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ORIGINAL PAPER

Invasion dynamics of round goby (*Neogobius melanostomus*) in Hamilton Harbour, Lake Ontario

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Abstract Most introduced non-native species fail to establish as a result of mortality or reproductive failure. An established population can increase the probability of survival and reproductive success of newly introduced individuals by reducing both Allee effects and demographic stochasticity. Previously, attention has been paid to the establishment phase of the invasion process and its probability modelled as a stochastic process, while the spread phase has received less attention. By analyzing data collected during the spread phase of an invasion of the round goby, *Neogobius melanostomus*, in Hamilton Harbour, Lake Ontario, we develop an analytical approach to backcalculate the time to establishment and to determine the time to habitat saturation. Our modelling shows that: (1) during the transition between arrival and establishment, propagule pressure in the form of new adults entering the area can be very low and still represent a significant probability of establishment; (2) much higher concentrations of juveniles would be needed to pose a significant risk of invasion; (3) the demographic contribution of propagule pressure during the spread phase is low and its total elimination will not halt population growth and spread; (4) a short elapsed time between arrival and establishment indicated that the transition between these two phases can be characterized as a deterministic process with high propagule pressure and low adult mortality rates; and, (5) very aggressive management actions would be needed to halt population growth after population establishment, suggesting that preventative measures are the most effective management options available to reduce risk of future invasions.

Keywords Gobidae · Great Lakes · Propagule pressure · Habitat saturation · Establishment probability · Invasive species

Introduction

Once an invasive species is widespread with long-established populations, the opportunity for rapid eradication has been lost. However, research on established populations of non-native species can

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answer fundamental questions in ecology and guide future control methods and effective maintenance management (Simberloff 2003). Population biological research can also generate important information on invasion dynamics such as the role of propagule pressure (Lockwood et al. 2005), the time lag between arrival and establishment (Jerde and Lewis 2007), and ecological resistance to biological invasion (Von Holle and Simberloff 2005). In this paper, we address these aspects of the invasion dynamics of round goby (*Neogobius melanostomus*) in Hamilton Harbour, Lake Ontario.

After it was first detected in 1990 in the St Clair River, western Lake Erie (Jude et al. 1992), the round goby rapidly invaded all Laurentian Great Lakes (Stepien and Tumeo 2006). Accidentally introduced and continuously reintroduced by ballast water (Corkum et al. 2004), round goby were present in all of the five Great Lakes by the year 2000 (Jude 2001). By the year 2001, round goby were common in the littoral zone of Hamilton Harbour (Chant 2002), the most important natural embayment in Lake Ontario (Roy et al. 1994). Apparently, round goby invaded this site sometime between 1996 and 2001 with the first round goby detected in the harbour in 1999 (Balshine et al. 2005).

There is evidence that the range expansion and aggressive behaviour of round goby has caused declines in several native species of benthic fishes (Janssen and Jude 2001), altered benthic communities by removal of invertebrates and cascade effects on benthic plants and nutrient cycles (Kuhns and Berg 1999), and displaced native species such as mottled sculpins (*Cottus bairdii*) and logperch (*Percina caprodes*) via the monopolization of shelter (Dubs and Corkum 1996; Balshine et al. 2005). In addition, round goby exert high predation on eggs of native fishes (Chotkowski and Marsden 1999), including endangered species such as lake sturgeon (*Acipenser fulvescens*; Nichols et al. 2003). Round goby also accumulate high concentrations of polychlorinated biphenyls (PCBs), opening a new transfer route for these toxic substances and threatening the health of fishes that prey on round goby (Morrison et al. 2000).

Any invasion process can be broken down into four phases: entry, establishment, spread, and impact (Andersen et al. 2004). The entry phase consists of the arrival of a non-indigenous species. The establishment phase is characterized by an incipient self-sustaining population large and dense enough to escape immediate local extinction. In the spread phase individuals increase occupation of the available habitat within the new environment while the impact phase is characterized by the persistence and integration (low impact) into the food web (e.g., gizzard shad, *Dorosoma cepedianum*, in Lake Powell; Vatland and Budy 2007) or by alteration (high impact) of the food web (e.g., sea lamprey, *Petromizon marius*, into the Great Lakes; Eshenroder and Burnham-Curtis 1999). Such food web alterations usually cause economic impacts (Pimentel et al. 2000). Both, entry and establishment phases of an invasion are directly related to propagule pressure (Lockwood et al. 2005). While most introduced species fail to establish soon after introduction (Williamson and Fitter 1996), the presence of a previously established population increases the probability of survival and reproductive success of newly released individuals. An already established population prevents both Allee effects and demographic stochasticity (Roman and Darling 2007), and may result in an accelerated invasion rate characteristic of the spread phase of the invasion process (Shigesada and Kawasaki 1997). Population regulation in invasion advancement is a widespread phenomenon in nature (Arim et al. 2006). As the non-indigenous species saturates the occupied habitat and population density approaches the carrying capacity of the system, population growth rates at particular locations are expected to decrease as a result of local density-dependent processes and increased propensity to disperse (Fretwell and Lucas 1970; Taylor and Norris 2007).

