimated at 766,000 kg (bootstrap 95% confidence interval: 401,411–1,185,665 kg), or 122 kg ha^{-1} in summer habitat shallower than 18.4 m (bootstrap 95% confidence interval: 64.0–189.1 kg ha^{-1}).

DISCUSSION

Our assessment of round goby habitat use throughout an annual cycle using videography and hierarchical statistical modeling to control for imperfect detection provides fine scale insight into the ecology of round gobies in newly invaded habitats in North America. Together these analyses stress the importance of correcting for observation errors and behavioral responses to sampling gear when attempting to reconstruct the density and biomass of cryptic species with videography. Indeed, by incorporating variation among multiple observers into our analyses (Figure S2), we were able to account for imperfect detection in video quadrat data by generating a detection probability subsequently used in N-mixture species distribution models and biomass estimates. Furthermore, through the novel integration of smooth terms into hierarchical species distribution models, our analytical approach provides a flexible method of assessing non-linear relationships between covariates and occupancy or abundance that is useful for investigating the importance of environmental thresholds, as we identified in the relationship between round goby habitat use and depth.

Using these methods, we find evidence of seasonally differentiated habitat use by round gobies in Cayuga Lake, splitting the year between shallow summer habitats and deeper winter habitats in this temperate climate. The summer niche is characterized by complex habitat with a mixture of vegetation, dreissenid mussels, and open habitat in a narrow band of shallow depths (<18.4 m) in the littoral zone of the lake, thus concentrating goby biomass in a relatively small area. In contrast, round goby biomass is diffuse in the winter, occupying habitats over a wider range of greater depths (47.2–104.2 m) that are dominated by open habitat with sparser dreissenid mussel cover. During the summer, estimated round goby biomass reached 122 kg ha^{-1} in the occupied nearshore area (< 18.4 m), indicating this species can become a significant component of the food web with high potential for ecological impacts of gobies in shallow environments during this season.

To our knowledge, this is the first study to estimate round goby biomass in North American inland lakes and predicts higher biomass than has been documented within the Great Lakes proper, including nearshore Lake Ontario (40 kg ha^{-1}, Pennuto, Howell, & Makarewicz, 2012; 50–112 kg ha^{-1}, Taraborelli, Fox, Johnson, & Schaner, 2010) and western Lake Erie (approx. 72.1 kg ha^{-1}, Johnson, Allen, Corkum, & Lee, 2005). However, caution may be warranted when comparing data collected using disparate sampling methodologies, as they vary in their round goby capture efficiency. For instance, benthic videography and direct observation are more effective for assessing round goby density than trawls, seining, and minnow traps across many substrate types (Jackson et al., 2019; Johnson, Allen, Corkum, & Lee, 2005) but may be limited in highly vegetated or turbid environments.

A seasonal shift of round gobies to deeper water in the winter months is known to occur within their native range (Charlebois et al., 1997) and is presumed to occur within invaded habitats (Johnson, Bunnell, & Knight, 2005; Lynch & Mensinger, 2012; Sapota & Skóra, 2005), including a possible winter out-migration to the Great Lakes from tributaries when temperatures decrease below 5–15º C (Pennuto, Krakowiak, & Janik, 2010). This migration may be due to round goby preference for warmer temperatures closer to their energetic temperature optimum at 26º C (Lee & Johnson, 2005). Our results document this shift in inland lakes, suggesting that the seasonal depth-mediated life history observed in this study may manifest in other inland lakes along the invasion path. In light of this, lake depth appears to be an important mediating factor driving the potential for species interactions with round gobies in invaded systems.

Round gobies in Cayuga Lake reach their highest abundance in the narrow shallow band around the lake perimeter during the summer months, and we therefore expect biotic interactions to be strongest in the littoral zone from May to October. This season coincides with the spawning period of several fish in nearshore areas including pumpkinseed sunfish (Lepomis gibbosus), yellow perch (Perca flavescens), largemouth bass (Micropterus salmoides), and smallmouth bass (M. dolomieu). Because round gobies consume fish eggs, larvae, and young of year (Steinhart, Marschall, & Stein, 2004), the strongest impacts of round goby predation on fish populations in deep lakes may therefore be limited to summer-spawning species. Similarly, while gobies may serve as prey items to a wide range of piscivores in the summer months, they may only be vulnerable to predation by deep ranging piscivores during the winter portion of the year. Thus, seasonal and spatial differences in round goby habitat use will likely have variable impacts on certain species depending on life history. However, such seasonally dependent trophic impacts may not be realized in shallower lakes along the invasions path, where the absence of deep habitats may lead to greater spatiotemporal overlap between gobies and other fish species or predators throughout the year.

While round gobies have potential for deleterious impacts to native fish and invertebrate communities, they are also one of few species in North America that consume invasive dreissenids and may serve an important role of mobilizing energy trapped in mussels to higher trophic levels in invaded systems (Ray & Corkum, 1997; Johnson, Bunnell, & Knight, 2005). When present, dreissenids can make up a dominant proportion of round goby diets and may contribute to supporting large goby populations (Charlebois et al., 1997; Pennuto, Howell, & Makarewicz, 2012). Indeed, in Cayuga Lake our distribution models associate mussel coverage with goby abundance during the summer. With high reliance on dreissenid prey, round gobies could theoretically suppress mussel recruitment with sustained high predation mortality, initiating a boom and bust goby population trajectory after initial establishment (Blackburn et al., 2011). However, in deep waterbodies such as Cayuga Lake, seasonally differentiated habitat use by round gobies may attenuate predation pressure on shallow nearshore versus deep offshore dreissenid populations across winter and summer, potentially mitigating the possibility of mussel collapse. In contrast, shallow lakes may result in sustained mussel predation mortality across all habitats throughout the year. For example, while there has been some evidence of round goby altering size distributions of dreissenids in the Great Lakes, they have not yet suppressed mussel populations after 25 years of coexistence (Johnson, Bunnell, & Knight, 2005; Pennuto, Howell, & Makarewicz, 2012). Yet, evidence from Onondaga Lake, an inland shallow (maximum depth < 19 m) waterbody in the Lake Ontario watershed, indicates round gobies may be having a rapid and strong impact on dreissenids (Rudstam & Gandino, 2016). Round gobies were first confirmed in Onondaga Lake in 2010, and benthic surveys have since indicated a replacement of thinner-shelled quagga mussels (preferred by gobies) with more armored zebra mussels less than a decade post-invasion (Rudstam & Gandino, 2016). Further observations of seasonal mussel-goby dynamics in inland lakes along the invasion path will be important for understanding the long-term stability of round goby populations.

