Forecasting the distribution of the invasive round goby (*Neogobius melanostomus*) in Wisconsin tributaries to Lake Michigan

Matthew S. Kornis and M. Jake Vander Zanden

Abstract: The Laurentian Great Lakes host more than 180 non-native species, including several that have resulted in major economic and ecological effects. This list includes the round goby (*Neogobius melanostomus*), an aggressive, benthic Ponto-Caspian fish that has established large populations in coastal Great Lakes habitats. Here, we document the inland dispersal of round gobies into Wisconsin tributaries of Lake Michigan. Round gobies were detected in 26 of 73 streams (36%) and found >10 km upstream of Lake Michigan in nine watersheds. Round goby presence–absence was modeled using landscape-scale data from these invaded streams. We forecasted the future spread of round goby within Wisconsin's Lake Michigan basin using our best model (80% accuracy), which included watershed area, stream gradient, and watershed slope as predictors. Round gobies were predicted to invade 1369 km of stream habitat up to the first stream barrier, and 8878 km of stream was identified as suitable looking beyond barriers at the broader Lake Michigan watershed (Wisconsin only). Our results depict the Great Lakes as a springboard for invasive species to disperse into inland ecosystems and, because round gobies are not usually reported in small streams in their native range, emphasize the utility of data from invaded regions when forecasting invasive species distributions.

Résumé : Les Grands Lacs Laurentiens contiennent >180 espèces non indigènes dont plusieurs ont eu des effets économiques et écologiques importants. Cette liste comprend le gobie à taches noires (*Neogobius melanostomus*), un poisson agressif d'origine ponto-caspienne, qui a formé de grandes populations dans les habitats côtiers des Grands Lacs. Nous apportons des informations sur la dispersion vers l'intérieur des gobies à taches noires dans les tributaires du lac Michigan au Wisconsin. Les gobies à taches noires se retrouvent dans 26 de 73 cours d'eau (36 %) et à >10 km en amont du lac Michigan dans neuf bassins versants. Nous avons modélisé la présence–absence des gobies à taches noires à l'aide de données à l'échelle du paysage provenant des cours d'eau envahis. Nous prédisons la dispersion future du gobie à taches noires dans le bassin versant du lac Michigan au Wisconsin à l'aide de notre meilleur (80 % d'exactitude) modèle qui inclut la surface du bassin versant, le gradient du cours d'eau et la pente du bassin comme variables prédictives. Notre prédiction est que les gobies à taches noires vont envahir 1369 km d'habitat lotique jusqu'à la première barrière dans les cours d'eau; de plus, 8878 km de cours d'eau au-delà des barrières paraissent des habitats convenables dans le bassin élargi du lac Michigan (dans le seul Wisconsin). Nos résultats décrivent les Grands Lacs comme des tremplins pour les espèces envahissantes vers les écosystèmes de l'intérieur; comme les gobies à taches noires ne se retrouvent pas généralement dans les petits cours d'eau dans leur aire de répartition indigène, nos résultats soulignent l'utilité de données provenant des régions envahies pour la prédiction des répartitions des espèces envahissantes.

[Traduit par la Rédaction]

Introduction

Increases in global transport and trade have resulted in an accelerating pace of species invasions at substantial ecological and economic costs (Mack et al. 2000; Pimentel et al. 2005). Understanding the nature and consequences of species invasions continues to be an urgent challenge facing the scientific community (Kolar and Lodge 2001; Sakai et al. 2001). Historically, invasive species studies have focused on documenting the human-facilitated movement of species and their effects on ecosystems and native biota. The realization that most successful invasions are irreversible has motivated ecologists to attempt to forecast species movements before populations become irreversibly entrenched in new ecosystems (Ricciardi and Rasmussen 1998; Vander Zanden 2005). This problem has been approached by evaluating the invasive potential of species not yet observed in a given ecosystem (Ricciardi and Rasmussen 1998; Kolar and

Received 29 January 2009. Accepted 18 November 2009. Published on the NRC Research Press Web site at cjfas.nrc.ca on 19 February 2010.
J21032

Paper handled by Associate Editor William Tonn.

M.S. Kornis[1] and M.J. Vander Zanden. Center for Limnology, University of Wisconsin, 680 N. Park Street, Madison, WI 53706, USA.

[1] Corresponding author (e-mail: kornis@wisc.edu).

doi:10.1139/F10-002

Lodge 2002) and by modeling the dispersal of species that have already invaded neighboring ecosystems (Leung et al. 2006; Keller et al. 2008). Despite such efforts, producing quantitative predications about invader success continues to challenge the scientific community (Vander Zanden 2005; Lodge et al. 2006; Hastwell et al. 2008).

One challenge in forecasting the spread of invasive species is acquiring appropriate data on which to base predictions. Forecasting invader distributions is commonly done using ecological niche modeling, which assumes that species will be able to invade areas that have the same ecological characteristics as their native range (Peterson 2003; Mercado-Silva et al. 2006). Yet species populations often behave differently in invaded ecosystems due to a release from certain predators, competitors, or parasites (Keane and Crawley 2002; Blumenthal 2006). In some cases, models based on data from regions already invaded by a given species (hereafter called invaded range data) have been found to be more accurate at forecasting that species' distribution than data from its native range (Loo et al. 2007). The greater utility of invaded range data is likely due to the fact that species may act unpredictably outside of their native range by adapting to novel habitats (Mooney and Cleland 2001; Peterson and Vieglais 2001).

The prevalence of round gobies (*Neogobius melanostomus*) in the Great Lakes region provides an alternative to using habitat data from the species' native range in developing models to predict species spread. The round goby is a small benthic fish (2–20 cm) native to the Black, Caspian, and Azov seas and the lower reaches of large associated rivers (Charlebois et al. 1997). The species was first observed in the Great Lakes in 1990, has since spread to all five Great Lakes, and is still expanding in the region (Jude et al. 1992; Jude 2001). Despite being limited to large lakes and rivers in their native range, round gobies have been found in four small (drainage area of 30–140 km^2) tributaries to Lake Erie (Phillips et al. 2003; Donald Luttman, Pennsylvania Department of Environmental Protection, 230 Chestnut Street, Meadville, PA 16335, USA, personal communication, 21 January 2009), illustrating the potential for round gobies to invade small lotic systems. Though the round goby was likely transported to the Great Lakes via ballast water in large freight ships (Hensler and Jude 2007), the species has access to the extensive network of Great Lakes tributaries independent of human assistance. In such cases, the range of a species expands as a result of population growth and natural dispersal such that vulnerable ecosystems can be identified by coupling species life history information with habitat suitability data (Vander Zanden et al. 2004). Although high predator abundance could slow or limit round goby expansion, physical barriers such as dams and waterfalls will ultimately limit upstream migration, and habitat suitability will likely dictate the range of round goby in inland streams up to the first stream impediment.