Although attention has been placed on the establishment phase of the invasion process and the probability of establishment has usually been modelled as a stochastic process (e.g., Haccou and Iwasa 1996; Drake 2004), important aspects of the spread phase such as the probability of monopolizing available habitat (i.e., habitat saturation) and the time lag between establishment and habitat saturation have not been sufficiently investigated. A better understanding of these invasion attributes is crucial for decisions related to pest control and maintenance management (Simberloff 2003). The main goal of this study is to investigate the invasion dynamics of round goby in Hamilton Harbour, Lake Ontario. Our specific objectives are: (a) to backcalculate the time of arrival and establishment; (b) to determine the elapsed time between establishment and habitat saturation, (c) to infer the relative demographic contribution of propagule pressure to the invasion process; and, (d) to identify points in the life cycle and invasion dynamics most sensitive to management actions.

Methods

Adult round gobies were collected from 2002 to 2008 in Hamilton Harbour, Lake Ontario, in four specific locations. Fish were collected approximately bi-weekly from late April or early May to late October or early November with a set of four minnow traps at 1 meter depth and separated from each other by at least 10 m and left for 24 h in each location and sampling event. The four sampling locations, separated from one another by distances ranging from 1.25 to 7.95 km (average distance between sites was 4.72 km), were characterized by different substrates (mud, sand, cobble, and boulder). Adults were sexed, and their standard length and body mass were measured to the nearest 0.1 mm and 0.0001 g, respectively.

Our approach included five steps. First, population attributes such as annual survival, fecundity rates, and population growth rates for each sampling year were estimated. Second, these population parameters were used to construct age-structured transition matrices for each sampling year. Juvenile (age-0) survival was derived from these matrices by solving for observed population growth. Third, time of arrival and time of establishment of round goby were backcalculated analytically from the relationship between density and critical population thresholds. Fourth, using a hierarchical model of invasion we estimated propagule pressure and converted it into a demographic rate. Finally, we used perturbation analysis of age-structured transition matrices, incorporating propagule pressure as a rate, to identify the relative vulnerability of different points in the life cycle and invasion process to management intervention.

Estimating survival

Annual survival rate (S_i) for adult fish 1-year old and older was estimated from age distributions using a catch curve analysis following the method introduced by Chapman and Robson (1960). Maximum age observed in Hamilton Harbour round goby is 4 years old (S. Balshine, McMaster University, Hamilton ON, unpublished data), which is shorter than the maximum age observed in Europe (age-5; Charlebois et al. 1997). MacInnis and Corkum (2000a) showed that in the upper Detroit River, length intervals exhibited by round goby of different ages overlapped considerably as well as the length-at-age intervals of males and females. Based on these data (MacInnis and Corkum 2000a), we ascribed non-overlapping (to avoid double counting of individuals) standard length intervals to males and females of ages 0–4 as follows: age 0 (juveniles) $\leq$ 56.5 mm, 56.6 mm $\leq$ age 1 $\leq$ 62.5 mm, 62.6 mm $\leq$ age 2 $\leq$ 72.9 mm, 73.0 mm $\leq$ age 3 $\leq$ 92.2 mm, age 4 $\geq$ 92.3 mm. Note that this procedure serves for modelling purposes in the absence of direct age information but discrete, non-overlapping length-at-age intervals rarely occur in animal populations. Age distributions defined by these intervals were determined for each sampling year, substrate type, and gender and further incorporated into individual catch curves analyses to estimate adult survival rates (S_A). This approach produced a single adult survival rate per catch curve that was assigned to age classes 1–4. Single catch curve analyses, including males and females from all substrates, were conducted for each sampling year after non-parametric analyses indicated non-significant differences in adult survival among substrates (Kruskall-Wallis: $\chi^2 = 1.95$; $df = 3$; $P = 0.58$) and sexes (Wilcoxon: $\chi^2 = 2.71$; $df = 1$; $P = 0.10$). The survival rate of age-0 fish (S_0) for each sampling year and site was estimated indirectly by solving for the population growth rates determined from the analysis of time series (see below).

