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Bycatch, bait, anglers, and roads: quantifying vector activity and propagule introduction risk across lake ecosystems

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Abstract. Long implicated in the invasion process, live-bait anglers are highly mobile species vectors with frequent overland transport of fishes. To test hypotheses about the role of anglers in propagule transport, we developed a social-ecological model quantifying the opportunity for species transport beyond the invaded range resulting from bycatch during commercial bait operations, incidental transport, and release to lake ecosystems by anglers. We combined a gravity model with a stochastic, agent-based simulation, representing a 1-yr iteration of live-bait angling and the dynamics of propagule transport at fine spatiotemporal scales (i.e., probability of introducing n propagules per lake per year). A baseline scenario involving round goby (*Neogobius melanostomus*) indicated that most angling trips were benign; irrespective of lake visitation, anglers failed to purchase and transport propagules (benign trips, median probability $P = 0.99912$). However, given the large number of probability trials (4.2 million live-bait angling events per year), even the rarest sequence of events (uptake, movement, and deposition of propagules) is anticipated to occur. Risky trips (modal $P = 0.00088$ trips per year; $\approx$1 in 1136) were sufficient to introduce a substantial number of propagules (modal values, Poisson model = 3715 propagules among 1288 lakes per year; zero-inflated negative binomial model = 6722 propagules among 1292 lakes per year). Two patterns of lake-specific introduction risk emerged. Large lakes supporting substantial angling activity experienced propagule pressure likely to surpass demographic barriers to establishment (top 2.5% of lakes with modal outcomes of five to 76 propagules per year; 303 high-risk lakes with three or more propagules per year). Small or remote lakes were less likely to receive propagules; however, most risk distributions were leptokurtic with a long right tail, indicating the rare occurrence of high propagule loads to most waterbodies. Infestation simulations indicated that the number of high-risk waterbodies could be as great as 1318 (zero-inflated negative binomial), whereas a 90% reduction in bycatch from baseline would reduce the modal number of high risk lakes to zero. Results indicate that the combination of invasive bycatch and live-bait anglers warrants management concern as a species vector, but that risk is confined to a subset of individuals and recipient sites that may be effectively managed with targeted strategies.

Key words: aquatic ecosystems; fishing; gravity model; invasive species; propagule pressure; social-ecological model; spread; transportation network.

Introduction

Species invasions are highly stochastic across space and time and, with a multitude of invaders and recipient sites globally, forecasting species and sites most at risk of invasion can be a daunting task (Moyle and Light 1996, Olden et al. 2010). Forecasting species invasions is difficult because it is a multistage, hierarchical process involving the arrival, survival, establishment, spread, and impact of the species: propagules are transported from donor to recipient ecosystem, propagules survive recipient conditions, propagules overcome demographic thresholds and the species experiences population expansion, and the species impacts native fauna within the surrounding environment (Kolar and Lodge 2001, Andersen et al. 2004, Leung et al. 2012). The arrival stage of the invasion process is arguably most critical, because propagule pressure below establishment thresholds effectively prohibits subsequent stages of the process (Vélez-Espino et al. 2010; see Lockwood et al. [2005] for the role of propagule pressure). These circumstances are notable when vectors transport species with negligible frequency or abundance; therefore, quantifying the spatiotemporal dynamics of propagule transport to, and introduction within recipient ecosystems is critical for enumerating the highly stochastic invasion process and directing management attention appropriately.

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Humans continue to be effective species vectors due to the development of trade and efficient transportation systems that facilitate propagule transport (Carlton and Ruiz 2005, Hulme 2009). The risk posed by humans as vectors (i.e., the vector risk profile) is contingent on the progression of specific activities leading to the uptake, movement, and deposition of viable propagules in relation to the local ecological context (i.e., the identity and characteristics of transported species and the biogeography of recipient landscapes). The incidence of specific context-dependent sequences indicates that individual patterns of behavior are a critical force structuring the vector risk profile and resulting patterns of propagule pressure. To date, few approaches quantifying invasions have explicitly accounted for individual vector behavior. Agent-based models (ABMs) are widely used in applied ecology, and allow the occurrence of a specific series of events undertaken by an individual (i.e., propagule uptake, movement, and deposition by a single vector) to influence the system in its entirety (i.e., patterns of propagule pressure across landscapes; see Grimm [1999] for a review of ABMs in ecology).

The present study explores the use of ABMs to quantify the vector risk profile and resulting spatiotemporal pattern of propagule introduction, which we characterize as a risk distribution (i.e., the probability of introducing *n* propagules per lake per year). We refer to this metric of introduction risk as absolute propagule pressure, which is estimated as a population-level statistic describing the total abundance of propagules introduced to a recipient site per unit of time. We define the term to clarify that propagule introduction is estimated at the statistical population as total propagules introduced per site per year, as opposed to approaches that estimate a surrogate measure of propagule abundance, such as the volume of vector activity (Drake and Mandrak 2010). This distinction is important, because estimating propagule pressure as a population statistic allows vectors and their propagules to be evaluated within an invasion framework against the abundances likely for species establishment.

Anglers have been repeatedly implicated as invasion vectors (e.g., Litvak and Mandrak 1993, Lodge et al. 2000, Kilian et al. 2012), but the lack of quantitative analyses of propagule transport at fine spatiotemporal scales has led to substantial uncertainty concerning their specific involvement in species introductions. Although anglers may unintentionally transport species via trailered boats (Johnson et al. 2001, Leung et al. 2006), and through gear and clothing fouling (Jacobs and MacIsaac 2007), we focus on anglers as vectors of invasive fishes resulting from the use of live bait fishes, and the transport of invasive fishes contained inadvertently within bait fish catches as bycatch. Where it occurs across North America and Europe, the use of live bait fishes for angling often constitutes a cultural norm. Bait fish practices vary according to climate, biological resources, and local management. Target bait fishes (usually small, abundant, native fishes) may be commercially cultured or harvested from the wild, or self-harvested by the angler, with varying degrees of harvester and angler regulation (i.e., species, harvest, or movement restrictions). Following commercial culture or harvest, target fishes are sold to bait fish retailers, which sell to anglers. Once purchased from the retailer, or following self-harvest, anglers may transport their captive fishes overland to the fishing destination. Most jurisdictions prohibit the release of leftover bait fishes by anglers; however, surveys indicate that, despite this prohibition, many respondents release their leftover bait fishes into the destination waterbody (Litvak and Mandrak 1993), facilitating the transport of fishes from donor to recipient ecosystems for species contained within bait buckets. Like most fisheries, the potential for bycatch associated with bait harvest exists during wild harvest (Drake and Mandrak 2012). Unlike most fisheries, bycatch forms the basis for invasion risk when invasive propagules are inadvertently harvested from invaded ecosystems. As bycatch, incidentally captured nontarget species may avoid detection during physical sorting by harvesters, aquaculture operators, retailers, and anglers. Species identification skill varies greatly (D. A. R. Drake, *unpublished data*), raising further concern about the detection and removal of bycatch from catches. Anglers are also highly mobile (Post et al. 2008, Hunt et al. 2011, Hunt and Lester 2011), and may travel long distances to reach desirable endpoints, potentially facilitating long-distance movements of propagules (Drake and Mandrak 2010). Quantifying the procession of bycatch and vector activities will allow bait activity, and the propensity for propagule introduction by anglers, to be evaluated within an invasion framework.

We developed a social-ecological model involving bycatch, anglers, road networks, and lakes to estimate the vector risk profile and quantify propagule introduction risk. We parameterized our model using empirical data from the bait fish pathway, including sampling of invasive propagules inadvertently contained as bycatch, and social characteristics of anglers, such as the propensity to release leftover bait fishes following travel to uninvaded lakes. We conducted an agent-based simulation of live-bait angling activity and propagule transport across a 1-yr period, and quantified propagule pressure (probability of introducing *n* propagules per lake per year) across a landscape of recipient sites to determine the relationship between individual vector behavior and propagule introduction. Specific objectives were (1) to test hypotheses about anglers as vectors of species introductions, given their propensity for effective propagule uptake, movement, and deposition, (2) to quantify spatiotemporal patterns and uncertainty of propagule transport to, and introduction within, lake ecosystems, and (3) to illustrate application of ABMs of species vectors at landscape scales.

Methods

To inform our social-ecological model and test hypotheses about anglers as vectors of species introductions, we required detailed information about the likelihood of species bycatch within the bait pathway, vector actions contributing to propagule transport, and landscape-level characteristics of ecosystems potentially receiving propagules, such as the distribution, accessibility, and biogeography of destination lakes. We focused on empirical data of bait, angling, and lake ecosystems in Ontario, Canada. Like most bait fish pathways, the Ontario pathway revolves around a legislated group of target species, but harvest from wild ecosystems allows for the possibility of fish bycatch, and inadvertent transport of nontarget species, by anglers (Drake and Mandrak 2012). This provides a suitable model system to explore the role of individual actions contributing to propagule introduction.

Substantial resident and nonresident angling activity exists in Ontario (1.4 million resident and nonresident anglers, 16.9 million angling days, $912 million [Canadian] in direct fishing-related expenditures; 2010 statistics [Fisheries and Oceans Canada 2012]) across a landscape of $>$225 000 lakes, of which $\sim$5% are greater than 1 km^2 in size (Cox 1978). Many of the large, accessible lakes support extensive angling activity (Drake and Mandrak 2010, Hunt et al. 2011). Recent estimates of commercial landings indicated a yearly harvest of 103 819 128 bait fishes sold by several hundred retail dealers to anglers (Ontario Ministry of Natural Resources and the Bait Association of Ontario 2006). A substantial portion of commercial bait fish harvest occurs in the southern, speciose portion of the province, primarily with harvest of emerald shiner (*Notropis atherinoides*) from within the nearshore Laurentian Great Lakes, their connecting channels, and Lake Simcoe and, secondarily, in tributary streams of the Great Lakes. These harvest areas support many nontarget fishes, including invasive fishes originating from the Ponto-Caspian region of Europe (Mandrak and Cudmore 2010), with the possibility of inadvertent sale and transport by anglers if fish invaders are not removed from catches during sorting (Drake and Mandrak 2012).