Accurately predicting the spread of round goby to inland streams is of great interest because of the detrimental effects that this species has wrought on the ecosystem of the Laurentian Great Lakes. Round gobies feed voraciously on benthic invertebrates and fish eggs (Diggins et al. 2002; Carman et al. 2006) and prefer rock or cobble substrate for spawning and feeding habitat (Jude et al. 1995; Charlebois et al. 1997; Corkum et al. 2004). Round gobies outcompete native benthivorous fish for feeding and spawning habitat because they are generally larger and more aggressive (Dubs and Corkum 1996; Janssen and Jude 2001; Balshine et al. 2005). Round gobies threaten to deplete food sources and extirpate native species in part because of their capacity to reach large population densities quickly, with females spawning four to five times per season and male nest-guarding resulting in a 95% egg hatching rate (MacInnis and Corkum 2000). Round gobies also provide a pathway for transferring contaminants such as mercury and polychlorinated biphenyls (PCBs) from *Dreissenid* mussels to piscivorous fishes potentially consumed by humans (Hogan et al. 2007; Ng et al. 2008).

Here we document the distribution of round goby in Wisconsin tributaries to Lake Michigan. We use habitat data (both field-based and landscape-scale) from the round goby's invaded range to model the distribution of the species in Wisconsin's Lake Michigan tributaries. Using this model, we then forecast the potential distribution of round gobies in the Lake Michigan watershed, both with and without dispersal barriers.

Materials and methods

Site selection

We conducted a census of all Wisconsin tributaries of Lake Michigan for round goby presence–absence from 9 June to 7 August 2007 (130 sites on 73 distinct streams; see Supplemental Table S1 for coordinates, available online from NRC Data Depository[2]). We defined a tributary as continuous flowing water that interfaced with Lake Michigan. Streams ranged in size from less than 1 m to over 600 m wide and provided a diverse range of habitat attributes. Sites were selected based on accessibility, with sampling occurring most often at bridge crossings, public parks, and, less frequently, on privately owned land. For a given stream, we sampled at or near the mouth of the stream first and continued to sample at sites upstream until no round gobies were detected. We assumed that if round gobies were not present at a given site, they would be absent upstream of that site as well. This was done to minimize the potential effect of an unsaturated landscape on our forecast of round goby distribution. We chose to maximize the geographic area covered by our study, and thus the number of systems examined, by sampling discrete sites (minimum distance of 1 stream km between sample sites from the same stream).

Fish collection

Two collection methods were required to adequately sample the wide range of stream sizes examined in this study. Sites that were wadeable (<1 m in depth) and exhibited

---

[2] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5348. For more information on obtaining material, refer to http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html.

high water clarity were sampled using a battery-powered backpack electrofishing unit with pulsed DC current. Rate (electric pulse frequency) and duty (pulse width divided by pulse period) were set to 80 and 90, respectively, to target smaller fish. Because of the variability in conductance between sites, we manipulated voltage settings by site to maintain a current between 3.5 and 4 amps. Rather than electrofishing a set area, we sampled for a set amount of time (20 min) at each site, working upstream and sampling from bank to bank.

We could not electrofish murky waters because round gobies lack a swim bladder and remain on the bottom when electrofished, making them difficult to see in dark water. Therefore, sites that were too turbid or deep (>1 m in depth) to electrofish were sampled using an overnight set of 10 cylindrical, wire-mesh, Gee-style minnow traps baited with chicken liver. Minnow traps had a mesh size of 6 mm with openings that were 30 mm in diameter. Traps were set in or near cobble or boulder substrate if available to maximize the likelihood that the traps would detect round goby presence. Traps were deployed for a minimum of 16 h overnight and were collected the following day.

Both of these capture methods have been recommended for use in capturing round gobies (Phillips et al. 2003; Diana et al. 2006). Probability of detection for both methods was assumed to be 1 in areas of high round goby abundance. Probability of detection at sites where round gobies were rare was 0.75 for electrofishing as determined by resampling sites where we had previously only captured one round goby and calculating the percentage of resamples in which we detected round gobies ($n = 12$). Probability of detection using minnow traps was not calculated but was assumed to be at least as high as the electrofishing method, as evidenced by the high percentage of sites where round goby presence was detected using this method (round gobies were detected at 57% of trapped sites compared with 40% of electrofished sites) and the high number of round gobies usually captured by minnow traps (geometric mean of 9.7 round gobies per set of 10 minnow traps at sites where round gobies were detected (95% confidence interval 0.9–108.1)).

Round gobies were euthanized using tricaine methanesulfonate (MS-222) and preserved in 95% ethanol. All other fish species were counted and released at the site of capture.

Habitat data

We collected a suite of local habitat characteristics specific to each site sampled (hereafter called field-based data). Water temperature and conductivity were collected using an YSI 85 meter (YSI Inc., Yellow Springs, Ohio). Bankfull width was measured using a Bushnell laser rangefinder (Bushnell Corp., Overland Park, Kansas). Stream depth was measured at 1/4, 1/2, and 3/4 of bankfull width, and values were averaged for each site. Percent substrate composition was visually assessed as silt, sand, gravel, cobble, boulder, or bedrock. In turbid and deep streams, substrate was assessed tactilely by wading throughout the site. Global positioning system (GPS) coordinates of each site were recorded using a Garmin GPSMap 76S unit (Garmin Ltd., Olathe, Kansas), and stream distance from Lake Michigan was determined for each site using a geographic information system (GIS).

Landscape-scale variables (watershed size, land use (percentage as urban, agriculture, forest, wetland), stream gradient, watershed slope, soil permeability, base-flow index (90% exceedance flow/watershed area), and mean July air temperature) and the coordinates of Wisconsin dams were obtained from a GIS database (US Geological Survey, Great Lakes Aquatic GAP Analysis Project). Landscape-scale variables were calculated on the scale of confluence-bound stream segments (each segment between the confluence of two streams was considered one unit).

Data analysis

Empirical round goby presence–absence data were mapped using a GIS, and landscape-scale variables associated with each site were determined. A correlation analysis was performed on all habitat variables, and those that were highly correlated with several other parameters were discarded ($r^2 > 0.6$ with two or more other covariates). The candidate set of predictors was composed of the remaining independent variables (Table 1). Two variables, watershed area and bankfull width, were log-normally distributed and were log-transformed to produce a nonskewed distribution. Nonskewed variables are not an assumption of generalized linear mixed models, but there is concern that comparing skewed variables with a set of relatively nonskewed variables would result in bias. Each variable was z-standardized using the equation

$$z = (x - \bar{x})/s$$

where z is the standardized value, x is the observed value, $\bar{x}$ is the mean of all observed values, and s is the standard deviation of all observed values. This converted all variables to the same unitless scale, allowing comparison of the relative effect of each predictor on round goby presence–absence.