Estimating fecundity

The regression between number of eggs (n) and standard length ($n = -332 + 8.95\ \mathrm{SL_{mm}}$) obtained by MacInnis and Corkum (2000b) in their study in the upper Detroit River was used to estimate mean annual fecundity at age as:

$$f_i = m_i \varsigma \tau \upsilon_t \qquad (1)$$

where ς is a constant that represents a fertilization rate of 0.95 as estimated by Charlebois et al. (1997), τ is a second constant representing an average number of three reproductive batches per year (MacInnis and

Corkum 2000b), υ_t represents the proportion of females in sampling year t, and m_i indicates the average number of eggs for age class i:

$$m_i = \frac{\sum_{f=1}^{c_i} n_f}{c_i} \tag{2}$$

In Eq. 2, n_f represents the number of eggs of a single female of length SL and c_i is the total number of females in age class i. The relationship between number of eggs and length obtained by MacInnis and Corkum (2000b) was applied to all females regardless of the substrate where they were sampled because there were not significant differences between slopes ($F = 0.45$; $P = 0.87$) or elevations ($F = 0.69$; $P = 0.63$) of substrate-specific length-weight relationships (see Fig. 1a), and similar reproductive allocations and maturation patterns are expected in females of similar size (Bolger and Connolly 1989). In addition, the use of the regression between number of eggs and standard length obtained by MacInnis and Corkum (2000b) in their study in the upper Detroit River to estimate mean annual fecundity in Hamilton Harbour was supported by the similarity of the length-weight allometric curve found in our study ($W = 0.000018\ \mathrm{SL}^{3.0811}$) with the one obtained by MacInnis (1997) in the upper Detroit River ($W = 0.000008\ \mathrm{SL}^{3.261}$; Fig. 1b).

Age-structured model

The round goby life cycle was modeled with a birth-pulse (i.e., seasonal reproduction), age-structured matrix model (Eq. 3) characterized by first maturity taking place during the second year of life (i.e., age 1;