The rapid expansion of round gobies in North America continues to progress inland from the Great Lakes. Round gobies and dreissenid mussels occupy similar habitats in both their native and invaded ranges, and thus it is conceivable that goby could occupy a similar geographic extent in North America as invasive zebra and quagga mussels if migration via connected waterways or human-assisted migration continues unabated. Our data suggest that in deep lakes, round goby migrations from low densities in deep waters to high densities concentrated in nearshore habitats could substantially alter species interactions across seasons. Conversely, an implication of this life history indicates that shallow lakes which may lack seasonally differentiated habitat niches may harbor proportionately higher round goby biomass relative to deeper inland lakes or the Great Lakes proper. For example, Cayuga Lake (total area = 172 km^2; total volume = 9.5 km^3, mean depth = 55 m) is considerably larger by volume, but comparable in area, than the nearby shallower Oneida Lake (total area = 207 km^2; total volume = 1.4km^3; mean depth = 6.7m) which contains a proportionately larger littoral zone and harbors round gobies across all depths in summer (Jackson et al., 2019). Video quadrat surveys in Oneida Lake indicate round gobies are found at similar densities in both shallow and deep sites (1.23 per m^2, 1.24 per m^2 respectively; Jackson et al., 2019), similar to those in Cayuga Lake summer nearshore habitats (2.7 per m^2). If we apply the shallow summer round goby biomass density estimated from Cayuga Lake to the entirety of Oneida Lake, the latter would have an estimated total standing stock goby biomass four times larger than that of the former. It follows that shallow lakes, which are numerous along the round goby invasion path, and the nearshore habitats of deep lakes in summer months may be most heavily impacted by high densities of round goby, emphasizing a need to investigate the role of lake depth and seasonal habitat use in predicting interactions between this rapidly expanding invader and resident species in infested or at-risk systems.

ACKNOWLEDGEMENTS

We thank A. Ullman, J.P. Hellenbrand, A. Hausner, and D. Kowalik for assistance with data collection and processing and L. Rudstam for insights into round goby ecology on Oneida Lake. C. Karbowski, two anonymous reviewers, and Journal editorial staff are thanked for comments which improved earlier drafts of this manuscript. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

DATA AVAILABILITY STATEMENT

Data available via Open Science Forum, https://osf.io/mz3he/.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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TABLES

Table 1 Hierarchical species distribution model results for round goby detection fit to summer or winter survey data. Values are on the probability scale with 95% highest posterior density (HPD) limits.

Model	Variable	Estimated probability of detection	
		Posterior mean	95% HPD limits
Summer	No vegetation	0.65	(0.42, 0.86)
	Low vegetation	0.63	(0.46, 0.79)
	High vegetation	0.49	(0.16, 0.74)
Winter	Intercept	0.78	(0.40, 1.00)

Table 2 Posterior inclusion probabilities for abundance covariates from hierarchical species distribution models fit to summer or winter round goby survey data. Inclusion probabilities characterize support from the data that a given variable is associated with the true model producing the observed count data, where values above 0.50 indicate sufficient variable support in each model. The reference 'high' categories for mussels, vegetation, and open habitats and 'no other fish present' are absorbed by the intercept.

Variable	Posterior inclusion probabilities	
	Summer model	Winter model
Intercept	0.95	0.75
Mussels – low	0.01	--
Mussels – zero	1.00	--
Vegetation – low	0.76	--
Vegetation – zero	0.22	--
Open habitat – low	0.06	0.13
Open habitat – zero	0.03	0.75
Other fish present	0.01	--
Depth (smooth)[†]	1.00	0.20

[†] See Figures 3–4 for visualizations of relationships between depth smooth terms and round goby abundance.