Eleven sites that were upstream of a dam (none of which had round gobies present) were removed from the analysis because the dam likely prohibited dispersal. A generalized linear mixed model was used to evaluate which habitat factors were the best predictors of round goby presence–absence at the remaining 119 sites. We used a mixed-effects model in which stream was represented as a random effect to account for correlation between sites from the same stream. The general form of this model is

$$y = \operatorname{logit} P = \beta_0 + \beta_n X_n + \rho_i$$

where β_0 is the intercept, β_n and X_n are the effects of the covariates, and ρ_i is the stream-specific random effect defined as $\rho_i \sim \mathrm{N}(0, \sigma^2)$. Probability of round goby presence can be calculated by

$$P(\text{goby presence}) = \mathrm{e}^y/(1 + \mathrm{e}^y)$$

We used model performance on independent data as our means of selecting the model used to make predictions about round goby distribution. Best subsets analysis (see below) was used to narrow the number of potential models to the 10 best models at each spatial scale (landscape-scale data only and landscape-scale data plus site-specific, field-based measurements). This distinction was made because landscape-scale data are more readily available for Wiscon-

Table 1. Description of potential covariates of round goby (*Neogobius melanostomus*) presence–absence in Wisconsin tributaries to Lake Michigan.

Habitat variables	Scale of measurement	Goby present (mean ± 1 SD)	Goby absent (mean ± 1 SD)	Significant $P < 0.05$
Conductivity (mS)	Field based	569.2±170.0	672.5±265.0	Yes
Soft substrate (%)	Field based	32.4±34.6	40.5±35.6	No
Hard substrate (%)	Field based	37.3±29.4	36.5±25.8	No
Bankfull width (m)	Field based	51.7±101.5	15.8±26.5	Yes
Water temperature (°C)	Field based	23.9±3.5	21.7±3.5	Yes
Distance upstream (m)	Field based	5829±5712	2982±5304	Yes
Reach gradient (vertical drop/reach length)	Landscape	0.0023±0.0057	0.0045±0.0039	Yes
Watershed slope	Landscape	0.88±0.39	0.83±0.37	No
Watershed area (km^2)	Landscape	1290±3304	223.6±570	Yes
Agricultural land (%)	Landscape	58.1±22.7	53.5±24.2	No
Urban land (%)	Landscape	2.4±6.1	6.4±12.1	Yes
Forested land (%)	Landscape	17.5±15.8	12.9±12.5	No
Wetland (%)	Landscape	13.5±7.8	15.9±15.5	No
Open water (%)	Landscape	0.87±1.6	0.57±2.3	No
Coarse-grained surficial geology (%)	Landscape	11.4±13.5	4.6±11.3	Yes

Note: Two-tailed *t* tests assuming unequal variance were conducted to detect significant differences between sites with and without round goby present. Distance upstream refers to distance from Lake Michigan "as the fish swims". n = 66 absent and 53 present. SD, standard deviation.

sin streams than field-based data, which are limited to a small subset of streams and would therefore limit the utility of a predictive model that required field-based data. Field-based data were included in 10 of the 20 models validated to determine how much predictive ability would be lost if field-based data were excluded. Best subsets analysis fits regression models for all possible combinations of predictor variables up to a set parameter limit and compares these models based on some model comparison criterion (Hosmer et al. 1989). Models were selected using the Bayesian information criterion (BIC) to select among models based on predictive ability. We chose to use BIC as a selection criterion because it selects for simpler models by penalizing the addition of a parameter to a greater degree than other commonly used selection criteria such as Akaike's information criterion (AIC). We wanted to select for more conservative, simple models because such models would likely generate more accurate predictions on novel data.

Each of our 20 "best" models was validated using a sevenfold cross validation in which six sets were combined to train each model and one set was used to test each model. This was repeated seven times such that each fold was the test set one time. This method of data portioning, known as *k*-fold cross validation, was recommended for models predicting presence–absence by Fielding and Bell (1997). We chose to perform a sevenfold cross validation because it resulted in subsets with an equal number of observations (17). For every validation, we established the optimal probability threshold using a receiver operating characteristic (ROC) analysis. ROC curves plot the percentage of correctly predicted presence (sensitivity) vs. the percentage of correctly predicted absence (specificity) over a range of probability thresholds distinguishing between predicted presence and predicted absence (Hosmer and Lemeshow 2000). ROC analysis has been used to evaluate logistic regression models using habitat data as predictors and is often used to determine the optimal probability (p_{opt}) that maximizes the overall percentage of correct predictions (Bonn and Schroder 2001; Jensen et al. 2005). We used the minimized difference threshold (MDT) criterion, which selected p_{opt} as the probability threshold that minimized the difference between sensitivity and specificity. The MDT criterion for selecting a probability threshold has previously been shown to produce more accurate predictions compared with other techniques (Jiménez-Valverde and Lobo 2007).

We used Cohen's kappa as the primary statistic of model performance, though we also report correct classification percentage because of its interpretability. Cohen's kappa is the proportion of agreement between actual and predicted data and is derived from a confusion matrix using the following equation:

$$\kappa = \frac{(a+d) - [(a+c)(a+b) + (b+d)(c+d)]/n}{n - [(a+c)(a+b) + (b+d)(c+d)]/n}$$

where a is a correct presence, b is a false presence, c is a false absence, d is a correct absence, and n is the number of observations. Validation, a step too often skipped in predicting fish species distribution, is needed to determine how robust models generalize to novel data (Olden et al. 2002). Cohen's kappa provides a measure of how often models correctly predict presence or absence after accounting for chance effects (Manel et al. 2001) and is considered a good measure of model predictability unless one case (presence or absence) far exceeds the other (Fielding and Bell 1997). This is not a problem with our data, as round gobies were present at 54 and absent from 65 sites (45% and 55%, respectively). Kappa values are considered to reflect model performance on the following scale: 0–0.4, poor to fair; 0.4–0.6, moderate; 0.6–0.8, excellent; and 0.8–1.0, almost perfect (Landis and Koch 1977).

A GIS was used to map the predicted presence–absence of round goby in Wisconsin streams both downstream of known dams and for the entire Lake Michigan basin. Predictions of round goby presence–absence were made on confluence-bound stream segments, the finest scale available in our GIS database. The landscape-scale-only model was used to generate these predictions because field-based variables were not available for the majority of stream segments in the state. All available data were used to construct the classification model of round goby distribution as recommended by Rencher (1995).

Generalized linear mixed models, best subsets analysis, correlation analysis, and *t* tests were performed using the R statistical package (version 2.7.0; www.r-project.org/). All mapping components of this project were done using ArcGIS software (ESRI, Redlands, California). ROC analysis and model validation were completed in Microsoft Excel®.