The use of live bait fishes in Ontario is legal in most waterbodies, and bait fish release by anglers, while illegal, occurs with varying prevalence. Although anglers may capture their own bait fishes from the wild for use as bait, we focused on the propensity for fish bycatch from commercial harvest operations and inadvertent sale to the angler by bait fish retailers because of the difficulty of reliably estimating capture location and species composition from personal catches of anglers. We focused on a baseline scenario of propagule introduction involving round goby (*Neogobius melanostomus*), a small, benthic fish invader established throughout the Laurentian Great Lakes and posing impacts to food web dynamics and native fish biodiversity and recruitment (Bunnell et al. 2005, Johnson et al. 2005, Poos et al. 2010). Despite establishment and proliferation throughout the Great Lakes proper, round goby has spread to only five inland lakes in proximity to invaded sources (see Appendix A for current distribution). More extensive overland spread beyond this region via any number of species vectors is possible; therefore, the bait pathway is of timely managerial concern.

Agent-based simulation of live-bait angling activity

To enumerate vector activity and quantify the probability of introducing n propagules per lake per year, we developed an ABM to quantify live-bait trips (U) involving vectors (live-bait anglers, V) from angler origins (i) to lake destinations (j). We incorporated vector characteristics such as the probability of purchasing invasive propagules inadvertently contained within bait fish catches at retailers, P(purchase[n propagules]), the probability of movement to a given lake from a given origin, P_{ij}, the probability of releasing purchased bait fish, P(release | purchase bait fish), and the distribution, accessibility, and fish species composition of destination lakes (Fig. 1). Table 1 provides the list of model parameters and their sources (e.g., empirical sampling or estimation). Details of empirical sampling, including biological sampling of bycatch within anglers' bait purchases, vector activities contributing to propagule transport, and surveys of vector activity, are given in Appendix B.

Propagule uptake by vectors.—We modeled propagule uptake, defined as the probability of propagule sale to the angler, P(purchase[n propagules]), as a function of the number of retailers in the bycatch region that could be positively identified (k, total = 181) and the probability of purchasing n propagules (R) during a single visit to one of these retailers. Empirical sampling of round goby propagules from bait fish retailers was used to estimate the occurrence (i.e., the encounter rate) of propagules during bait fish purchase by anglers, as the number of purchases containing round goby propagules, divided by the total number of purchases made from within the sample space. Because empirical sampling of purchases was conducted as a maximum abundance of purchased fishes (and may overestimate the prevalence of propagules in a single purchase of fewer individuals), we divided the encounter rate by two to represent a systematic 50% reduction in the prevalence of bycatch associated with a single purchase (i.e., some anglers may purchase the maximum volume of bait, others may purchase less, and volume reductions should lead to lower probabilities of bycatch; see Appendix C for an overview of model assumptions). We modeled three distinct contamination scenarios: (1) baseline, based on the results of empirical sampling and representing the status quo contamination of bait catches with propagules, (2) infestation, representing an outbreak of propagules within bait purchases (i.e., encounter rate

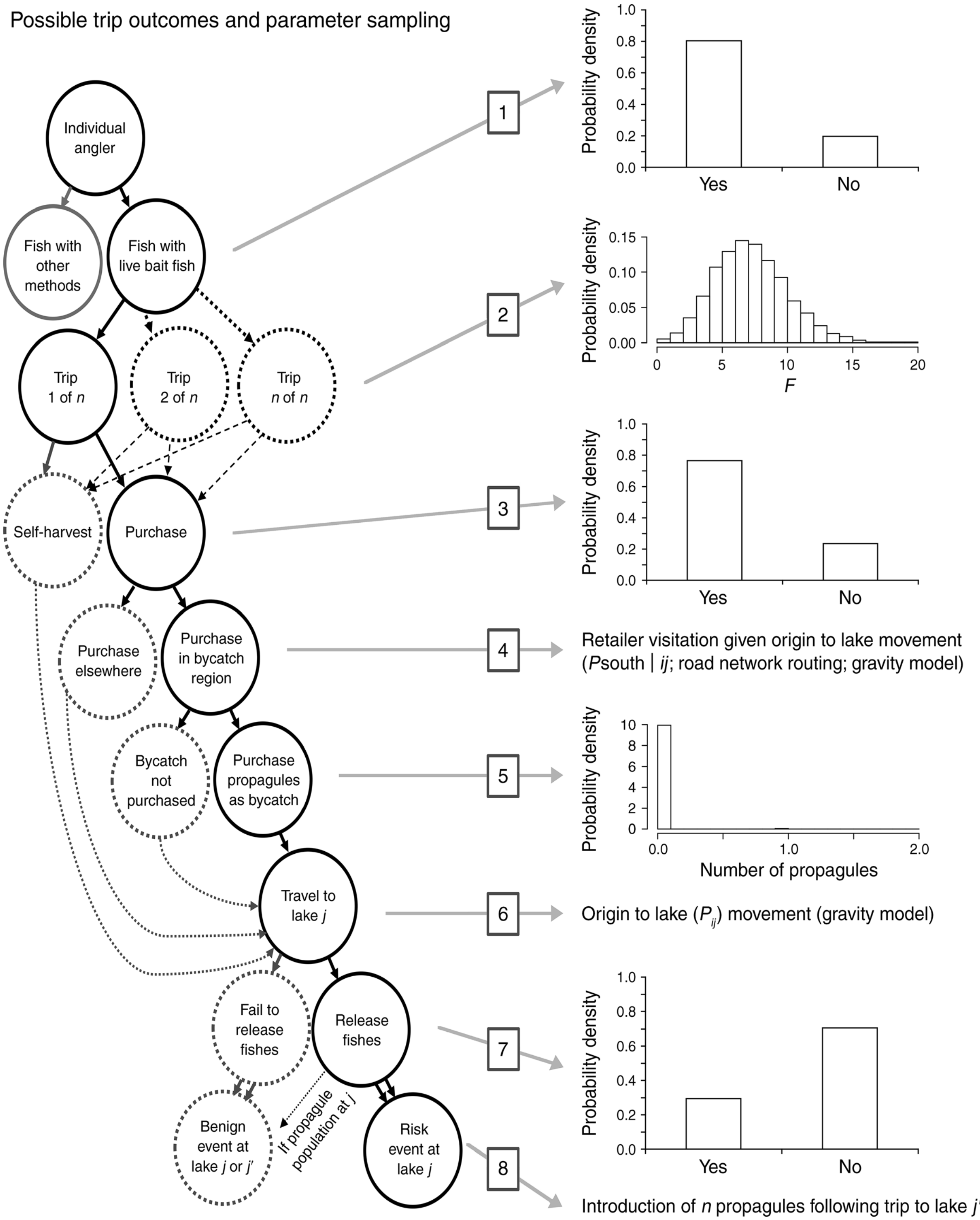

FIG. 1. Conceptual diagram of the agent-based process involving bycatch, anglers, road networks, and lakes. Key distributions include (1) the probability of live-bait fishing (yes/no, P(fish with live bait fish)), (2) the frequency of live-bait fishing (F), (3) the probability of purchasing, as opposed to self-harvesting, bait fish (yes/no, P(purchase | fish with live bait fish)), (4) the probability that a purchasing angler will visit a retailer in the bycatch region, given a trip to any one lake (P(south | ij; where origin is i and destination is j), (5) the probability that the angler will purchase n propagules, R, as bycatch, given a purchase from the bycatch region, P(purchase(n propagules)), (6) the probability of movement to a given lake (P_{ij}), (7) the probability that an angler will release their leftover or unwanted bait fish (yes/no, P(release | purchase bait fish), and (8) the introduction of n propagules to lake j' failing to contain the species. Following the selection of n anglers and trips, propagule arrival was catalogued for each visited lake

four times that of baseline), and (3) bycatch reduction, where the probability of encountering propagules experiences a 90% reduction from baseline. The bycatch reduction scenario represents reductions attributed to risk management, or the early stages of invasion where low contamination rates may be anticipated. Empirical sampling documented only a single adult round goby propagule; therefore, beyond the encounter rate, the shape of the probability distribution was unknown. For each scenario (baseline, infestation, bycatch reduction), we modeled the bycatch parameter P(purchase[n propagules]) using both Poisson and over-dispersed (zero-inflated negative binomial; hereafter ZINB) distributions (Table 1; see Appendix D for encounter rates and probabilities of purchasing one, two, or 10 propagules).