FIGURES

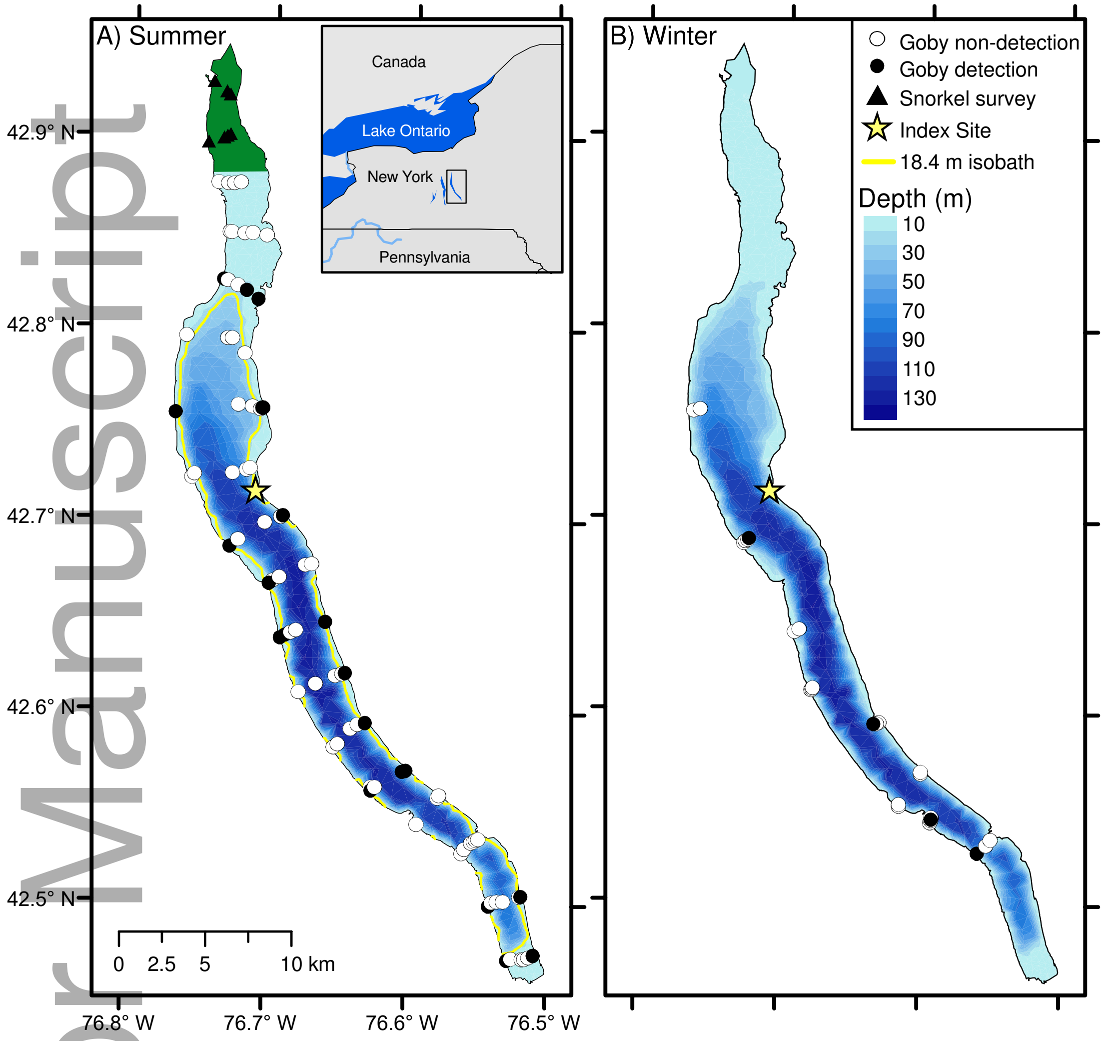


Figure 1 Round goby (Neogobius melanostomus) sampling during (A) summer and (B) winter videography surveys in Cayuga Lake. In summer, round goby presences (black circles) were found in depths shallower than 18.4 m (yellow isocline), whereas round gobies did not exhibit a significant depth association in winter. Seasonal offshore migrations were assessed at an index site at Long Point State Park (yellow star). Due to dense vegetation, round goby densities were assessed with snorkel surveys in the northern end of the lake (black triangles in the green shaded area).

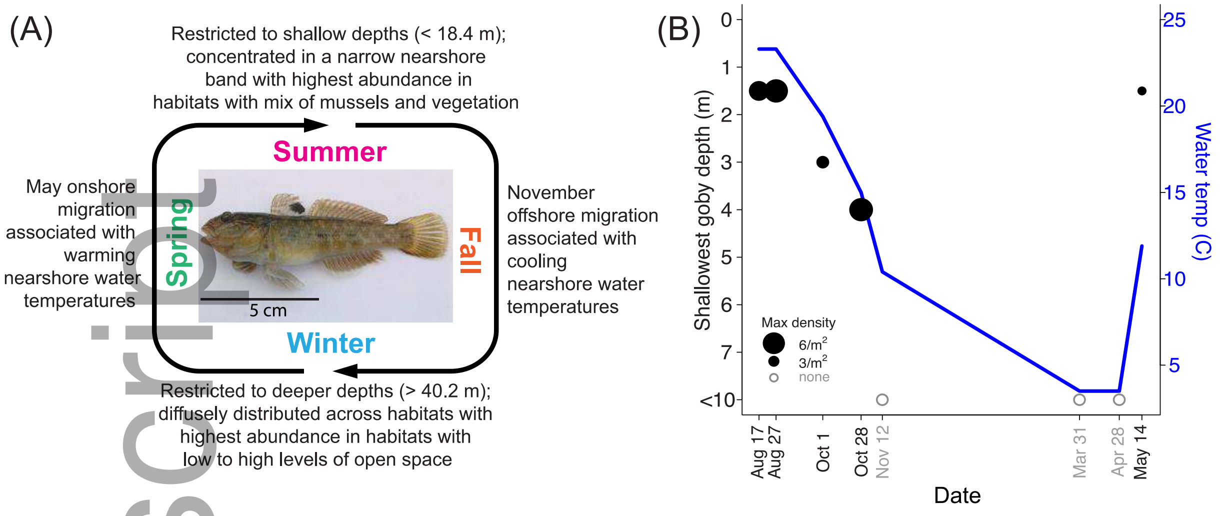
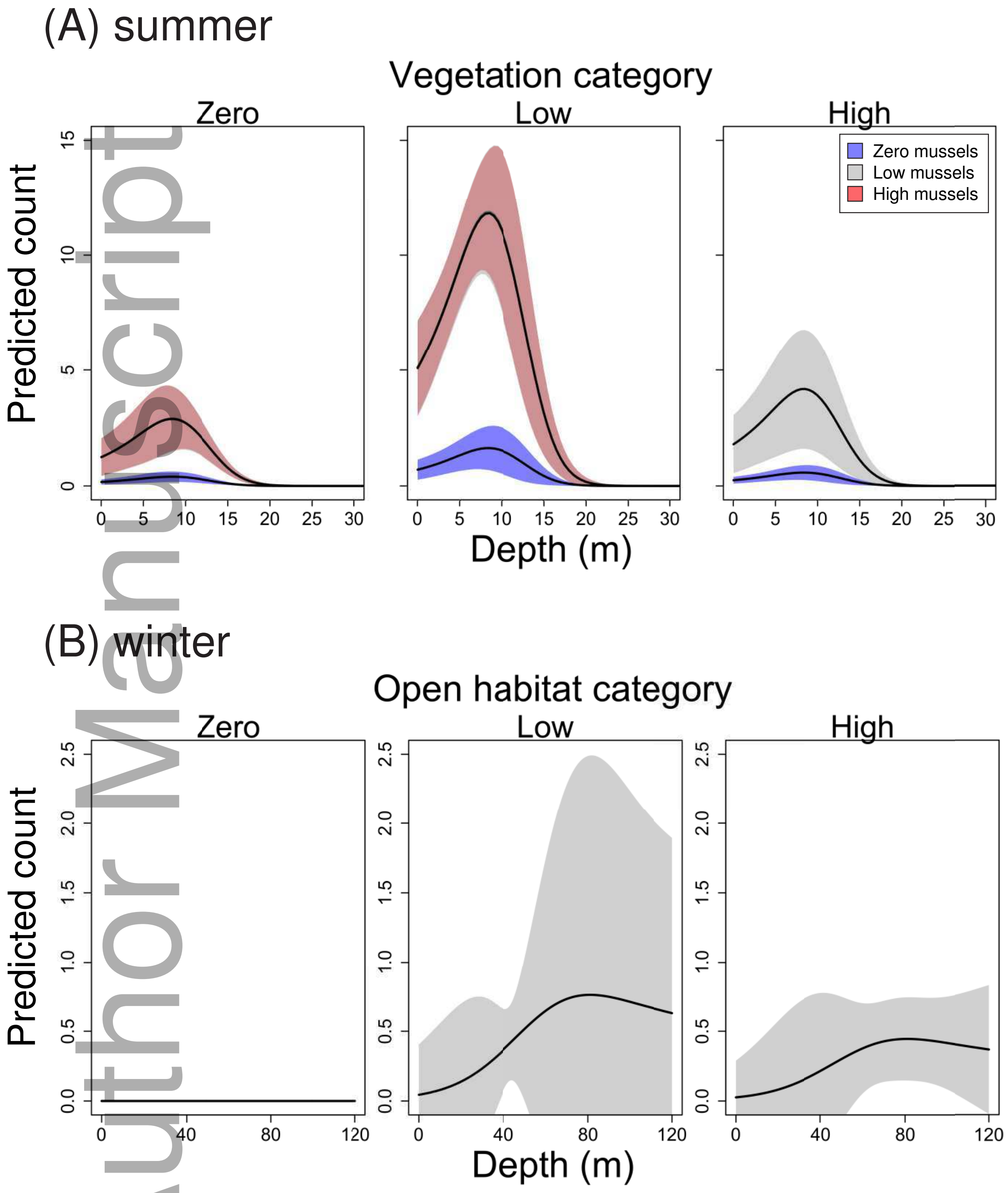