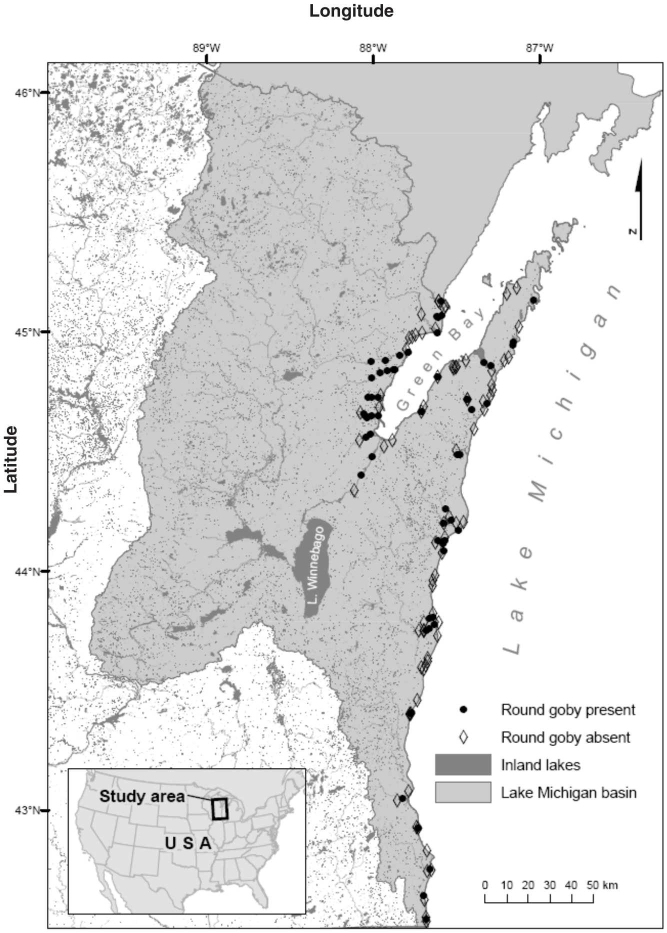
Results

We detected round goby presence in 26 of the 73 sampled watersheds (36%) and 54 of 119 sites (45%; Fig. 1). Round gobies were detected in nine streams at distances greater than 10 km upstream of Lake Michigan, with the farthest inland point recorded at 33.9 stream km in the Pensaukee River (Table 2). We also found round gobies immediately downstream of a physical barrier (dam or waterfall) at seven of the 26 streams (27%) in which round gobies were detected. We sampled upstream of several dams to test whether they served as impediments to round goby migration; no round gobies were detected at above-dam sites (n = 11). Spawning round gobies were captured at several upstream sites, and eggs were found 10.5 km upstream in one watershed. Habitat predictors were evaluated individually for effects on round goby occurrence, and significant differences between sites with and without round gobies were identified for four site-scale variables and four landscape-scale variables (Table 1). According to this analysis, round goby presence had positive relationships with bankfull width, water temperature, watershed area, and the percentage of surficial geology that was coarse-grained. Round goby presence had negative relationships with conductivity, stream gradient, and percentage of urban land.

Validated candidate models were evaluated by their performance on independent data using the mean Cohen's kappa value over the seven validation trials (Supplemental Table S2[2]). On average, models that contained only landscape-scale variables were not significantly different than models that contained both landscape-scale and field-based data (p = 0.76, n = 20, Mann–Whitney U test). Though the best model included both landscape-scale and field-based data (κ = 0.57), it did not perform significantly better on independent data than the best model including only landscape-scale data (κ = 0.55, p = 0.77, n = 7, Student's *t* test assuming equal variance).

We used the best landscape-scale model to forecast the distribution of round goby in Wisconsin tributaries of Lake Michigan. This model displayed moderate agreement between predicted and actual values and correctly classified independent sites 80% of the time. Coefficients in the model were analyzed to determine how the probability of round goby presence changed in relation to each of the variables included in the model. Round goby presence increased linearly with watershed area, decreased linearly with watershed slope, and decreased asymptotically with stream gradient (see Supplemental Table S2[2] for model coefficients). Because dams and waterfalls are barriers to round goby movement, we applied our model to the 3223 km of stream contiguously connected to Lake Michigan (i.e., downstream of any barriers to fish dispersal; Fig. 2*a*). Of these accessible stream reaches, 42% were identified as suitable habitat (1369 km, representing 7% of all Wisconsin streams in the Lake Michigan basin) and may presumably be invaded by round gobies without human assistance. Dam removals or human-assisted movement over dams present the possibility of round gobies circumventing physical barriers. We therefore expanded our forecast to all 20 172 km of Wisconsin streams in the Lake Michigan basin (Fig. 2*b*). Of these stream segments, 44% (8878 km) are predicted to be suitable for round gobies should they gain access to these waters.

Fig. 1. Round goby (*Neogobius melanostomus*) presence (solid circles) and absence (open diamonds) in Wisconsin tributaries of Lake Michigan. Sampling occurred from June to August 2007. Either electrofishing or minnow traps were used depending on the site. Watersheds were sampled at discrete sites upstream from the coast until absence was detected. n = 130 sites and 73 watersheds.



Discussion

Results presented here represent the most extensive documentation of round goby migration into tributary streams of all sizes. Round gobies are native to the Black, Caspian, and

Table 2. Farthest upstream occurrence of round goby (*Neogobius melanostomus*) in invaded Lake Michigan tributaries.

Stream name	Distance upstream (km)
Pensaukee River	33.9
Oconto River	23.2*
Fox River	19.5
Little Suamico River	17.6
East Twin	16.6*
Suamico River	13.3*
Ahnapee River	12.6*
Kewaunee River	11.4*
Sheboygan River	10.5
West Twin	9.6*
Duck Creek	6.4
Milwaukee River	5.5
Big Creek	5
Manitowoc River	4.7
Little River	4.2
Pigeon River	3.2
Menomonee River	3
Menominee River	2.9*
Pike River	2.7
Whitefish Bay Creek	1.6
Root River	0.5
Mud Lake Drainage	0.1
Little Manitowoc River	0.1
Silver Creek	0.1
Stony Creek	0.1
Peshtigo River	0.1

*Steams at which round gobies were found immediately downstream of a physical barrier (dam or waterfall).

Azov seas, as well as several of their larger tributaries (Charlebois et al. 1997), and have since invaded other larger rivers in Eurasia (Brown and Stepien 2008). Smaller tributaries in Eurasia may also be occupied by round gobies, but round goby ascension into flowing water has been reported to be limited and much slower than other Ponto-Caspian gobiids such as the tube-nosed goby (*Proterorhinus marmoratus*) and monkey goby (*Neogobius fluviatilis*) (Harka and Bíró 2007). In the Great Lakes, round gobies have been reported in a handful of small tributaries to Lake Erie (Phillips et al. 2003; Krakowiak and Pennuto 2008), several tributaries in Ontario known as species-at-risk hot spots (Poos et al. 2009), and have been introduced by anglers to a few other inland streams (Carman et al. 2006). Our data illustrate the pervasiveness of this species in a variety of stream habitats and suggest that round gobies are more widespread and abundant in streams than previously thought.