Vector dynamics contributing to propagule transport.—To model the role of vectors in propagule transport, we quantified the number (n = 659 496) and spatial residence (six-digit postal code, summarized by i) of licensed, resident anglers in Ontario, using 2007 provincial license records. We then quantified the probability of specific actions undertaken by vectors, such as the probability that an angler will fish with live bait fishes at least once throughout the year, P(fish with live bait fish), the yearly frequency of live-bait trips (F), and the probability of purchasing (as opposed to self-harvesting) bait fishes, P(purchase bait fish | fish with live bait fish). With the exception of F, which was modeled as a Poisson distribution, parameters were modeled as binomial distributions, representing the success or failure of each activity (Table 1). Parameters were based on results of social surveying, where the empirically derived proportions (e.g., proportion of anglers indicating bait-bucket release) were equal to the probability of success for each distribution. To allow the model to explicitly account for geographic differences of individual behavior, we quantified vector characteristics (P(fish with live bait fish), F, P(purchase bait fish | fish with live bait fish), P(release | purchase bait fish), at origin, i) for each geographic region (i.e., northern, eastern, and southwestern Ontario, the greater Toronto area, and metropolitan Toronto) based on empirical surveying (see Table 1 for specific values).

Because of the strong role of vector movement in the invasion process, we had previously developed a gravity model of the spatial interaction of live-bait anglers (T_{ij}, an index of aggregate spatial interaction between i and j; Drake and Mandrak 2010) as

$$T_{ij} = \beta_0 + \beta_1 \log(o_i) + \beta_2 \log(w_j, 1) + \beta_3 \log(w_j, 2) + \beta 4 \log(D_{ij})$$

where T_{ij} is the response variable, β are model coefficients, o_i describes the propensity for live-bait movements to leave each origin, w_j describes the attractiveness of destination lakes (w_j,1 represents lake surface area (ha), w_j,2 represents lake sport fish richness), and D_{ij} is the road travel distance associated with each optimal route (S_{ij}) through the provincial road network. Because T_{ij} units correspond to an index of origin-lake visitation, but not the frequency with which live-bait trips are made, we used T_{ij} scores to compute the probability of movement (P_{ij}) between each origin and destination lake as $P_{ij} = T_{ij}/\sum_{i=1}^{n} T_i$, where $\sum_{i=1}^{n} T_i$ represents the sum of all interaction values leaving an origin. Next, we calculated the probability of movement to retailer, k, given an ij trip ($P(k \mid ij)$), by identifying all of the stores accessible by road given a maximum travel deviation of 1 h from S_{ij} and allowing each store within the travel deviation an equal chance of visitation. Computing $P(k \mid ij)$ was necessary to determine the probability that a purchasing angler will visit a store within the bycatch region (i.e., the region in close proximity to the Great Lakes basin anticipated to pose greatest bycatch risk) as $P(\text{south} \mid ij)$ and, therefore, provides the initial conditions for the purchase (uptake) of propagules.

Estimating propagule pressure as probability density functions.—We were primarily interested in four metrics resulting from a yearlong iteration of the dynamics of V and R to j: the fraction of risky (vs. benign) trips, defined as those capable of propagule introduction, and estimates of lake-specific (R_j) and total ($\sum_{j=1}^{n} R_j$) propagule pressure (i.e., probability of introducing n propagules per year, to all lakes not currently containing the species, j'). We were also interested in the number of yearly live-bait trips ($\sum_{j=1}^{n} U_j$), the number of yearly live bait fish trips received at each destination lake (U_j), and trips involving introduction of propagules ($UR_{j'k}$; Table 1).

To initiate our agent-based simulation, each of Ontario's 659 496 resident, licensed anglers were subjected to a series of random draws (i.e., assignment into a value within a given probability distribution) with distributions specific to the region of origin (Fig. 1). First, we drew from the P(fish with live bait fish) binomial, representing the success (one) or failure (zero) that an angler will fish with live bait fishes at least once throughout the year, as opposed to fishing with other methods. Should they fish with live bait fishes (given the success of the random draw), a second draw was made from the frequency of live-bait fishing distribution, determining how many live-bait trips were made during a given year by that angler. Each of the angler's n trips were then subjected to a series of random draws determining the

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as the number of propagules introduced per year. Distributions at right represent parameters derived for a live-bait angler residing within the greater Toronto region. Gray circles and arrows towards left of flow chart represent benign progressions and outcomes, whereas black circles and arrows represent the progression necessary for a risk event (propagule release) to a given lake, j'. Dashed arrows in upper right of flowchart represent additional trials.

Table 1. Model parameters and response variables used in the social-ecological model involving bycatch, anglers, road networks, and lakes.

Variable name	Description	Values	Source
Propagule uptake			
k	bait fish retailers within bycatch region	$n = 181$ positively identified	OMNR (Ontario Ministry of Natural Resources) license records.
Bycatch parameter P(purchase[n propagules])	probability of purchasing n propagules within bycatch region	baseline Poisson $\lambda = 0.00735$; baseline ZINB $\mu = 0.8$, size = 0.3, zprob = 0.9773; infestation Poisson $\lambda = 0.0294$; infestation ZINB $\mu = 0.8$, size = 0.3, zprob = 0.9103; bycatch reduction Poisson $\lambda = 0.000735$; bycatch reduction ZINB $\mu = 0.8$, size = 0.3, zprob = 0.9977	Baseline: results of empirical sampling of retailers in OMNR southern region with empirical encounter rate of 0.0147 (Appendix B). Baseline encounter rate assumes 50% reduction from empirical in the probability that an individual angler will purchase propagules. Additional distributions (e.g., infestation) are in relation to baseline (Appendix D).
Vector characteristics			
V	number of licensed, resident anglers	overall (n) = 659 496, N = 122 849, SW = 148 979, GTA = 209 519, M = 59 802, E = 118 347†	OMNR license records.
P(fish with live bait fish)	probability of anglers fishing with live bait fish at least once per year	overall = 0.813, N = 0.922, SW = 0.792, GTA = 0.804, M = 0.774, E = 0.749†‡	Results of empirical sampling (social survey, Q.3; Appendix B).
F	yearly frequency of fishing with live bait fish	λ overall = 8.05, λ N = 9.048, λ SW = 7.896, λ GTA = 7.694, λ M = 7.662, λ E = 7.894†§	Results of empirical sampling (social survey, weighted mean of Q.3; Appendix B), fitted as Poisson distribution with λ = mean empirical values.
P(purchase | fish with live bait fish)	average per-trip probability of purchase (as opposed to self-harvest), given anglers fishing with live bait fish	overall = 0.727, N = 0.679, SW = 0.698, GTA = 0.756, M = 0.798, E = 0.704†‡	Results of empirical sampling (social survey, average per-trip probability of purchase, Q. 4,10; Appendix B).
P(release | purchase bait fish)	probability of anglers releasing leftover or unwanted bait fish, given they purchase live bait	overall = 0.292, N = 0.212, SW = 0.356, GTA = 0.307, M = 0.304, E = 0.284†‡	Results of empirical sampling (social survey, greatest per-trip probability of release given purchase, Q. 15,16; Appendix B).
Vector movement and lake characteristics			
j	destination lakes reasonably accessed by road	$n = 2920$	Spatial sampling (GIS), least-cost road network, gravity model (Drake and Mandrak 2010).
j'	subset of j currently lacking round goby populations	$n = 2910$	Regional lake sampling programs.
T_{ij}	spatial interaction (index of aggregate movements)	$n = 1\,246\,840$ (mean = 2.48, range of values = 0 −567 213)	Response variable of gravity model.
S_{ij}	optimal road travel route between origin, i, and destination lake, j	$n = 1\,246\,840$ optimal ij routes	Least-cost routing (GIS) of provincial road network, gravity model.
D_{ij}	distance of optimal travel route between origin, i, and j		Least-cost routing (GIS) of provincial road network, gravity model.
D_{ijk}	distance of optimal travel route between i, retailer, k, and j		Least-cost routing (GIS) of provincial road network, given k, S_{ij}, and ≤ 1 hr travel deviation.
P_{ij}	probability of movement between i and j		Estimated from gravity model output and least-cost routing.

TABLE 1. Continued.

Variable name	Description	Values	Source
$P(k \mid ij)$, $P(\text{south} \mid ij)$	probability of movement to k, given i and j; and probability of movement to k, within southern (bycatch) region, given an ij trip.		Estimated from gravity model output and least-cost routing.
Response variables			
V	potential vector (licensed, resident anglers who fish with live bait fish at least once per year)		Model output.
U	trip involving live bait fish		Model output.
U_j	yearly live bait fish trips received at j.		Model output.
$\sum_{j=1}^{n} U_j$	yearly live bait fish trips across all j		Model output.
R	round goby propagules		Model output.
$UR_{j'k}$	trips introducing propagules from k to j' (i.e., lakes not presently containing the species)		Model output.
R_j	lake-specific propagule pressure (absolute number of round goby propagules introduced per lake per year)		Model output.
$\sum_{j=1}^{n} R_j$	total propagule pressure (absolute number of propagules introduced per year across all destination lakes)		Model output.

Notes: Response variables were estimated following an agent-based simulation of a 1-yr iteration of live-bait angling activity to quantify propagule arrival as the introduction of n propagules per lake per year. Parameter values are given as proportions following empirical sampling unless otherwise indicated. Gravity model variables are described within Drake and Mandrak (2010). The symbol λ describes the mean and variance of the Poisson distribution, μ describes the mean of the negative binomial distribution, size describes the over-dispersion of the negative binomial distribution, and zprob describes the probability of structural zeroes within the ZINB model.

† The five geographic regions are N (northern Ontario, postal district P), SW (southwestern Ontario, postal district N), GTA (the greater Toronto area and surrounding region, postal district L), M (metropolitan Toronto, postal district M), and E (eastern Ontario, postal district K).

‡ Binomial distribution of probabilities of success.