Figure 2 Summary of the seasonally dependent habitat use and migrations by round gobies in Cayuga Lake. (A) Round goby habitat use in summer and winter was assessed from video quadrat data and hierarchical statistical modeling, while migration events in spring and fall were inferred nearshore snorkel surveys at the index site; (B) Round goby offshore migration timing over the fall 2017–spring 2018 period assessed by nearshore snorkel surveys at the index site. The blue line indicates nearshore water column temperature at 1 m depth. Points indicate the shallowest depth and maximum density of round goby observed within breath-hold diving depth limits (10 m) during each snorkel sampling occasion. Round goby photo credit: P. van der Sluijs, used with permission under creative commons license CC BY-SA 3.0 (scale bar added to demonstrate a typical adult specimen size).



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499 **Figure 3** Predicted round goby counts in video quadrats from the (A) summer and (B) winter species distribution models across different combinations of habitat cover ('zero' = absent, 'low' = 1–50%, 'high' = 51–100%) and depth. Lines indicate posterior mean predicted values and

polygons represent 95% credibility regions. The summer model (A) supported mussels (lines with color polygons) and vegetation (panels) influencing goby abundance, while the winter model (B) supported open habitat (panels) as influencing goby abundance. For summer data, the combination of high mussels and high vegetation was not observed and is excluded, and predictions overlap for low and high mussels at zero and low vegetation combinations. Winter predictions for goby counts at zero open habitat were close to zero (i.e., < 0.01 goby/quadrat). Y-axes for summer and winter panels are on different scales.

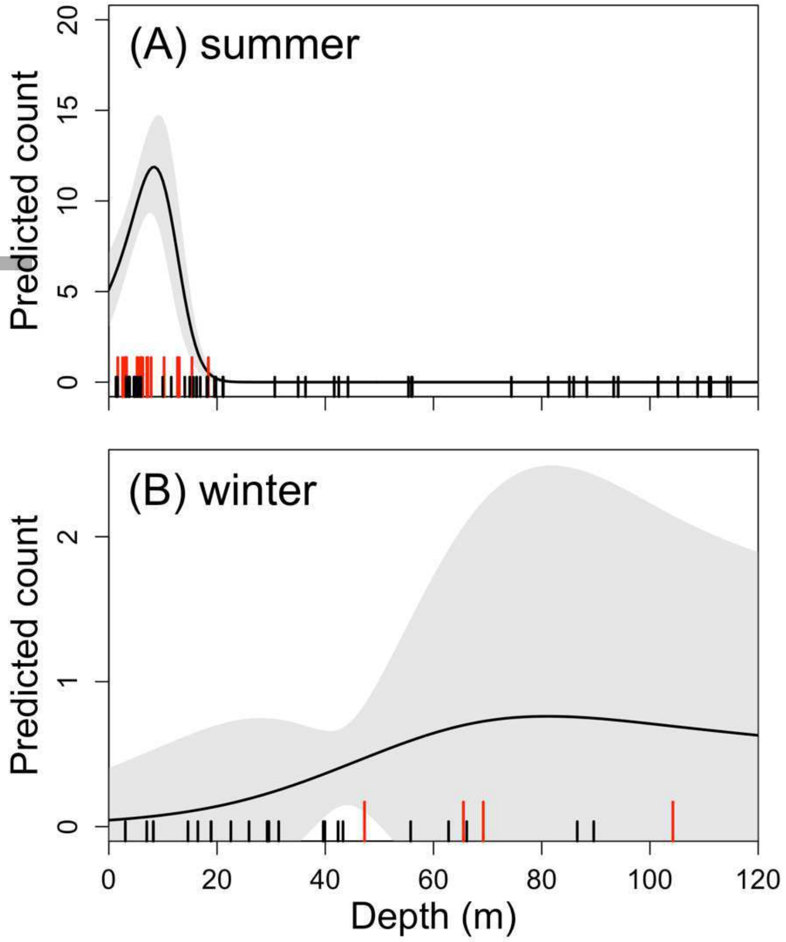

Figure 4 Observed round goby occurrences and predicted counts in video quadrats by depth for the (A) summer and (B) winter hierarchical species distribution models in habitats. Other model covariates were fixed at values associated with highest goby counts (‘high’ mussels and ‘low’ vegetation in summer; ‘low’ open habitat in winter). Depth was modeled as a smooth term; lines represent posterior median values and shaded polygons represent 95% credibility regions. Rugs along the X-axes represent the observed presence (red) or absence (black) of round gobies across sampled depths. Y-axes for summer and winter models are on different scales.