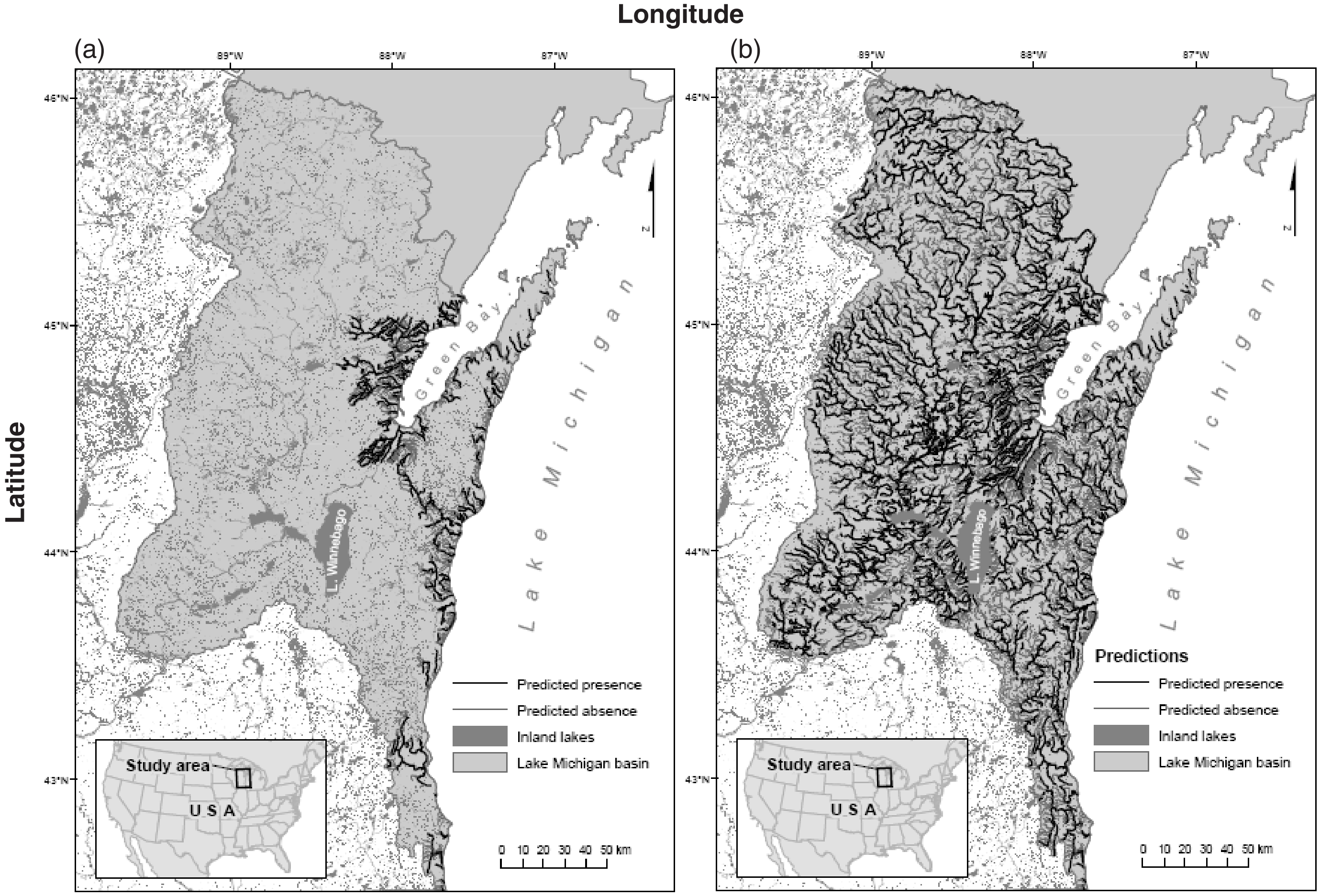
Our findings contribute to a growing body of evidence that species may not be limited to their native range habitats in invaded regions. In addition to invading stream habitat, round gobies can thrive in systems devoid of *Dreissenid* mussels (Carman et al. 2006), which are important forage of round goby in their native range and in the Great Lakes (Ghedotti et al. 1995; Ray and Corkum 1997; French and Jude 2001). Our results corroborate Carman et al. (2006), as *Driessenid* mussels were found at only 13% of sites where we detected round gobies. Other examples of species behaving unexpectedly in their invaded range include the rusty crayfish (*Orconectes rusticus*), which is native to streams in the Ohio River drainage, yet has prospered in north temperate lakes (Olden et al. 2006; Roth et al. 2007).

Ecological niche modeling, a tool commonly used to forecast species invasions, often assumes that species will establish in habitats similar to that of their native range (Peterson 2003). These studies also assume that a species is environment-limited in its native range and often only use presence data (instead of presence–absence data). Although this method has been used to predict the distributions of many invasive species (Peterson 2003; Thuiller et al. 2005; Mercado-Silva et al. 2006), the widespread round goby invasion of tributary streams would not have been predicted from native range data alone. Similarly, models based on invaded range data outperformed models based on native range data in forecasting the distribution of the New Zealand mudsnail (*Potamopyrgus antipodarum*) in Australia and North America (Loo et al. 2007) and cane toad (*Chaunus* [*Bufo*] *marinus*) in Australia (Urban et al. 2007). We encourage ecological niche modelers to include invaded range data when predicting species spread because species are not always limited to the habits and habitats of native range populations.

We found landscape-scale variables to be sufficient for describing and forecasting species distributions and detected no statistical difference between models that included landscape-scale and field-based data and models that included only landscape-scale data. In fact, our top three models (two including landscape-scale and field-based data and one including only landscape-scale data) were almost identical in their ability to predict round goby occurrence on independent data. This is useful because landscape-scale data are often easier to obtain than field-based data because of advances in spatial modeling techniques and availability of geographical databases (Wiley et al. 1997). Although fish distributions are often linked to field-based parameters such as habitat and temperature, landscape-scale variables such as watershed area, reach gradient, and geology are linked to fish habitat use and are dependable predictors of species presence–absence (Kruse et al. 1997; Porter et al. 2000; Creque et al. 2005). One study suggested that landscape-scale variables acting together could dictate field-based characteristics such as substrate and flow (Watson and Hillman 1997). Our results support these ideas, demonstrating that excluding field-based data does not necessarily result in inferior models.

This work is intended to help guide efforts to prevent the spread of harmful invasive species. Prevention is considered the most cost-effective strategy for dealing with species introductions (Leung et al. 2002; Keller et al. 2008). Upstream dispersal of round goby is likely occurring elsewhere in the Great Lakes basin, and the potential for human-assisted transport across stream barriers suggests that there are thousands of vulnerable streams in the region. The presence of round goby larvae in the water column provides a mechanism by which round gobies may be transported inland through water in the live wells of recreational boaters (Hensler and Jude 2007). The sizeable difference between the number of streams expected to be invaded by round gobies downstream of the first dams on Lake Michigan tributa-

Fig. 2. Forecasted distribution of round goby (*Neogobius melanostomus*) in tributary segments (*a*) downstream of the first impassable barrier and (*b*) ignoring the presence of impassable barriers. Black segments are predicted to be invaded by round goby and shaded segments are predicted to remain uninvaded by round goby. Predictions were made using a landscape-scale generalized linear mixed model for round goby presence–absence. Model was constructed based on data from 119 sites (excludes 11 sites upstream of dams).



ries and the number of streams suitable for round gobies regardless of dams highlights the importance of minimizing purposeful or accidental (bait-bucket or livewell) transport of round gobies. Round gobies have already been introduced to the Flint and Shiawassee rivers in inland Michigan (Jude 2001; Carman et al. 2006) and Lakes Simcoe and Rice in Ontario, Canada (Jason Borwick, Ontario Ministry of Natural Resources, Aquatic Research and Development Section, Laboratory of Fisheries Research, Third Floor North, 300 Water Street, Peterborough, ON K9J 8M5, Canada, personal communication, 26 September 2008), via bait-bucket transportation. Education efforts should be a key piece of the strategy to minimize further spread and impacts of round gobies and invasive species in general.