§ Poisson distribution.

trip destination and specific elements of the trip that could lead to propagule transport and introduction. First, we drew from the P_{ij} distribution to determine the specific route and location of the destination waterbody. Next, we drew from the $P(\text{purchase} \mid \text{fish with live bait fish})$ binomial, to determine if bait fishes were purchased (as opposed to self-harvested) during the trip. When a purchase was made, we then drew from the $P(\text{south} \mid ij)$ distribution, to determine for the ij route whether bait fishes were purchased from a retailer in the bycatch region, as opposed to northern retailers, which were hypothesized to pose a reduced risk of bycatch. When purchasing from the bycatch region, a subsequent random draw was made of the $P(\text{purchase}[n \text{ propagules}])$ distribution, to determine the occurrence (and abundance, when present) of propagules inadvertently contained within bait purchases when traveling to j. Following travel to j, and given the incidence of bait purchase, we drew from the $P(\text{release} \mid \text{purchase bait fish})$ distribution, to determine if fishes were released into the destination waterbody. Lakes failing to contain round goby populations were noted for each release event, resulting in the failure ($R = 0$) or success ($R > 0$) of introduction of n propagules released to each destination lake during each live-bait trip, and ending the series of random draws for a single trip. The process was repeated for remaining trips for that angler, and for all remaining anglers, until each vector had been subjected to random draws resulting in the failure or success of n propagules, across destination lakes (Fig. 1). Response variables, such as live-bait trips and deposition of propagules, were summarized at the lake level for each variable of interest. This formed a single model iteration. Anglers were selected again each of 499 times (i.e., 500 iterations of n selections of V, and 500 random permutations of parameter distributions) to account for the inherent variability within the system, and to allow response variables, such as overall and lake-specific propagule pressure, to be modeled as probability density functions given various outputs of the model resulting from stochasticity.

To determine the robustness of the model, we systematically changed parameter values ($P(\text{purchase} \mid \text{fish with live bait fish})$, $P(\text{purchase}[n \text{ propagules}])$, P(re-

TABLE 2. Key live-bait trip actions contributing to propagule uptake, movement, and deposition, following the agent-based simulation of a 1-yr span of live-bait angling activity (baseline, Poisson with $\lambda = 0.00735$) involving bycatch, anglers, road networks, and lakes.

Vector, trip, and propagule characteristics	Median proportion of vectors or trips	Median number (n) or value
Yearly live-bait trips, U, irrespective of risk status		4 244 824 absolute trips
Trips purchasing bait, given angling with bait fish, U(purchase | fish with live bait fish)	0.721 (0.698, 0.708, 0.734, 0.741)	3 061 493 trips (2 963 406, 3 007 754, 3 116 133, 3 147 036)
Trips self-harvesting bait, given angling with bait fish, U(self-harvest | fish with live bait fish)	0.278 (0.259, 0.266, 0.291, 0.301)	1 183 332 trips (1 097 788, 1 128 691, 1 237 070, 1 281 418)
Trips purchasing and releasing bait, given angling with bait fish, U(purchase ∩ release | fish with live bait fish)	0.21 (0.195, 0.201, 0.220, 0.230)	893 029 trips (826 617, 851 572, 934 772, 975 266)
Trips involving propagule uptake, but failed deposition; successful transition of U, purchase, k, R, irrespective of release behavior or lake biogeography (e.g., j vs. j')	0.0036 (0.00046, 0.0014, 0.0064, 0.0081)	15 206 trips (1961, 5774, 26 981, 34 556)
Risky trips: propagule uptake, movement, and deposition $U_{rj'k}$ (subset of U, introducing R, to j')	0.00085 (0.000051, 0.000278, 0.00162, 0.00199)	3629 trips (218, 1178, 6887, 8482)

Note: Values in parentheses are the minimum, 2.5th percentile, 97.5th percentile, and maximum values.

lease | purchase ∩ fish with live bait fish)) ± 25%, while observing changes in the total propagule pressure ($\sum_{j=1}^{n} R_j$) density function as the primary response variable. Sensitivity analysis was conducted for each parameter change over 500 iterations, allowing the effect of the changed parameter to be interpreted, given the stochasticity and structure of the model. All statistical analyses were conducted using the statistical language and software program R, version 2.12.1 (R Development Core Team 2008).

RESULTS

Propagule uptake, movement, and deposition: trip risk profiles

Simulations revealed a substantial yearly volume of vectors and trips, attributed to the high probability and frequency of live-bait angling across a large resident angling population; overall P(fish with live bait fish) = 0.813, overall F $\lambda = 8.05$ trips per yr (λ describes the mean and variance of the Poisson distribution; Table 1), absolute $V = 526\,713$ anglers, absolute sum of $U = 4\,244\,824$ trips associated with live bait (see Appendix E for estimates of live-bait angling effort). Risk profiles for baseline scenarios indicated that the majority of trips were benign (median proportion benign $U = 0.99912$), given our criteria for risk (effective propagule arrival as the introduction of ≥ 1 propagule to a lake not containing the species). Benign trips were generally the result of the rarity of inadvertent bycatch sale to the angler (e.g., baseline encounter rate, $P > 0$ propagules = 0.007323; probability of purchasing one, two, or 10 propagules within the bycatch region = 0.0073, 0.000027, and 1.25×10^{-28}, respectively, when $\lambda = 0.00735$; see Appendix D for additional bycatch parameters). Should propagules be purchased, most trips exhibiting effective uptake (i.e., fishing with live bait fish and purchasing propagules from within the bycatch region, median proportion $U = 0.0036$; Table 2) did so without effective movement or deposition, such as by traveling to lakes already containing the species or by failing to release leftover or unwanted fishes (Table 2). Fewer trips exhibited effective uptake and movement (i.e., by fishing with bait fishes, purchasing propagules, and traveling to lakes lacking the species) and, of those exhibiting effective uptake and movement, fewer still deposited their propagules effectively (i.e., released) to the uninvaded destination lake.

Based on modal values, risky trips (i.e., consecutive uptake, movement, and deposition of propagules: baseline $P = 0.00088$; ≈1 in 1136 trips), overcame the behavioral and biogeographic constraints necessary for propagule introduction, resulting in 3715 trips per yr to lakes not currently supporting the species (modal values; Poisson model, 3715 propagules among 1288 lakes, per-trip range of propagules 0–1; ZINB model, 6722 propagules among 1292 lakes, per-trip range of propagules 0–9; Fig. 2A, B; Appendices F, G). Although the subset of risky trips ($UR_{j'k}$) displayed travel distances similar to the distribution of all live-bait angling trips, risky trips experienced a distinct southern shift, primarily due to the importance of the bycatch region (i.e., spatial availability of propagules for purchase; Fig. 3). Irrespective of risk status, the distribution of travel distances was leptokurtic with a long right tail and generally consistent with overall spatial interaction from Drake and Mandrak (2010). The infestation scenario, representing a fourfold increase in the propagule encounter rate, would substantially increase the probability of risky trips, the overall number of propagules introduced, and the number of lakes receiving propagules per year (modal outcomes; Poisson model, 15 461 propagules among 1707 lakes, per-trip range 0–4; ZINB model, 30 621 propagules among 1687 lakes, per-trip range 0–9); whereas a 90% reduction in the propagule encounter rate would reduce the modal number of propagules