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FIGURE LEGENDS

Figure 1 Round goby (Neogobius melanostomus) sampling during (A) summer and (B) winter videography surveys in Cayuga Lake. In summer, round goby presences (black circles) were found in depths shallower than 18.4 m (yellow isocline), whereas round gobies did not exhibit a significant depth association in winter. Seasonal offshore migrations were assessed at an index site at Long Point State Park (yellow star). Due to dense vegetation, round goby densities were assessed with snorkel surveys in the northern end of the lake (black triangles in the green shaded area).

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Figure 3 Predicted round goby counts in video quadrats from the (A) summer and (B) winter species distribution models across different combinations of habitat cover (‘zero’ = absent, ‘low’

= 1–50%, ‘high’ = 51–100%) and depth. Lines indicate posterior mean predicted values and polygons represent 95% credibility regions. The summer model (A) supported mussels (lines with color polygons) and vegetation (panels) influencing goby abundance, while the winter model (B) supported open habitat (panels) as influencing goby abundance. For summer data, the combination of high mussels and high vegetation was not observed and is excluded, and predictions overlap for low and high mussels at zero and low vegetation combinations. Winter predictions for goby counts at zero open habitat were close to zero (i.e., < 0.01 goby/quadrat). Y-axes for summer and winter panels are on different scales.

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SUPPLEMENTARY FILES

SUPPLEMENTARY METHODS

Text S1: N-mixture model implementation

SUPPLEMENTARY FIGURES

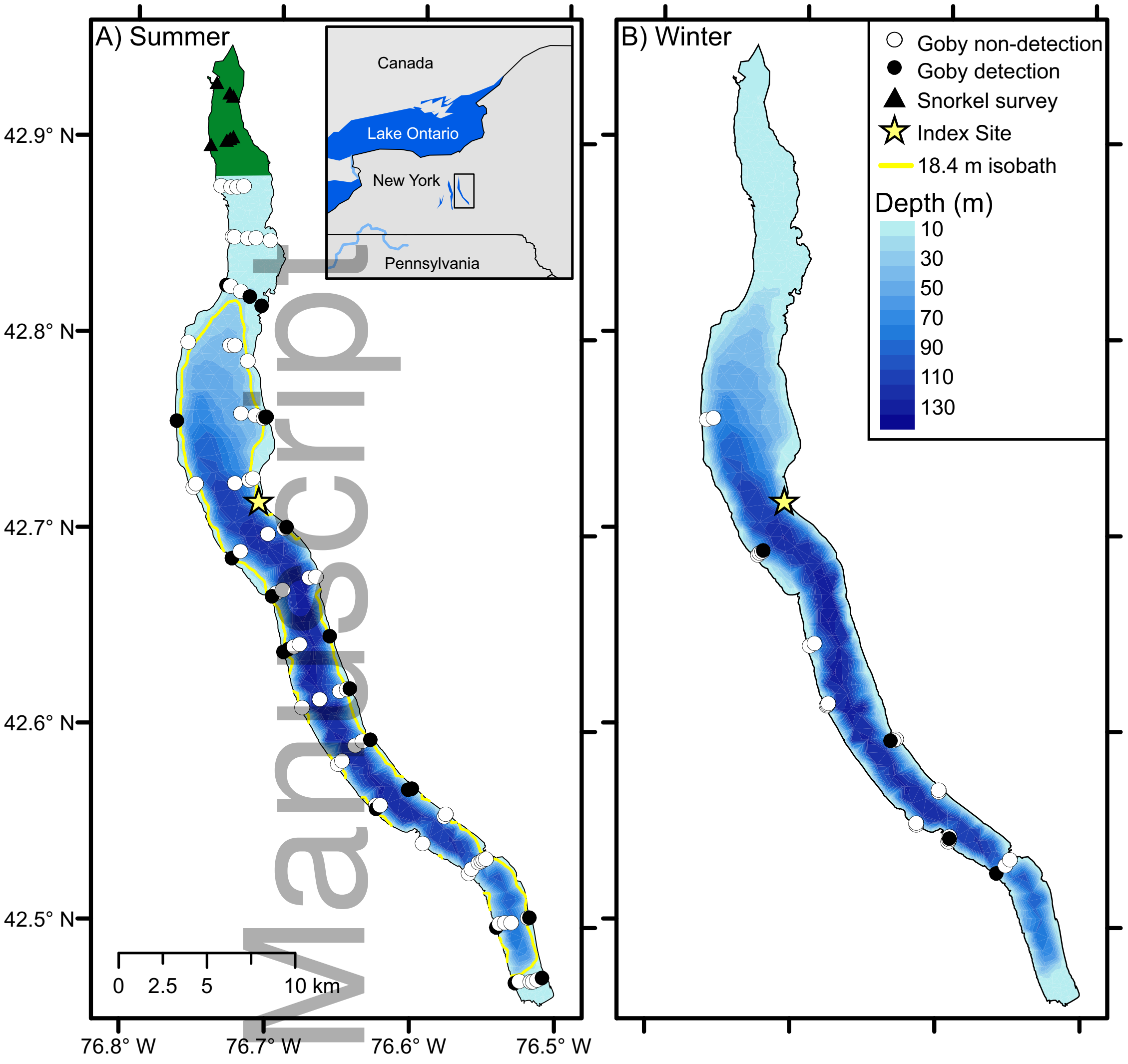
Figure S1 Schematic bird's eye perspective of the benthic video quadrat nominal sampling area (a; 0.65 m^2), and effective sampling area (b; 2.56 m^2) encompassing the zone of attraction of round gobies. GoPro videos looking outward from the video quadrat cage (c) were used to calculate the round goby attraction distances.