Efforts to increase stream connectivity by removing dams can also open new habitats to the natural dispersal of aquatic invasive species. Increasingly, decision makers are choosing to remove rather than repair aging and obsolete dams (Stanley and Doyle 2003). Although the ecological benefits of dam removals are well documented (Hart et al. 2002; Catalano et al. 2007; Doyle et al. 2008), invasive species add a level of complexity to improving stream connectivity. The removal of dams that are the first barrier between a Great Lake and its upstream watershed, for example, would open up new stream habitats not only to desirable fish species (Bednarek 2001; Bowman 2002), but also to aquatic invasive species. The general issue of stream connectivity facilitating invasive species spread is likely to be relevant in other regions of the world, though perhaps with a different set of invasive species.

Though efforts to forecast species distributions have done much to advance our understanding of species invasions, pre-invasion data on invaded ecosystems are necessary to answer questions involving ecosystem changes wrought by an invader (Hengeveld 1999). Pre- and post-invasion studies of ecosystems are rare because of the difficulty associated with predicting suitable systems (Hengeveld 1999), but results of this study provide such predictions for the round goby. Further work should address what effects round gobies have on native communities and energy pathways in streams, as such work has been done in the Great Lakes (Johnson et al. 2005) but not in tributaries (but see Krakowiak and Pennuto 2008). Further examination of potential biological barriers to round goby expansion (e.g., high predator abundance) would also be of great interest and would highlight ecological integration as a potential barrier to species invasions even when propagule pressure and habitat suitability are adequate for establishment.

This study provides strong evidence of the Great Lakes as a source population for aquatic invasive species to inland watersheds. We show that round gobies are thriving in relatively small tributary streams across a wide geographic scale, a surprising discovery considering that round gobies are usually associated with large lakes. Researchers who deal with predicting invasive species dispersal should not rely on native range data alone if invaded range data are available. Although there is much to be learned from the historical distribution of a species in its native range, only invaded range data incorporate unknown factors such as rapid adaptation and release from predators in forecasting the spread of an invader.

Acknowledgements

Erik Kopperud and Jedchada Carlson assisted with data collection. James Kitchell, Anthony Ives, and Brian Weidel helped develop collection and analysis protocols and provided valuable input on the manuscript. We thank David Jude and Hugh MacIsaac for their signed reviews; Gretchen Hansen, Matthew Diebel, and Scott Higgins also offered beneficial comments on the manuscript. Jeffrey Maxted assisted with creating and polishing GIS maps. Nicholas Keuler provided counsel regarding statistical analysis. This research was supported by the Wisconsin Sea Grant Institute, the Wisconsin Department of Natural Resources, and by graduate research grants from the University of Wisconsin Zoology Department.

References

Balshine, S., Verma, A., Chant, V., and Theysmeyer, T. 2005. Competitive interactions between round gobies and logperch. J. Great Lakes Res. **31**(1): 68–77.

Bednarek, A.T. 2001. Undamming rivers: a review of the ecological impacts of dam removal. Environ. Manage. **27**(6): 803–814. doi:10.1007/s002670010189. PMID:11393315.

Blumenthal, D.M. 2006. Interactions between resource availability and enemy release in plant invasion. Ecol. Lett. **9**(7): 887–895. doi:10.1111/j.1461-0248.2006.00934.x. PMID:16796578.

Bonn, A., and Schroder, B. 2001. Habitat models and their transfer for single and multi-species groups: a case study of carabids in an alluvial forest. Ecography, **24**(4): 483–496. doi:10.1034/j.1600-0587.2001.d01-204.x.

Bowman, M.B. 2002. Legal perspectives on dam removal. Bioscience, **52**(8): 739–747. doi:10.1641/0006-3568(2002)052[0739:LPODR]2.0.CO;2.

Brown, J.E., and Stepien, C.A. 2008. Ancient divisions, recent expansions: phylogeography and population genetics of the round goby *Apollonia melanostoma*. Mol. Ecol. **17**(11): 2598–2615. doi:10.1111/j.1365-294X.2008.03777.x. PMID:18466236.

Carman, S.M., Janssen, J., Jude, D.J., and Berg, M.B. 2006. Diel interactions between prey behaviour and feeding in an invasive fish, the round goby, in a North American river. Freshw. Biol. **51**(4): 742–755. doi:10.1111/j.1365-2427.2006.01527.x.

Catalano, M.J., Bozek, M.A., and Pellett, T.D. 2007. Effects of dam removal on fish assemblage structure and spatial distributions in the Baraboo River, Wisconsin. N. Am. J. Fish. Manage. **27**(2): 519–530. doi:10.1577/M06-001.1.

Charlebois, P.M., Marsden, J.E., Goettel, R.G., Wolfe, R.K., Jude, D.J., and Rudnika, S. 1997. The round goby *Neogobius melanostomus* (Pallas): a review of European and North American literature with notes from the Round Goby Conference, Chicago, IL. Illinois–Indiana Sea Grant Program and Illinois Natural History Survey, INHS Special Publication No. 20, Champaign, Illinois.

Corkum, L.D., Sapota, M.R., and Skora, K.E. 2004. The round goby, *Neogobius melanostomus*, a fish invader on both sides of the Atlantic Ocean. Biol. Invasions, **6**(2): 173–181. doi:10.1023/B:BINV.0000022136.43502.db.

Creque, S.M., Rutherford, E.S., and Zorn, T.G. 2005. Use of GIS-derived landscape-scale habitat features to explain spatial patterns of fish density in Michigan rivers. N. Am. J. Fish. Manage. **25**(4): 1411–1425. doi:10.1577/M04-121.1.

Diana, C.M., Jonas, J.L., Claramunt, R.M., Fitzsimons, J.D., and Marsden, J.E. 2006. A comparison of methods for sampling round goby in rocky littoral areas. N. Am. J. Fish. Manage. **26**(3): 514–522. doi:10.1577/M05-049.1.

Diggins, T.P., Kaur, J., Chakraborti, R.K., and DePinto, J.V. 2002. Diet choice by the exotic round goby (*Neogobius melanostomus*) as influenced by prey motility and environmental complexity. J. Great Lakes Res. **28**(3): 411–420.

Doyle, M.W., Stanley, E.H., Havlick, D.G., Kaiser, M.J., Steinbach, G., Graf, W.L., Galloway, G.E., and Riggsbee, J.A. 2008. Environmental science: aging infrastructure and ecosystem restoration. Science (Washington, D.C.), **319**(5861): 286–287. doi:10.1126/science.1149852. PMID:18202277.

Dubs, D.O.L., and Corkum, L.D. 1996. Behavioral interactions between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). J. Great Lakes Res. **22**(4): 838–844.