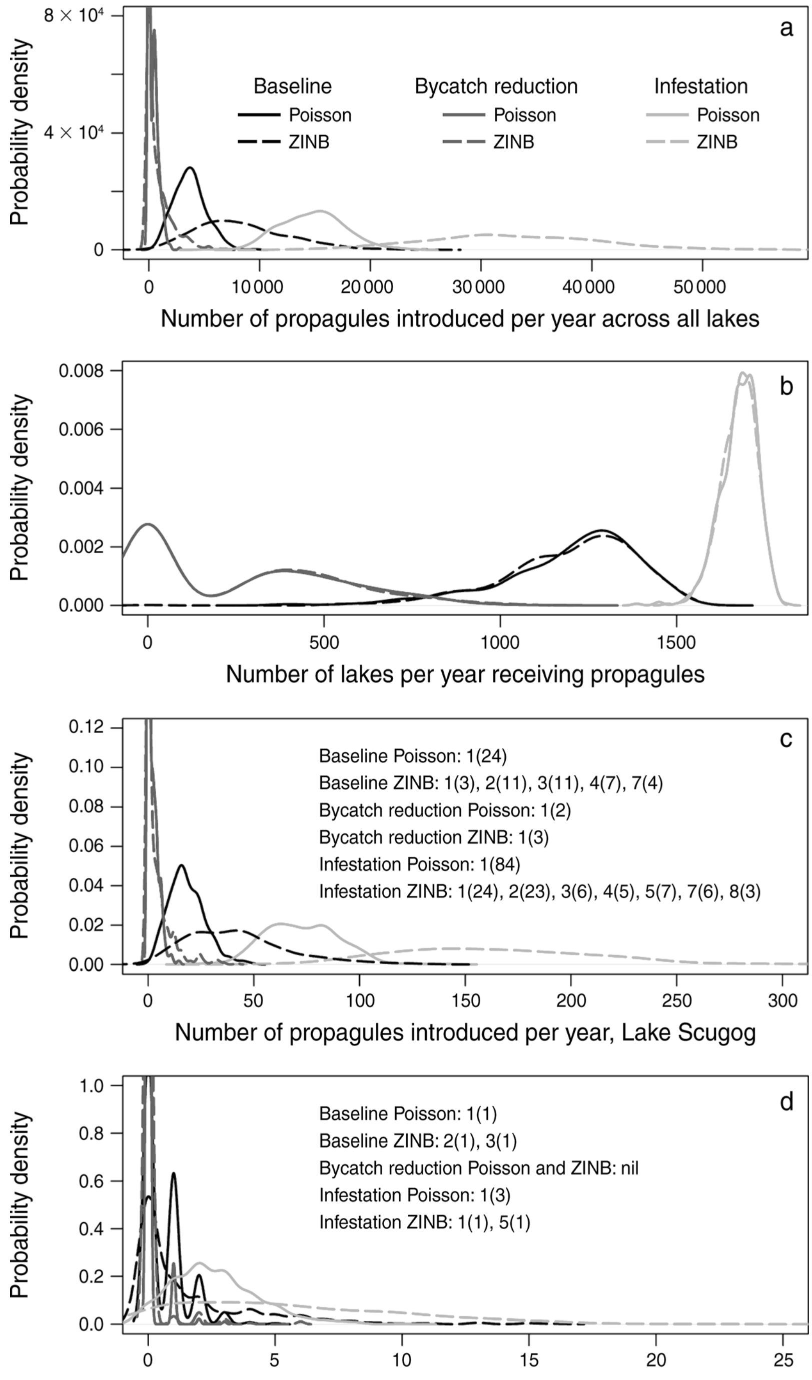

FIG. 2. Probability density functions of propagule pressure, (a) as the probability density of the introduction of *n* propagules across all lakes, attributed to bycatch and live-bait angling in Ontario, Canada. Density functions are shown for baseline, bycatch reduction, and infestation scenarios exhibiting propagule encounter rates of ≈1 in 137, ≈1 in 1369, and ≈1 in 35, respectively, for Poisson and zero-inflated negative binomial (ZINB) bycatch parameters. Also shown is (b) the number of lakes per year anticipated to receive propagules under each scenario, (c) an example of a high-risk lake (e.g., experiences a high probability of receiving >0 propagules per year; Lake Scugog in southern Ontario is shown), and (d) an example of a low-risk lake (e.g., experiences a high probability of receiving zero propagules per year; Shannon Lake, northeastern Ontario). Panels c and d also show the per-trip number of propagules released, with the yearly frequency of introduction shown in parentheses, for a randomly selected single iteration to each lake. For example, baseline ZINB to Shannon Lake resulted in two propagules released during a single angling event, and three propagules released during another event.

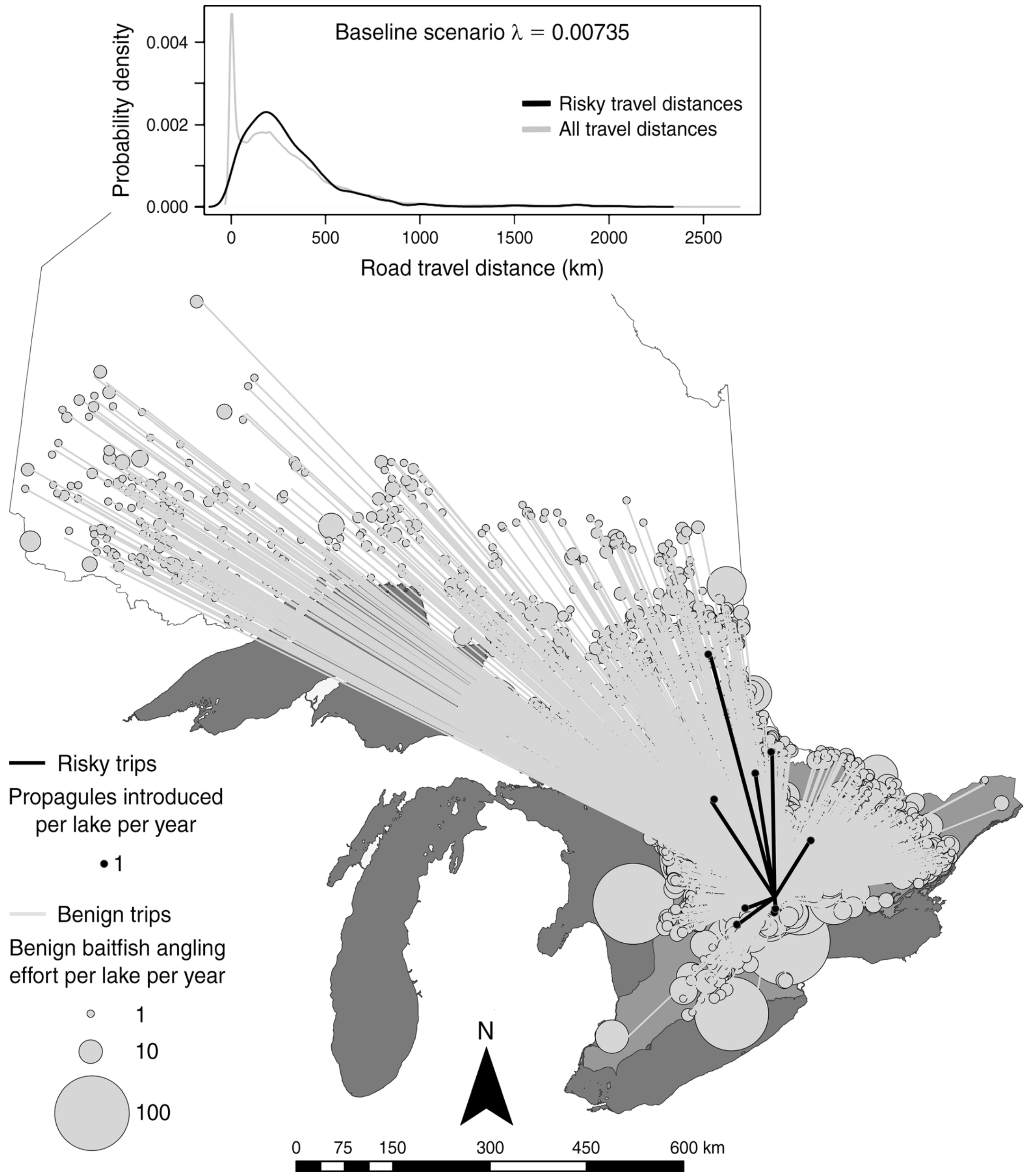

FIG. 3. Spatial distribution of benign trips (gray lines; *ij* route shown as Euclidean origin-destination path), and benign trip outcomes at the lake level (gray circles; i.e., live-bait angler effort as trips per year per lake failing to introduce propagules) based on a single yearly iteration of trip outcomes (baseline Poisson) for a single angler origin, *i*, located in the southern portion of the province of Ontario. Also shown is the subset of risky (risk of propagules being released) trips per year (black lines; $n = 9$) and propagule introductions per year ($n = 9$ risky trips associated with one propagule each) for the same yearly iteration of trips leaving the southern origin. Lines represent the origin (centroid of cluster) to destination (terminal portion of line segment) *ij* route of live-bait trips outbound from the single origin within a given year. The distance-frequency distance function describes all live bait trips (gray line) and the subset of risky trips (black line). In the inset, λ describes the mean and variance of the Poisson distribution.

introduced per year to zero for Poisson and ZINB models, respectively (Fig. 2); per-trip range 0–1 (Poisson) and 0–9 (ZINB).

Lake-specific propagule pressure

The stochastic nature of yearly vector activity led to lake-specific probability density functions exhibiting a relatively large range of potential outcomes of propagule pressure (e.g., Fig. 2C, D). Patchy propagule introductions across the $n = 2920$ destination lakes experiencing live-bait angling effort was the result of spatiotemporal variability of angling effort and stochastic processes leading to risky vs. benign trip outcomes (Fig. 3). Nonetheless, two groups of lake-specific propagule pressure emerged. Most lakes (baseline Poisson, n = 1870, proportion = 0.64; baseline ZINB, n = 1928, proportion = 0.66; infestation Poisson, n = 1360, proportion = 0.47; infestation ZINB, n = 1421, proportion = 0.49; bycatch reduction Poisson and ZINB, n = 2920, proportion = 1.0) exhibited negligible or low propagule pressure (i.e., low-risk lakes exhibiting a high probability of receiving zero propagules per year, with substantially lower probability of receiving one or more propagules per year). Low propagule pressure to certain lakes was attributed to the predominance of benign trips or overall lack of angling effort, especially to small, remote northern lakes and certain small southern lakes, and many northern waterbodies at the lengthiest travel distances from the bycatch region. The second group (almost one-third of lakes visited for live-bait angling, baseline Poisson), exhibited high probabilities of receiving one or more propagules per year (Fig. 4; see inset for the number of high-risk lakes with modal outcomes of receiving $\geq$3 propagules/year). The highest-risk lakes (i.e., the top 1%, $n \approx 30$ lakes) were generally large lakes in close proximity to the bycatch region experiencing frequent angling activity (modal outcomes; baseline Poisson, 7–76 propagules per yr, Table 3; baseline ZINB, 12–138 propagules per yr; infestation Poisson, 30–247 propagules per yr; infestation ZINB, 66–801 propagules per yr; bycatch reduction Poisson and ZINB, 0 propagules per yr; Fig. 4, see Appendix H for top 100 lakes in each scenario and Appendix I for landscape patterns of minimum and maximum per lake outcomes). Results indicated a skewed, patchy introduction of propagules irrespective of contamination scenario; most lakes received negligible or low propagules, with a subset receiving substantially more, due to dominant movement and activity patterns.

Model sensitivity

Generally, the model was sensitive to changes in key parameters. Changes in the bycatch parameter (i.e., per-trip probability of purchasing n propagules as bycatch) had the greatest influence towards median overall propagule pressure. A 25% reduction in λ reduced median introduction risk by 28.1%, whereas a 25% increase would lead to a 30.9% increase of median risk values (Fig. 5). The per-trip probability of release or probability of angler purchase held slightly less influence ($\leq$26.1% for median shifts in either direction). Generally, an increase in any parameter resulted in decreased leptokurtis for total and lake-specific distributions, whereas leptokurtis was increased when parameters were decreased (Fig. 5).