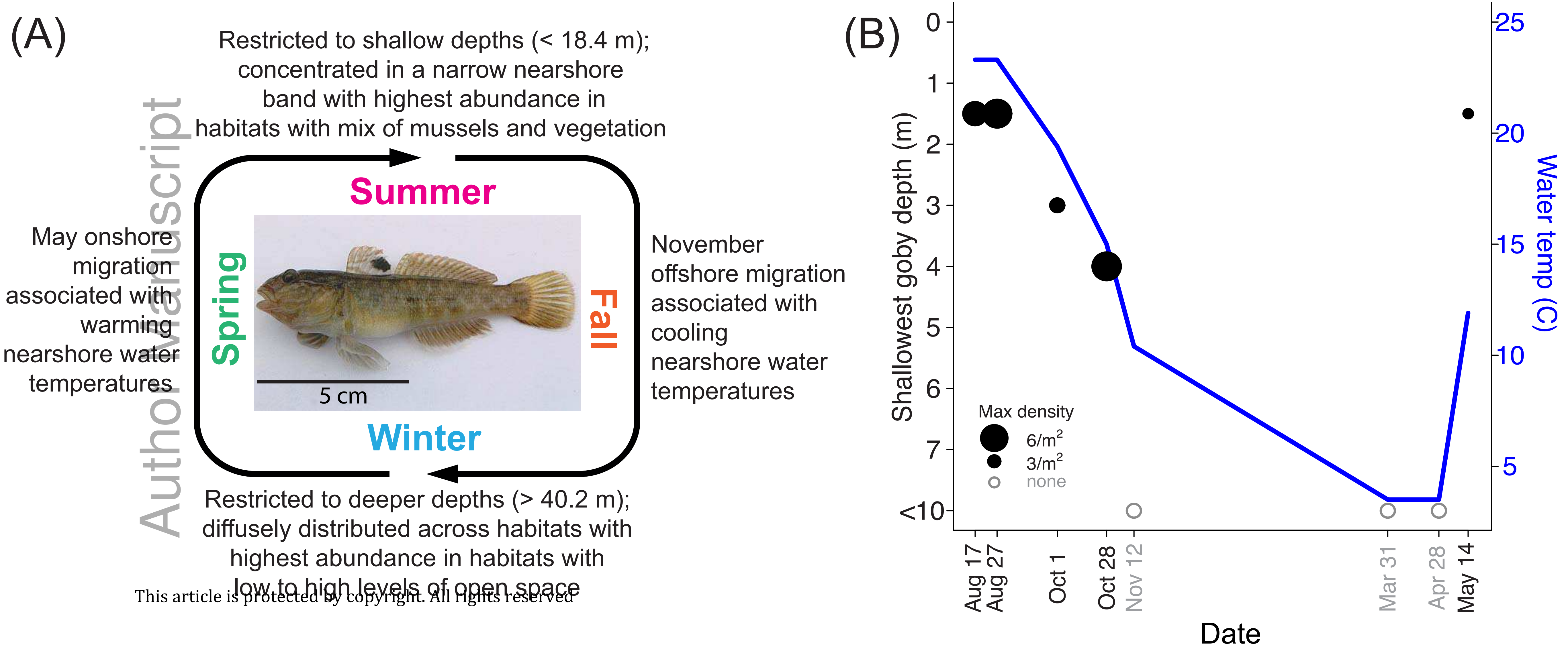
Figure S2 Maximum round goby (Neogobius melanostomus) counts per 0.65 m^2 video quadrat observed over one-minute intervals. Values are averaged for each observer across quadrats for positive-presence sites (n = 20 sites). Because mean round goby counts peaked at six minutes (gray line), we retained the maximum goby count through minute six of each video as the raw data representative of round goby density for subsequent species distribution modeling.

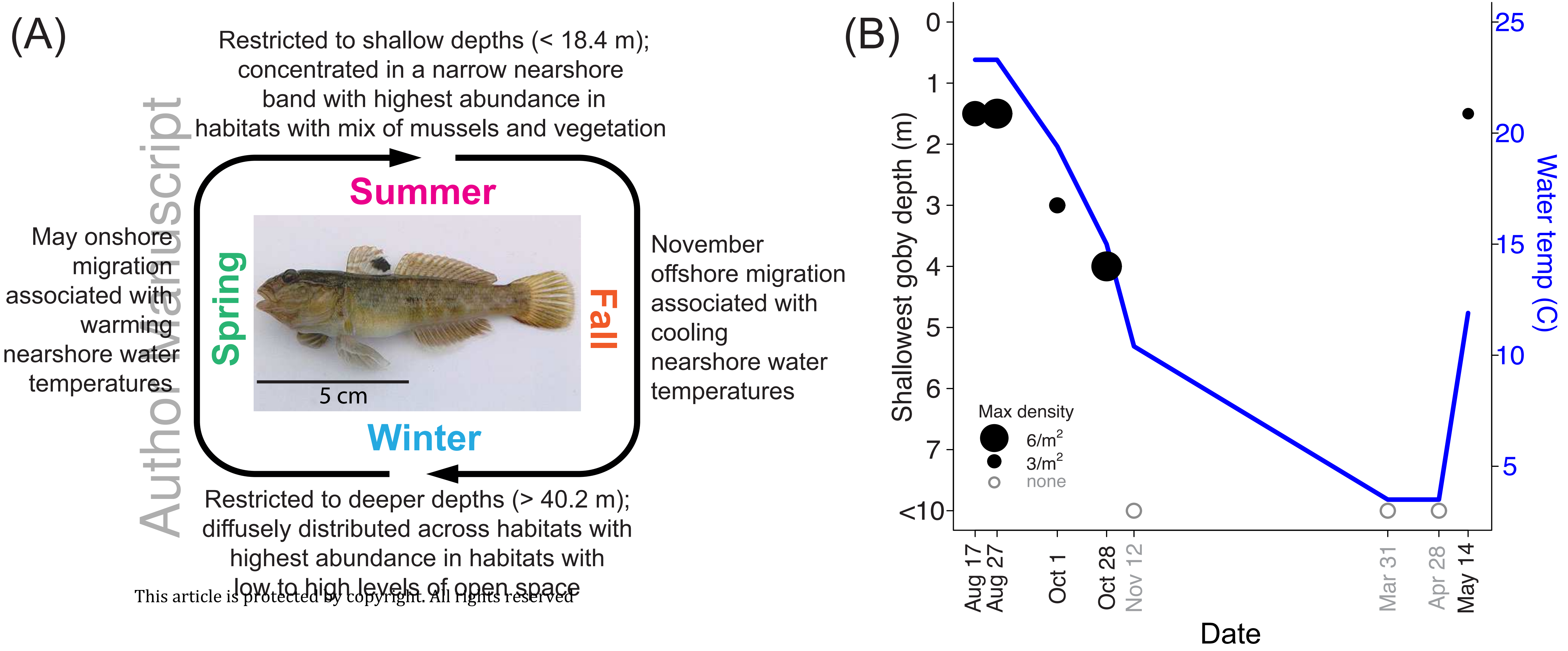
Figure S3. Benthic habitat characterization (vegetation, mussels, open space) with percent cover scores ('zero' = absent, 'low' = 1–50%, 'high' = 51–100%) at summer and winter videography survey sites in Cayuga Lake. The presence of round gobies at a site is indicated with a red outline.