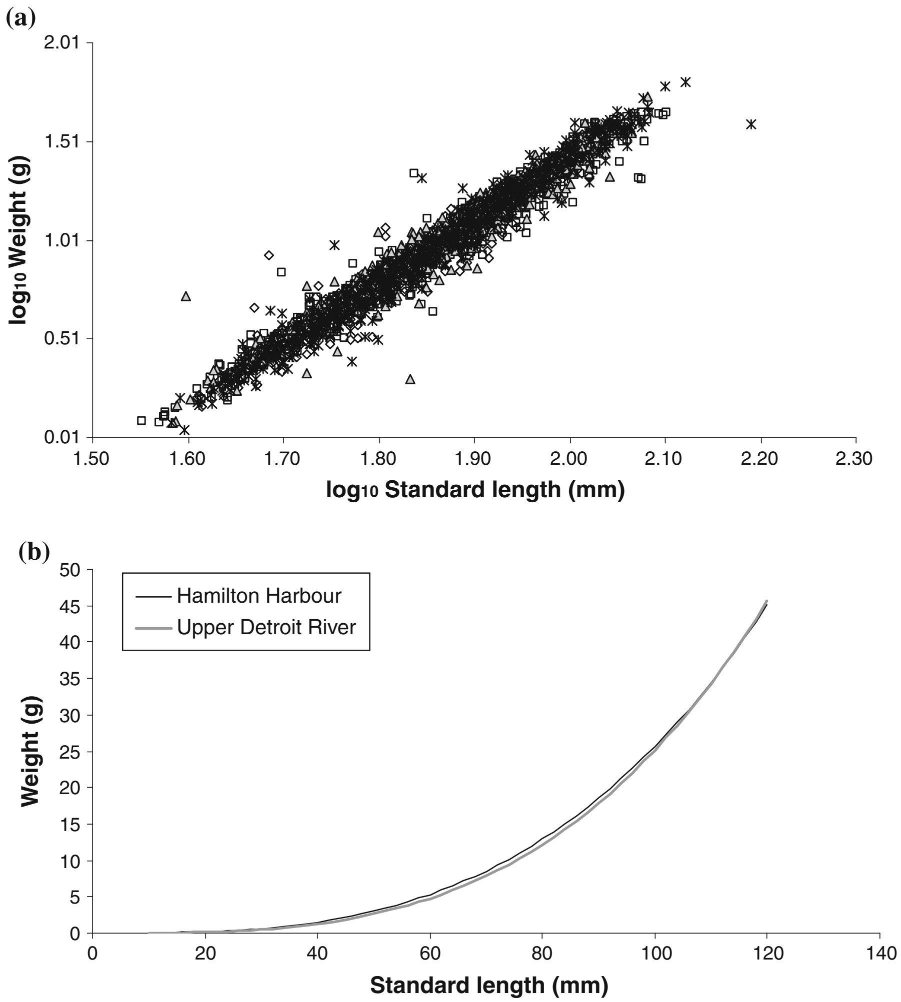

Fig. 1 Length weight relationships. **a** The relationship between standard length and weight of round goby sampled on four different substrate types in Hamilton Harbour: mud (*diamonds*), sand (*squares*), cobble (*triangles*), and boulder (*stars*). **b** The relationship between standard length and weight of round goby sampled in Hamilton Harbour ($W = 0.000018\ \mathrm{SL}^{3.0811}$). A length-weight curve for the upper Detroit River (MacInnis 1997; $W = 0.000008\ \mathrm{SL}^{3.261}$) is included for comparison

MacInnis and Corkum 2000b), maximum reproductive age of four years, survival S_i, and fecundity rate F_i computed as the product of the mean fecundity and the annual survival of age class i, $F_i = f_i\,Si$ (i.e., post-breeding variant of the matrix model; see Caswell 2001). Elements S_i and F_i were incorporated into individual transition matrices representing each sampling year and site:

$$\mathbf{M}_t = \begin{pmatrix} 0 & F_{1(t)} & F_{2(t)} & F_{3(t)} & F_{4(t)} \\ S_{0(t)} & 0 & 0 & 0 & 0 \\ 0 & S_{1(t)} & 0 & 0 & 0 \\ 0 & 0 & S_{2(t)} & 0 & 0 \\ 0 & 0 & 0 & S_{3(t)} & 0 \end{pmatrix} \qquad (3)$$

The dominant eigenvalue of matrix $\mathbf{M}_t$, λ_t, represents the annual population growth rate such that $N_{t+1} = \lambda_t\, N_t$. Given that the value of age-0 survival ($S_{0(t)}$) is still unknown, population growth rates were estimated from the analysis of time series. Aggregated monthly captures were incorporated into a Leslie-Davis depletion model to compute annual population size (N_t), population growth for sampling year t (λ_t) was calculated as N_{t+1}/N_t, and the mean intrinsic rate of increase (r) was determined from the best of a set of three models of population growth (see below). The survival rate for the first year of life ($S_{0(t)}$) for each sampling year and site was estimated by solving each matrix $\mathbf{M}_t$ for the annual population growth rate λ_t.

Modelling population growth

Annual density (D_t) was computed as the Leslie-Davis estimate of population size divided by the potential area of influence of a single minnow trap. Previous studies indicate that site fidelity in round goby is strong (Wolfe and Marsden 1998) with an average home range of 2.65–7.35 m^2 (Ray and Corkum 2001). If a minnow trap were placed in the center of a quadrant divided into four identical squares, each representing individual home ranges, fish from the four home ranges could potentially be captured by the minnow trap occupying one corner of each of the home-range squares. Using the 2.65 m^2 lower and 7.35 m^2 upper limits of round goby home range size, we calculate that the area of influence of a single minnow trap varies from approximately 10–30 m^2. Therefore, the area of influence of each of the four minnow traps did not overlap since they were placed more than 10 m apart. Data from all substrates were pooled after a non-parametric analysis indicated non-significant differences in density among substrates (Kruskall-Wallis: $\chi^2 = 2.43$; $df = 3$; $P = 0.49$). The final estimates of density (D_t) were computed as the average density across all traps in each location and included low and high estimates of density generated by upper and lower home range limits, respectively.

Three models of population growth were fitted to the density data using nonlinear least-squares regression of $\log(D_{t+1}/D_t)$ against D_t: (1) the Ricker model was represented with the equation $\log(D_{t+1}/D_t) = r(1 - D_t/K)$; (2) the theta logistic model $\log(D_{t+1}/D_t) = r(1 - (D_t/K)^\theta)$; and, (3) a model incorporating Allee effects as $\log(D_{t+1}/D_t) = \log(D_t) - \log(\theta + D_t) + r - KD_t$, where r represents the intrinsic rate of increase, K is the carrying capacity, and θ is a model parameter that determines how r changes with D_t (Morris and Doak 2002). A density-independent model ($\log(D_{t+1}/D_t) = r$) was not included in the model selection process because preliminary analyses showed a clear density-dependent pattern (Fig. 2).