Discussion

Propagule pressure is a primary determinant of invasion success (Lockwood et al. 2005). Quantifying the variability, rarity, and spatiotemporal context of propagule arrival represents a major step towards understanding, forecasting, and mitigating invasions across landscapes with many potential vectors, propagules, and sites (Simberloff 2009). Our agent-based approach provides insight into landscape patterns of propagule introduction, the dynamic and patchy nature of propagule transport and deposition, and the uncertainty of propagule arrival. Three main conclusions can be drawn from our model that advance understanding of the role of propagule pressure (Lockwood et al. 2009) and the ability to forecast invasions. These factors may also explain the imperfect discriminative ability of gravity models as predictive tools (e.g., Jerde and Bossenbroek 2009, Muirhead and MacIsaac 2011, Rothlisberger and Lodge 2011).

First, many plausible propagule arrival outcomes were possible due to the stochastic nature of humans as species vectors. The number of trips received at a destination lake will vary across years, so too will the arrival of releasing (vs. non-releasing) anglers, the arrival of anglers from specific origins, and so on (Jerde and Bossenbroek 2009). Some years may be characterized by relatively benign outcomes, while others may be risky due to stochasticity, where by chance alone, a high incidence of conditional sequences (i.e., uptake through deposition) leads to greater propagule arrival. Variation among sites is also possible. Lake Scugog, a popular angling destination in southern Ontario, will probably receive 16 propagules/yr (modal outcome, baseline Poisson; Fig. 2C). Certain patterns of angling activity could result in more (50) or fewer (one) arriving propagules, but both of these alternative scenarios are equally unlikely as 1 in 500 yearly outcomes. Although Lake Scugog ranks the second-highest of uninvaded destination lakes based on its modal outcome, it could be ranked as low as 1058th, should it experience its lowest outcome relative to all other modal lake values. Shannon Lake, a low-risk waterbody (ranked 2596th; Fig. 2D) due to its remote location in northern Ontario, will probably receive 0 propagules/yr, but could also experience a riskier outcome; P(Shannon Lake[5 propagules/yr]) = 0.002. Lake Scugog could receive five times fewer propagules than Shannon Lake, P(LakeScugog[1 propagule/yr]) $\cap$ P(ShannonLake[5 propagules/yr]) = 0.000004, but this is extremely unlikely as a 1 in 250 000 yearly event.

Second, and related to the variability of predictions, most lakes exhibited relatively narrow differences in the numbers of arriving propagules, and unlike the extreme example involving Shannon Lake, the switching of lake rank is probable for closely ranking waterbodies. Narrow differences between ranks also exist for the gravity scores of lakes visited by recreational boaters, and were suggested as the reason for the relatively poor predictive ability of gravity models (Rothlisberger and Lodge 2011). Lake-specific density functions of propagules introduced by anglers confirm that the narrow range of gravity scores may be reflective of the actual deposition of n propagules per year, but combining trip volumes with per-trip propagule contamination will

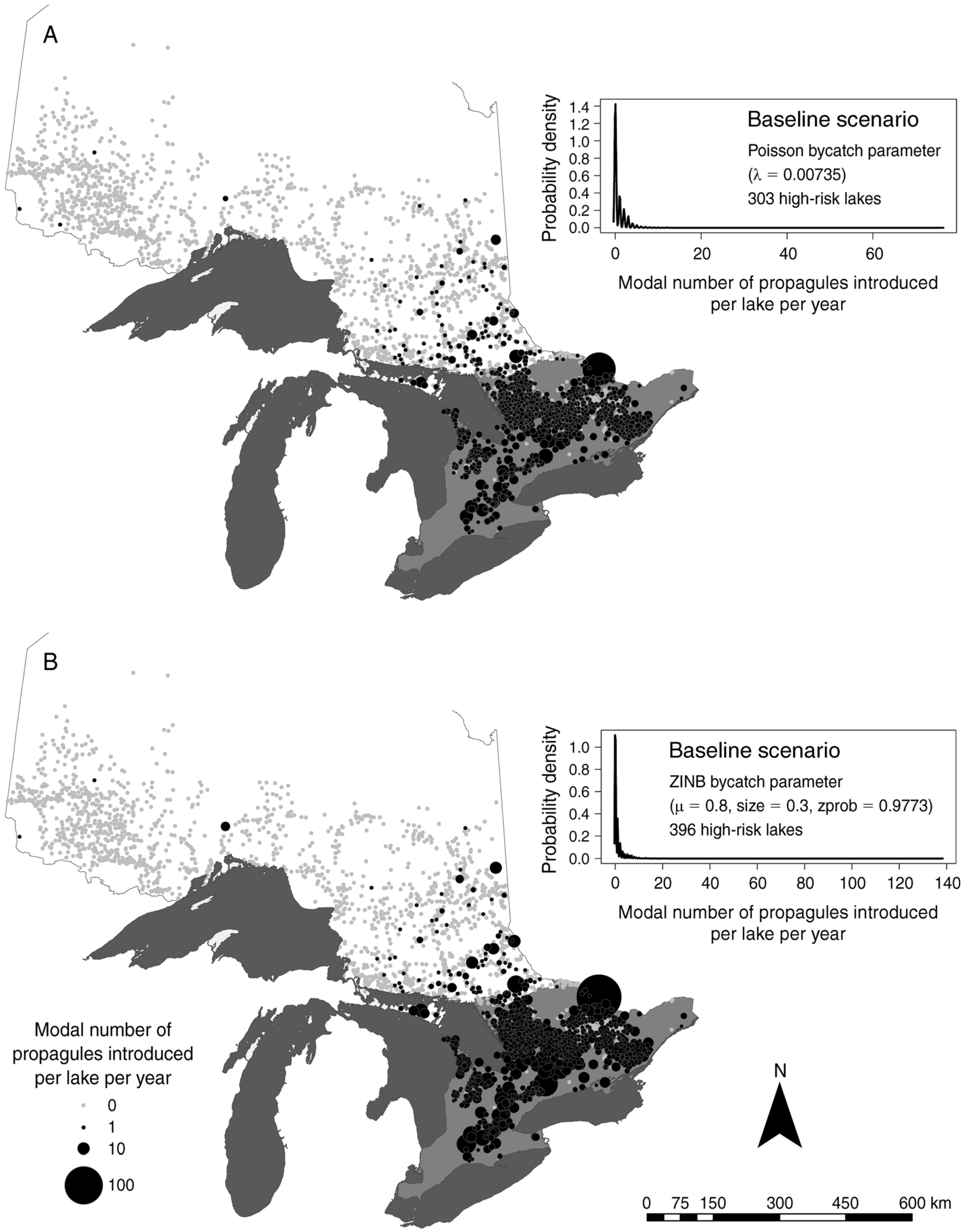

FIG. 4. Landscape patterns of yearly absolute propagule pressure (modal per-lake outcomes; black circles) attributed to bycatch and risky angling activities in Ontario. Risk maps indicate the outcomes following 500 iterations of yearly live-bait angling activity for (A, B) baseline and (C, D) infestation. High risk classification (inset) indicates the number of lakes receiving three or more propagules per year within a given scenario. Gray circles represent the subset of lakes visited for live bait fish angling but failing to receive propagules. The bycatch region is represented by the shaded area in the southern portion of the province. Not shown are the outcomes for bycatch reduction scenarios, in which all lakes visited for live-bait angling exhibited modal outcomes of zero propagules per year. Landscape patterns of lake-specific minimum and maximum absolute propagule pressure are given in Appendix I. In the insets, μ describes the mean of the negative binomial distribution, size describes the over-dispersion of the negative binomial distribution, and zprob describes the probability of structural zeroes within the zero-inflated model.