Fielding, A.H., and Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservations presence/absence models. Environ. Conserv. **24**(1): 38–49. doi:10.1017/S0376892997000088.

French, J.R.P., III, and Jude, D.J. 2001. Diets and diet overlap of nonindigenous gobies and small benthic native fishes co-inhabiting the St. Clair River, Michigan. J. Great Lakes Res. **27**(3): 300–311.

Ghedotti, M.J., Smihula, J.C., and Smith, G.R. 1995. Zebra mussel predation by round gobies in the laboratory. J. Great Lakes Res. **21**(4): 665–669.

Harka, A., and Bíró, P. 2007. New patterns in Danubian distribution of Ponto-Caspian gobies — a result of global climatic change and/or canalization? Electrononic J. Ichthyol. **3**: 1–14.

Hart, D.D., Johnson, T.E., Bushaw-Newton, K.L., Horwitz, R.J., Bednarek, A.T., Charles, D.F., Kreeger, D.A., and Velinsky, D.J. 2002. Dam removal: challenges and opportunities for ecological research and river restoration. Bioscience, **52**(8): 669–681. doi:10.1641/0006-3568(2002)052[0669:DRCAOF]2.0.CO;2.

Hastwell, G.T., Daniel, A.J., and Vivian-Smith, G. 2008. Predicting invasiveness in exotic species: do subtropical native and invasive exotic aquatic plants differ in their growth responses to macronutrients? Divers. Distrib. **14**(2): 243–251. doi:10.1111/j.1472-4642.2007.00367.x.

Hengeveld, R. 1999. Modelling the impact of biological invasions. *In* Invasive species and biodiversity management. *Edited by* O.T. Sandlund, P.J. Schei, and A.Viken. Kluwer Academic Publishers, Boston, Mass. pp. 127–138.

Hensler, S.R., and Jude, D.J. 2007. Diel vertical migration of round goby larvae in the Great Lakes. J. Great Lakes Res. **33**(2): 295–302. doi:10.3394/0380-1330(2007)33[295:DVMORG]2.0.CO;2.

Hogan, L.S., Marschall, E., Folt, C., and Stein, R.A. 2007. How non-native species in Lake Erie influence trophic transfer of mercury and lead to top predators. J. Great Lakes Res. **33**(1): 46–61. doi:10.3394/0380-1330(2007)33[46:HNSILE]2.0.CO;2.

Hosmer, D.W., and Lemeshow, S. 2000 Applied logistic regression. John Wiley & Sons, New York.

Hosmer, D.W., Jovanovic, B., and Lemeshow, S. 1989. Best subsets logistic regression. Biometrics, **45**(4): 1265–1270. doi:10.2307/2531779.

Janssen, J., and Jude, D.J. 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, Southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. J. Great Lakes Res. **27**(3): 319–328.

Jensen, O.P., Seppelt, R., Miller, T.J., and Bauer, L.J. 2005. Winter distribution of blue crab *Callinectes sapidus* in Chesapeake Bay: application and cross-validation of a two-stage generalized additive model. Mar. Ecol. Prog. Ser. **299**: 239–255. doi:10.3354/meps299239.

Jiménez-Valverde, A., and Lobo, J.M. 2007. Threshold criteria for conversion of probability of species presence to either/or presence–absence. Acta Oecol. **31**(3): 361–369. doi:10.1016/j.actao.2007.02.001.

Johnson, T.B., Bunnell, D.B., and Knight, C.T. 2005. A potential new energy pathway in central Lake Erie: the round goby connection. J. Great Lakes Res. **31**(Suppl. 2): 238–251.

Jude, D.J. 2001. Round and tubenose gobies: 10 years with the latest Great Lakes phantom menace. Dreissena! (National Aquatic Species Clearinghouse, SUNY, Brockport, New York), **11**(4): 1–14.

Jude, D.J., Reider, R.H., and Smith, G.R. 1992. Establishment of Gobiidae in the Great Lakes basin. Can. J. Fish. Aquat. Sci. **49**(2): 416–421. doi:10.1139/f92-047.

Jude, D.J., Janssen, J., and Crawford, G. 1995. Ecology, distribution, and impact of the newly introduced round and tubenose gobies on the biota of the St. Clair and Detroit rivers. *In* The Lake Huron ecosystem: ecology, fisheries and management (Ecovision World Monograph Series). *Edited by* M. Munawar, T. Edsall, and J. Leach. SPB Academic Publishing, Amsterdam, Netherlands. pp. 447–460.

Keane, R.M., and Crawley, M.J. 2002. Exotic plant invasions and the enemy release hypothesis. Trends Ecol. Evol. **17**(4): 164–170. doi:10.1016/S0169-5347(02)02499-0.

Keller, R.P., Frang, K., and Lodge, D.M. 2008. Preventing the spread of invasive species: economic benefits of intervention guided by ecological predictions. Conserv. Biol. **22**(1): 80–88. doi:10.1111/j.1523-1739.2007.00811.x. PMID:18254855.

Kolar, C.S., and Lodge, D.M. 2001. Progress in invasion biology: predicting invaders. Trends Ecol. Evol. **16**(4): 199–204. doi:10.1016/S0169-5347(01)02101-2. PMID:11245943.

Kolar, C.S., and Lodge, D.M. 2002. Ecological predictions and risk assessment for alien fishes in North America. Science (Washington, D.C.), **298**(5596): 1233–1236. doi:10.1126/science.1075753. PMID:12424378.

Krakowiak, P.J., and Pennuto, C.M. 2008. Fish and macroinvertebrate communities in tributary streams of eastern Lake Erie with and without round gobies (*Neogobius melanostomus*, Pallas 1814). J. Great Lakes Res. **34**(4): 675–689. doi:10.3394/0380-1330-34.4.675.

Kruse, C.G., Hubert, W.A., and Rahel, F.J. 1997. Geomorphic influences on the distribution of Yellowstone cutthroat trout in Absaroka Mountains, Wyoming. Trans. Am. Fish. Soc. **126**(3): 418–427. doi:10.1577/1548-8659(1997)126<0418:GIOTDO>2.3.CO;2.

Landis, J.R., and Koch, G.G. 1977. The measurement of observer agreement for categorical data. Biometrics, **33**(1): 159–174. doi:10.2307/2529310. PMID:843571.

Leung, B., Lodge, D.M., Finnoff, D., Shogren, J.F., Lewis, M.A., and Lamberti, G. 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proc. R. Soc. Lond. B, **269**(1508): 2407–2413. doi:10.1098/rspb.2002.2179.

Leung, B., Bossenbroek, J.M., and Lodge, D.M. 2006. Boats, pathways, and aquatic biological invasions: estimating dispersal potential with gravity models. Biol. Invasions, **8**(2): 241–254. doi:10.1007/s10530-004-5573-8.

Lodge, D.M., Williams, S., MacIsaac, H.J., Hayes, K.R., Leung, B., Reichard, S., Mack, R.N., Moyle, P.B., Smith, M., Andow, D.A., Carlton, J.T., and McMichael, A. 2006. Biological invasions: recommendations for U.S. policy and management. Ecol. Appl. **16**(6): 2035–2054. doi:10.1890/1051-0761(2006)016[2035:BIRFUP]2.0.CO;2. PMID:17205888.