Figure S4 Water temperature (1.0 m above lake bottom) and depth at benthic videography sites in the summer survey (24 July 2017–1 August 2017). The round goby summer shallow distribution depth threshold (18.4 m; gray dotted line) occurs near the deepest part of thermocline.

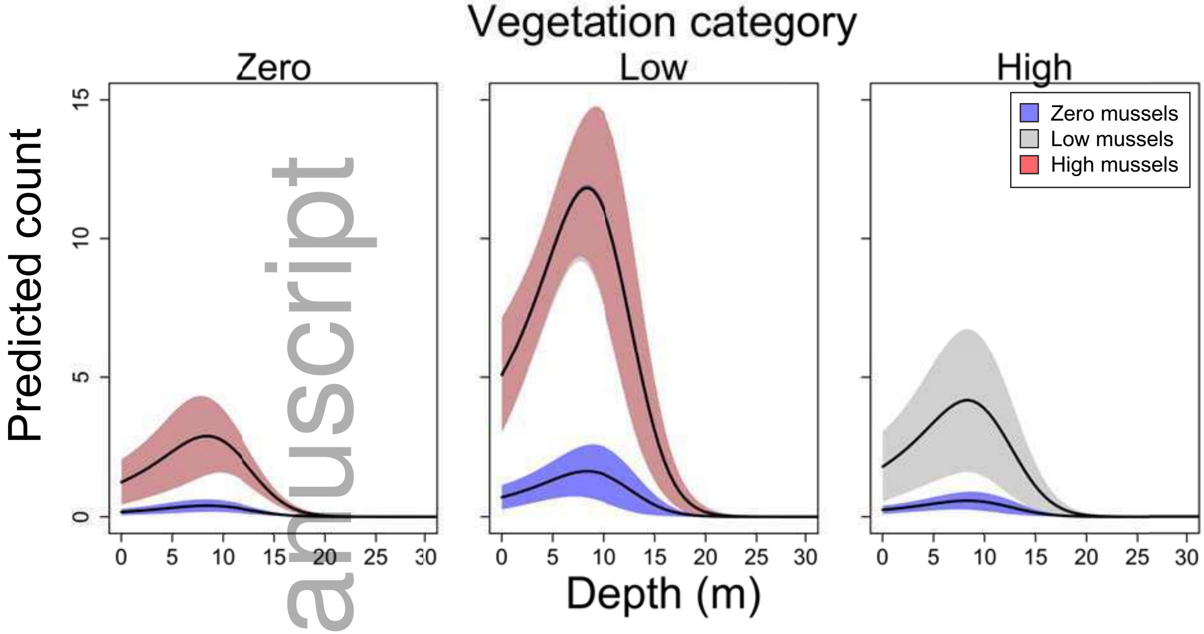
Figure S5 (A) Fitted relationship (equation and gray line; $F_{1,104} = 7408$, $p < 0.001$, $R^2 = 0.99$) between round goby head widths and weights analyzed from 150 specimens collected with small mesh stick seines at Long Point State Park, Cayuga Lake, NY, U.S.A. in July 2018. The grey line represents the fitted regression line to the data. Axes are on logarithmic scales. (B) Histogram of round goby head widths measured from summer videography. Mean head width (14.26 mm; gray dotted line) was associated with a predicted weight of 8.28 g in the summer season standing stock biomass estimation.


A) Summer
B) Winter
Canada
Lake Ontario
New York
Pennsylvania
Goby non-detection
Goby detection
Snorkel survey
Index Site
18.4 m isobath
Depth (m)
10
30
50
70
90
110
130
42.9° N
42.8° N
42.7° N
42.6° N
42.5° N
0
2.5
5
10 km
76.8° W
76.7° W
76.6° W
76.5° W