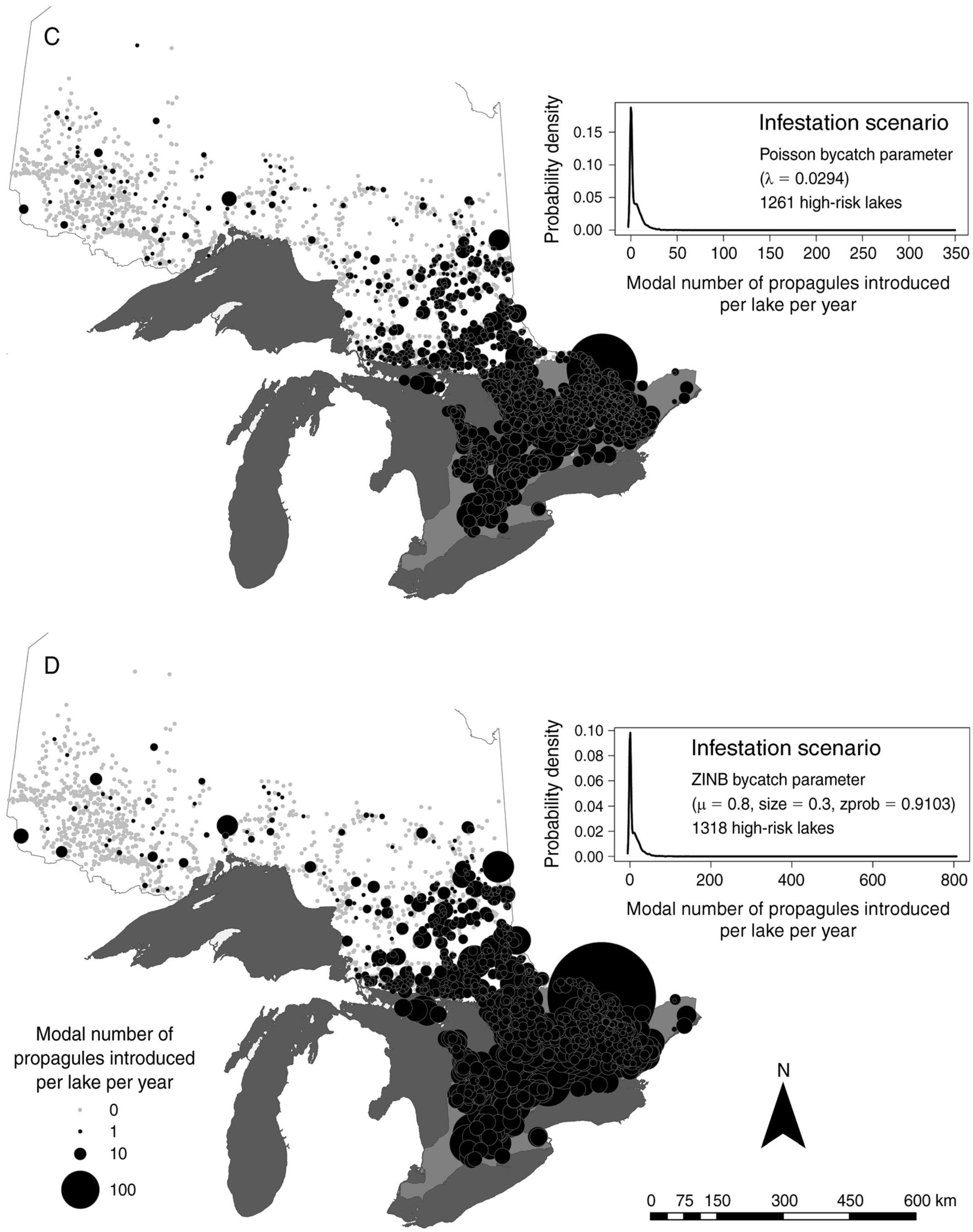

FIG. 4. Continued.

provide insight into the patterns of arriving propagules for other vectors (e.g., recreational boats, ballast water).

Third, substantial epistemic uncertainty concerns the degree of contamination of an individual trip. For example, under a baseline Poisson scenario, a single iteration led to 16 independent introductions of individual propagules to Lake Scugog. The same baseline scenario with strongly over-dispersed contamination would be characterized by the release of multiple propagules per trip (e.g., Fig. 2C). Vélez-Espino et al. (2010) modeled the probability of establishment of round goby, where establishment approached 95% at or above 3 adult propagules$\cdot$m$^{-2}\cdot$yr^{-1} (the same 95% chance of establishment would require upwards of 3000 juvenile propagules$\cdot$m$^{-2}\cdot$yr^{-1}; see Fig. 4 for number of lakes with modal outcomes $\geq$3 propagules per yr). Therefore, single trips involving adult propagules may be sufficient to establish founding populations for over-

TABLE 3. Lake-specific absolute propagule pressure per year following the agent-based simulation of live-bait angling activity in Ontario.

Lake identity	Surface area (ha)	Min	2.5th	25th	50th	75th	97.5th	Max	Mean	Mode
Ottawa River	127 100	3	18	63	95	137	242	321	104.48	76
Lake Scugog	8 256	1	5	12	17	23	38	49	18.244	16
Fanshawe Reservoir	217	0	3	8	13	17	27	36	13.08	13
Lake Nipissing	87 330	0	2	8	12	15	27	41	12.158	12
Pigeon Lake	5 344	1	3	8	12	16	26	41	12.268	12
Gordon Pittock Reservoir	770	0	3	8	12	16	26	34	12.474	12
Lake Manitou	10 400	0	3	8	12	16	26	34	12.474	12
Wildwood Reservoir	713	0	3	9	13	18	28	46	13.918	12
Sturgeon Lake	4 495	0	2	8	12	16	25	33	12.428	11
Orangeville Reservoir	171	0	2	8	11	15	24	33	11.8	11
Balsam Lake	4 665	1	3	7	11	15	24	32	11.434	10
Lake Muskoka	12 206	0	3	10	15	20	32	37	15.328	10
Lake Eugenia	723	0	2	7	10	13	22	32	10.294	10
Lake of Bays	6 904	1	2	8	11	15	24	36	11.536	10
Buckhorn Lake	3 189	0	2	6	9	13	20	30	9.864	9
Guelph Reservoir	688	0	1	6	10	13	21	32	9.998	9
Lake Rosseau	6 374	0	2	6	9	13	20	27	9.842	9
Skeleton Lake	2 156	0	1	5	8	11	18	25	8.772	9
Canal Lake	1 084	0	2	6	9	12	19	24	9.046	8
Chemong Lake	2 278	0	2	6	9	12	20	36	9.312	8
Bark Lake	3 799	0	1	5	8	10	16	26	7.858	8
Conestogo Reservoir	735	0	1	5	8	11	18	25	8.462	8
Golden Lake	3 552	0	1	5	8	11	18	22	8.61	8
Kagawong Lake	5 556	0	1	4	7	10	16	23	7.338	8
Lake Abitibi	79 772	0	1	5	7	11	18	26	7.892	7
Big Rideau Lake	6 479	0	1	5	7	10	17	23	7.826	7
Cameron Lake	1 303	0	1	5	7	10	16	21	7.734	7
Stony Lake	2 825	0	1	6	8	11	20	28	8.894	7
Lake Wanapitei	62 200	0	1	5	7	10	16	23	7.846	7
Lake Joseph	5 156	0	2	6	9	13	20	25	9.59	7

Notes: Propagule pressure statistics (minimum, mean, 2.5th percentile, and so on) represent the absolute number of round goby propagules (R) introduced per lake per year, for the top 30 lakes (rank based on modal value) lacking established round goby populations and predicted to receive propagules under the baseline scenario ($\lambda = 0.00735$).

dispersed scenarios, especially given the propensity for introduced propagules to remain in close proximity following release. Collectively, these factors related to propagule pressure (spatiotemporal variability of propagule arrival, narrow ranges of arrival between lakes, and the degree of over-dispersion) explain some of the difficulty of predicting invasions at scales relevant for management intervention (Jerde and Bossenbroek 2009).

Analysis of predictions for invaded lakes provides further insight into the role of propagule pressure across landscapes and suitability of propagule arrival models for predicting invasions. Generally, the few inland lakes supporting established round goby populations ranked highly based on the modal number of propagules introduced per year (baseline Poisson; Lake Simcoe/Couchiching, second-highest modal outcome across all inland lakes; Belwood Reservoir, 13th; Rice Lake, 65th). Deer Creek Reservoir, an invaded waterbody in southern Ontario, held a low arrival rank, suggesting that (1) other vectors were responsible, (2) our model of propagule arrival is incorrect, or Deer Creek Reservoir experienced its maximum lake-specific outcome relative to all other sites, or (3) the contamination parameter is over-dispersed such that a single risky trip was sufficient for founding propagules to establish. Species establishment is also a highly variable process (Jerde and Lewis 2007), so logically the combined uncertainty of arrival and establishment can lead to patterns of invasion that deviate from predictions of arrival alone (Olden et al. 2011). Although it ranked highly, Lake Simcoe was invaded by another vector, raising broader issues about the suitability of comparing the invasion status of sites against propagule arrival models (or gravity model scores) as means of model validation. Landscape patterns in Ontario indicate that the modal number of propagules per year is correlated with a lake's invasion status (as with gravity scores; Muirhead and MacIsaac 2005, 2011). High propagule pressure alone does not dictate the certainty of invasion within a given time step, but the cumulative arrival of propagules across large timescales (e.g., decades) strongly increases the probability that high-risk sites become invaded. Propagule pressure as a null model for invasions (Lockwood et al. 2009) is sensitive to the influence of time and, at certain scales, plagued by joint uncertainties of arrival and species establishment (e.g., Buchan and Padilla 2000). Despite these overarching uncertainties, highly ranked waterbodies remain a top ecological priority, given the correlation between propagule arrival and invasion status.