Loo, S.E., Mac Nally, R., and Lake, P.S. 2007. Forecasting New Zealand mudsnail invasion range: model comparisons using native and invaded ranges. Ecol. Appl. **17**(1): 181–189. doi:10.1890/1051-0761(2007)017[0181:FNZMIR]2.0.CO;2. PMID:17479844.

MacInnis, A.J., and Corkum, L.D. 2000. Fecundity and reproductive season of the round goby *Neogobius melanostomus* in the upper Detroit River. Trans. Am. Fish. Soc. **129**(1): 136–144. doi:10.1577/1548-8659(2000)129<0136:FARSOT>2.0.CO;2.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., and Bazzaz, F.A. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol. Appl. **10**(3): 689–710. doi:10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2.

Manel, S., Williams, H.C., and Ormerod, S.J. 2001. Evaluating presence–absence models in ecology: the need to account for prevalence. J. Appl. Ecol. **38**(5): 921–931. doi:10.1046/j.1365-2664.2001.00647.x.

Mercado-Silva, N., Olden, J.D., Maxted, J.T., Hrabik, T.R., and Vander Zanden, M.J. 2006. Forecasting the spread of invasive rainbow smelt in the Laurentian Great Lakes region of North America. Conserv. Biol. **20**(6): 1740–1749. doi:10.1111/j.1523-1739.2006.00508.x. PMID:17181809.

Mooney, H.A., and Cleland, E.E. 2001. The evolutionary impact of invasive species. Proc. Natl. Acad. Sci. U.S.A. **98**(10): 5446–5451. doi:10.1073/pnas.091093398.

Ng, C.A., Berg, M.B., Jude, D.J., Janssen, J., Charlebois, P.M., Amaral, L.A., and Gray, K.A. 2008. Chemical amplification in an invaded food web: seasonality and ontogeny in a high-biomass, low-diversity ecosystem. Environ. Toxicol. Chem. **27**(10): 2186–2195. doi:10.1897/07-636.1. PMID:18544008.

Olden, J.D., Jackson, D.A., and Peres-Neto, P.R. 2002. Predictive models of fish species distributions: a note on proper validation and chance prediction. Trans. Am. Fish. Soc. **131**(2): 329–336. doi:10.1577/1548-8659(2002)131<0329:PMOFSD>2.0.CO;2.

Olden, J.D., McCarthy, J.M., Maxted, J.T., Fetzer, W.W., and Vander Zanden, M.J. 2006. The rapid spread of rusty crayfish (*Orconectes rusticus*) with observations on native crayfish declines in Wisconsin (U.S.A.) over the past 130 years. Biol. Invasions, **8**(8): 1621–1628. doi:10.1007/s10530-005-7854-2.

Peterson, A.T. 2003. Predicting the geography of species' invasions via ecological niche modeling. Q. Rev. Biol. **78**(4): 419–433. doi:10.1086/378926. PMID:14737826.

Peterson, A.T., and Vieglais, D.A. 2001. Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. Bioscience, **51**(5): 363–371. doi:10.1641/0006-3568(2001)051[0363:PSIUEN]2.0.CO;2.

Phillips, E.C., Washek, M.E., Hertel, A.W., and Niebel, B.M. 2003. The round goby (*Neogobius melanostomus*) in Pennsylvania tributary streams of Lake Erie. J. Great Lakes Res. **29**(1): 34–40.

Pimentel, D., Zuniga, R., and Morrison, D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol. Econ. **52**(3): 273–288. doi:10.1016/j.ecolecon.2004.10.002.

Poos, M., Dextrase, A.J., Schwalb, A.N., and Ackerman, J.D. 2009. Secondary invasion of the round goby into high diversity Great Lakes tributaries and species at risk hotspots: potential new concerns for endangered freshwater species. Biol. Invasions (e-view). doi: 10.1007/s10530-009-9545-x.

Porter, M.S., Rosenfeld, J., and Parkinson, E.A. 2000. Predictive models of fish species distribution in the Blackwater Drainage, British Columbia. N. Am. J. Fish. Manage. **20**(2): 349–359. doi:10.1577/1548-8675(2000)020<0349:PMOFSD>2.3.CO;2.

Ray, W.J., and Corkum, L.D. 1997. Predation of zebra mussels by round gobies, *Neogobius melanostomus*. Environ. Biol. Fishes, **50**(3): 267–273. doi:10.1023/A:1007379220052.

Rencher, A.C. 1995. Methods of multivariate analysis. John Wiley & Sons, Inc., New York.

Ricciardi, A., and Rasmussen, J.B. 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Can. J. Fish. Aquat. Sci. **55**(7): 1759–1765. doi:10.1139/cjfas-55-7-1759.

Roth, B.M., Tetzlaff, J.C., Alexander, M.L., and Kitchell, J.F. 2007. Reciprocal relationship between exotic rusty crayfish, macrophytes, and *Lepomis* species in northern Wisconsin lakes. Ecosystems (N.Y., Print), **10**(1): 75–86. doi:10.1007/s10021-006-9004-9.

Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, T.N., and Weller, S.G. 2001. The population biology of invasive species. Annu. Rev. Ecol. Syst. **32**(1): 305–332. doi:10.1146/annurev.ecolsys.32.081501.114037.

Stanley, E.H., and Doyle, M.W. 2003. Trading off: the ecological effects of dam removal. Front. Ecol. Environ. **1**(1): 15–22.

Thuiller, W., Richardson, D.M., Pysek, P., Midgley, G.F., Hughes, G.O., and Rouget, M. 2005. Niche-based modeling as a tool for predicting the risk of alien plant invasions at a global scale. Glob. Change Biol. **11**(12): 2234–2250. doi:10.1111/j.1365-2486.2005.001018.x.

Urban, M.C., Phillips, B.L., Skelly, D.K., and Shine, R. 2007. The cane toad's (*Chaunus* [*Bufo*] *marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. Proc. Biol. Sci. **274**(1616): 1413–1419.

Vander Zanden, M.J. 2005. The success of animal invaders. Proc. Natl. Acad. Sci. U.S.A. **102**(20): 7055–7056. doi:10.1073/pnas.0502549102. PMID:15886283.

Vander Zanden, M.J., Olden, J.D., Thorne, J.H., and Mandrak, N.E. 2004. Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. Ecol. Appl. **14**(1): 132–148. doi:10.1890/02-5036.

Watson, G.W., and Hillman, T.W. 1997. Factors affecting the distribution and abundance of bull trout: an investigation at hierarchical scales. N. Am. J. Fish. Manage. **17**(2): 237–252. doi:10.1577/1548-8675(1997)017<0237:FATDAA>2.3.CO;2.

Wiley, M.J., Kohler, S.L., and Seelbach, P.W. 1997. Reconciling landscape and local views of aquatic communities: lessons from Michigan trout streams. Freshw. Biol. **37**(1): 133–148. doi:10.1046/j.1365-2427.1997.00152.x.