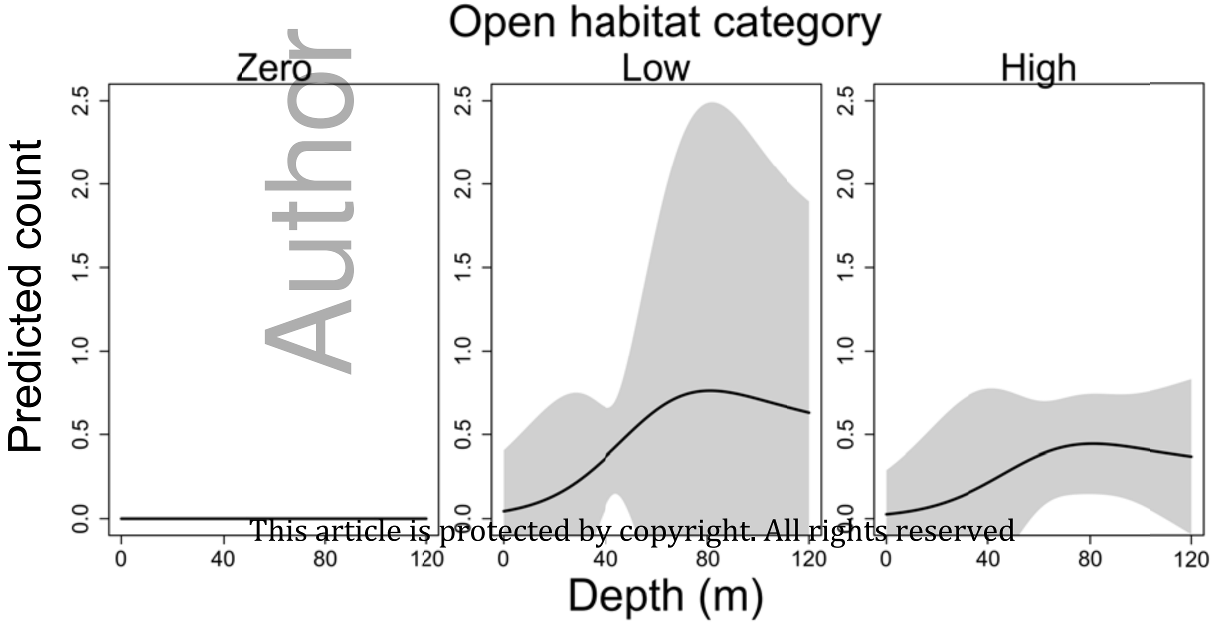

(A)
Restricted to shallow depths (< 18.4 m); concentrated in a narrow nearshore band with highest abundance in habitats with mix of mussels and vegetation
Summer
Spring
Fall
Winter
5 cm
May onshore migration associated with warming nearshore water temperatures
November offshore migration associated with cooling nearshore water temperatures
Restricted to deeper depths (> 40.2 m); diffusely distributed across habitats with highest abundance in habitats with low to high levels of open space
(B)
Shallowest goby depth (m)
0
1
2
3
4
5
6
7
<10
Water temp (C)
25
20
15
10
5
Max density
6/m²
3/m²
none
Aug 17
Aug 27
Oct 1
Oct 28
Nov 12
Mar 31
Apr 28
May 14
Date

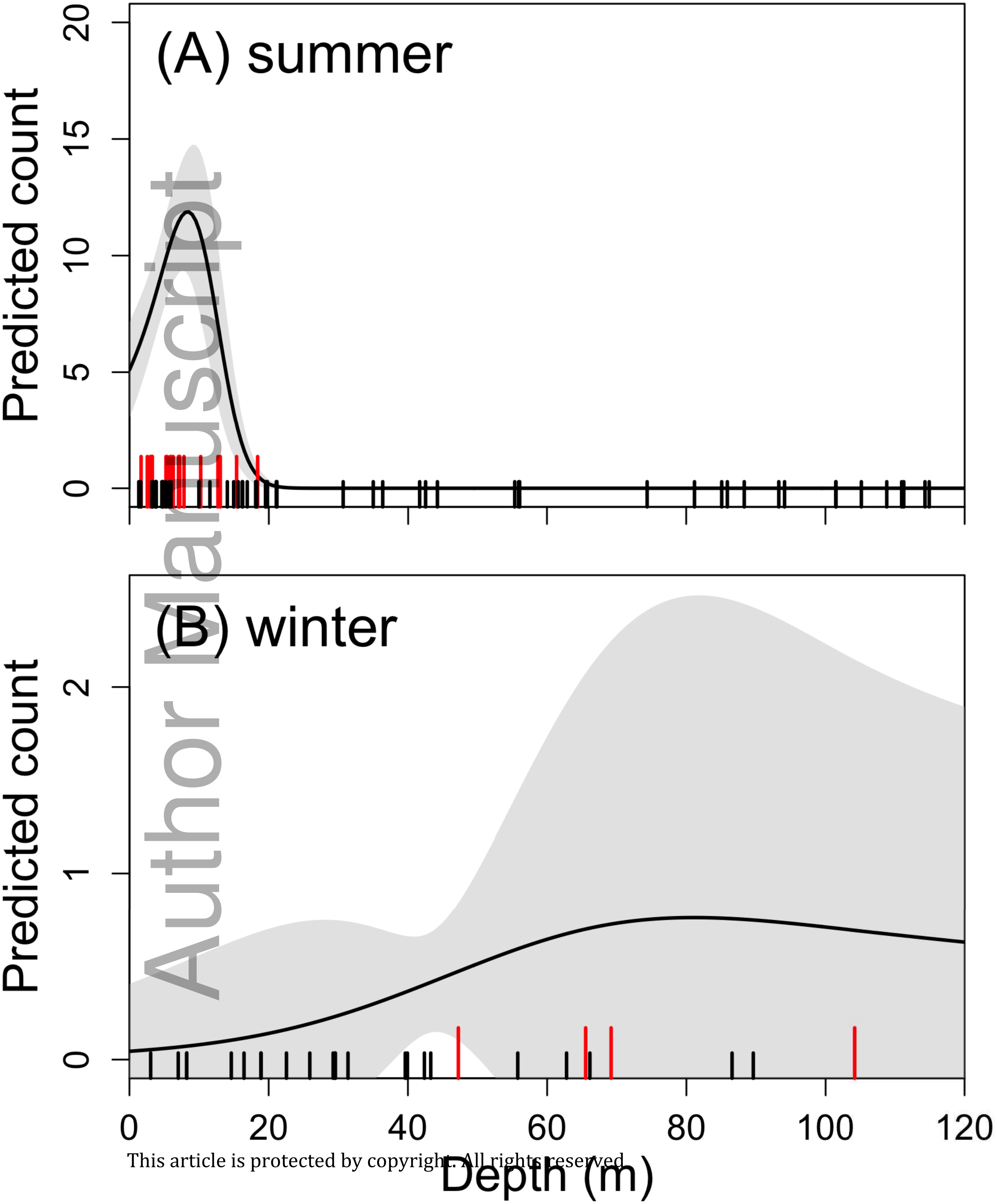

(A)
Restricted to shallow depths (< 18.4 m); concentrated in a narrow nearshore band with highest abundance in habitats with mix of mussels and vegetation
Summer
Spring
Fall
Winter
5 cm
May onshore migration associated with warming nearshore water temperatures
November offshore migration associated with cooling nearshore water temperatures
Restricted to deeper depths (> 40.2 m); diffusely distributed across habitats with highest abundance in habitats with low to high levels of open space
(B)
Shallowest goby depth (m)
0
1
2
3
4
5
6
7
<10
Water temp (C)
25
20
15
10
5
Max density
6/m²
3/m²
none
Aug 17
Aug 27
Oct 1
Oct 28
Nov 12
Mar 31
Apr 28
May 14
Date

(A) summer



(B) winter




(A) summer
Predicted count
20
15
10
5
0
(B) winter
Predicted count
2
1
0
0
20
40
60
80
100
120
Depth (m)