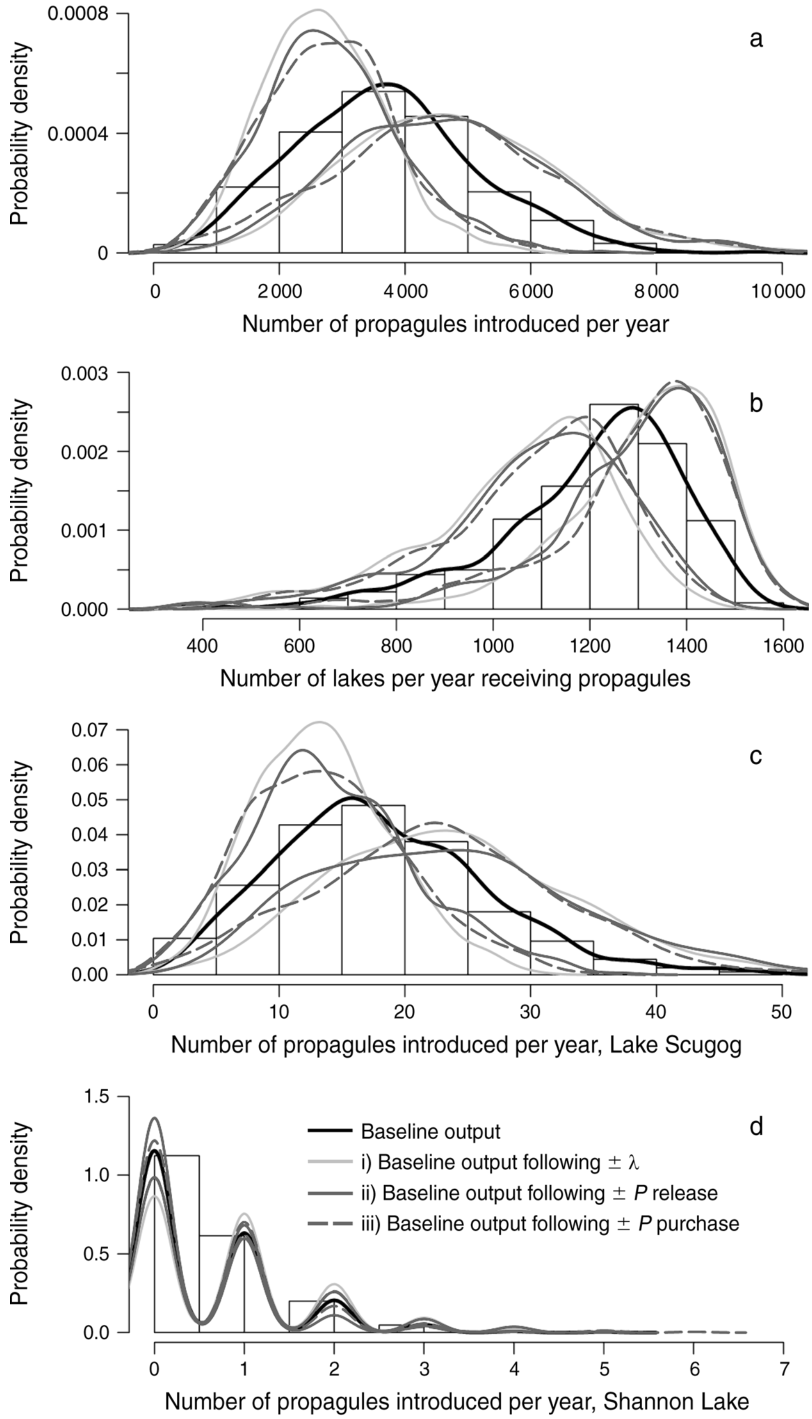

FIG. 5. Sensitivity to changes in model parameters of (a) the probability of introducing *n* propagules per year among all lakes, (b) the number of lakes per year receiving propagules, (c) the probability of introducing *n* propagules/year to Lake Scugog, and (d) the probability of introducing *n* propagules per year to Shannon Lake. The agent-based model output (baseline scenario with Poisson bycatch parameter) is shown as the black line overlaying histogram bars. Light gray, dark gray, and dashed lines represent the response of the baseline model output to 25% increases or decreases (right vs. left distributional shifts, respectively) of (1) the parameter λ for P(purchase[n propagules]), describing the mean prevalence of n invasive propagules as bycatch within angler purchases (light gray), (2) the region-specific probability of releasing leftover bait fishes at the destination waterbody (dark gray), and (3) the probability of purchasing (as opposed to self-harvesting) bait fishes (dashed line). Note changes in x- and y-axis labels between panels.

Anglers have long been implicated as invasion vectors (Lodge et al. 2000, Keller et al. 2007, Kilian et al. 2012), but like many vectors globally, there is substantial uncertainty concerning the frequency and extent of propagule transport (Hulme 2009), thus limiting appropriate management response (Vander Zanden and Olden 2008). Although previous studies have quantified bycatch effort–capture relationships in commercial bait fisheries (Drake and Mandrak 2012), we provide perspective to the risk of contamination of bait catches, where the modal probability of any live-bait trip resulting in propagule introduction is ≈1 in 1136 for a baseline scenario involving round goby. A sizable number of propagules are introduced across destination lakes, but specific outcomes (e.g., baseline Poisson; 3715 propagules among 1288 lakes, vs. baseline ZINB; 6722 among 1292 lakes) depend on the degree of overdispersion associated with the contamination of bait purchases by propagules. The incidence and magnitude of introduction is chiefly attributed to the large volume (4.2 million per yr) of live-bait trips, where even the rarest sequence of events (i.e., the consecutive uptake, movement, and deposition of propagules during an individual trip) is anticipated to occur across a large number of probability trials. Substantial trip volumes probably play a role in the effectiveness of other species vectors (e.g., trailered recreational boats) by providing increased opportunity for a successful context-dependent trip involving the consecutive progression from contamination through establishment.

Landscape configuration and other spatial factors, such as the availability of bycatch and the accessibility (via road networks) and size of lakes, were strong drivers of lake risk status. Low-risk lakes were typically small waterbodies located in southern or northern regions, resulting from relatively low angling effort due to their small size or lengthy travel time, confirming the distance decay of propagule transport during human-mediated species introductions (e.g., Muirhead and MacIsaac 2005, Leung et al. 2006). High-risk lakes were generally large, southern lakes in close proximity to the invaded range, and each of the highest-risk waterbodies (e.g., Ottawa River, Lake Scugog, Fanshawe Reservoir, Lake Nipissing, Pigeon Lake in the Kawartha region) exhibited multiple risk factors: large physical size and diverse sportfish populations (each as drivers of live-bait angling effort; Drake and Mandrak 2010) and proximity to large angling populations and the bycatch region. Collectively, these factors led to a proportional increase of risky inbound trips and higher cumulative probabilities of introduction across yearly iterations of vector activity.

Effective vector assessment and management requires an understanding of how intervention strategies influence ecological risk across landscapes (Carlton and Ruiz 2005). Within our model, the notable result of risk management strategies (i.e., reducing bycatch or the per-trip probability of release) was a greater reduction in propagule pressure for high-risk lakes because of the larger number of inbound risky trips upon which management would be influential. A 90% reduction in the probability of encountering propagules would substantially reduce propagule pressure (most likely outcome, zero propagules introduced per year). However, the long right tail of most lake-specific density functions (Fig. 2C, D) indicated that relatively common iterations of yearly activity can lead to non-negligible propagule pressure to some lakes, and certain rare iterations can lead to sizable propagule loads. Predicting these rare events remains a perpetual challenge for invasion ecologists (Franklin et al. 2008).

Results indicate that even infrequent contamination of bait pathways with large distribution networks (e.g., aquaculture facilities) are of ecological concern, given the large number of probability trials (commercial distribution, angling events) by which contaminated bait may be released to the wild. Therefore, while bycatch reduction provides a sound mechanism to reduce the risk of propagule arrival, it will not eliminate the risk of arrival due to the volume of vector activity and the stochasticity of relevant social and ecological processes. Bycatch reduction will reduce the uncertainty of propagule arrival, which may be perceived positively by managers; thus, bycatch reduction and management of bait pathways are activities strongly dependent on risk tolerance. Infestation would result in a 4.2–4.6-fold increase in the modal number of propagules introduced, but only a 1.3-fold increase in the modal number of lakes receiving propagules. The prominent effect of infestation is increased intensity of propagule arrival (as opposed to saturation across all destination lakes) because of the prevailing attractiveness of certain sites and higher proportions of risky arrivals, so infestation sharply increases the per-lake probability of establishment for high-ranking waterbodies.

Given our models involving round goby as a species sold incidentally from the Great Lakes and certain inland waterbodies, we provide a coarse surrogate for the introduction of other species and pathogens anticipated through similar mechanisms (e.g., the potential contamination of bait catches with other Great Lakes fishes or viral hemorrhagic septicemia virus). Nonetheless, application to other species of concern requires a thorough assessment of encounter rates, the dispersion of contamination, and relevance of existing spatial factors. We confirm live-bait anglers as highly mobile vectors of species introductions; however, risk is confined to a subset of individuals and recipient sites that may be effectively managed with targeted strategies.

In conclusion, our study provides perspective to the role and rarity of humans as species vectors. We provide a process for species arrival to be evaluated within an invasion framework that, when adopted, will foster a better understanding of ecological consequences among vectors so that management resources can be allocated effectively. Lastly, we illustrate the complexity of social-ecological systems and the dynamic process of species arrival, which represents a significant accomplishment towards understanding and forecasting the ecological mechanisms of change associated with species invasions.

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Supplemental Material

Appendix A

Distribution of inland lakes with established populations of round goby (*Neogobius melanostomus*) in Ontario, Canada (*Ecological Archives* A024-051-A1).

Appendix B

Empirical data for estimating model parameters (*Ecological Archives* A024-051-A2).

Appendix C

Overview of model assumptions (*Ecological Archives* A024-051-A3).

Appendix D

Probability distributions describing the availability of n propagules as bycatch to purchasing anglers (*Ecological Archives* A024-051-A4).

Appendix E

Live bait fish angling effort for lakes, irrespective of risk status, following the agent-based simulation of resident, licensed anglers in Ontario, Canada (*Ecological Archives* A024-051-A5).

Appendix F

The vector (trip) risk profile following the agent-based simulation of bycatch, anglers, road networks, and lakes with mean, $\lambda = 0.00735$ (i.e., baseline Poisson) (*Ecological Archives* A024-051-A6).

Appendix G

Propagule pressure summary statistics for baseline, infestation, and bycatch reduction simulations (*Ecological Archives* A024-051-A7).

Appendix H

Lake-specific absolute propagule pressure under various bycatch scenarios *Ecological Archives* A024-051-A8).

Appendix I

Landscape patterns of absolute propagule pressure under various bycatch scenarios (*Ecological Archives* A024-051-A9).