The Akaike Information Criterion (AIC) was used for model selection. The AIC identifies the best model based on the model's likelihood to fit the data and the number of parameters. More complex models (with more parameters) are more heavily penalized. The AIC was corrected for small sample size and Akaike weights ($\mathrm{AIC}_{\mathrm{weight}}$) were computed following procedures described by Burnham and Anderson (1998). Akaike weights quantify the probability that a given model is the best representation of the data.

Backcalculating time of arrival and establishment

Arrival and establishment are two separate phases of a non-native invasion (Vermeij 1996). Small incipient populations of non-native species fail to establish if they do not reach population densities enabling them to cope with environmental and demographic stochasticity and with Allee effects (Lockwood et al. 2005). For a species with strong site fidelity and small home range such as the round goby (Wolfe and Marsden 1998; Ray and Corkum 2001), overcoming Allee effects is of great importance in the invasion process (Leung et al. 2004). Based on home range estimates of 2.65 and 7.35 m^2, finding a mate would require at least a population density of 0.38 and 0.14

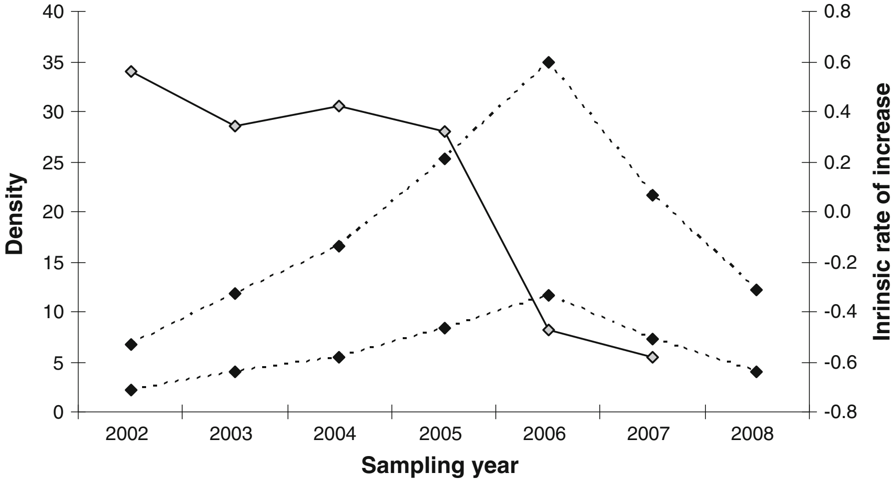

Fig. 2 Density (fish/m^2; *dashed lines*) and intrinsic rate of increase (r; y^{-1}; *solid line*) during the study period (2002–2008). Lower and upper density bounds produced by the possible home range sizes (see methods) and their effect on the area of influence of traps are presented. Intrinsic rate of increase for year 2008 is not shown because its computation requires 2009 density data

adult fish per square meter (i.e., the inverse of the home range), respectively, to overcome this kind of Allee effect and have a chance of establishment. Thus, using these density limits as the range of critical density for establishment (D_E), we followed an analytical approach to backcalculate the time of establishment (T_E) that also facilitated the backcalculation of time of arrival. Deterministically, time of establishment was calculated as:

$$T_E = \left[\frac{\log\left(\frac{D_C}{D_E}\right)}{r}\right] \tag{4}$$

where D_C represents the density at the beginning of the time series and r is the Ricker's population growth rate. T_E was calculated for the two critical densities for establishment (D_E) determined by the range in adult home range size.

Backcalculated time of arrival (T_A) would be the limit of Eq. 4 as density (D) approaches a value of zero:

$$T_A = \lim_{D \to 0}\left[\frac{\log\left(\frac{D_C}{D}\right)}{r}\right] \tag{5}$$

Since T_A tends to infinity as D approaches zero, T_A was approximated with a third-order polynomial of T on D for the range $D = (0.01, 0.38)$, where the upper limit of this range represents the largest of the critical densities for establishment:

$$T_A = \lim_{D \to 0}\left(aD^3 + bD^2 + cD + d\right) = d \tag{6}$$

The third-order polynomial explained 98.4% of the variation in T_A computed with Eq. 5.

Propagule pressure

Propagule pressure is a composite measure of the average number of non-native individuals of a given species released into a region in a single introduction event (propagule size) and the number of discrete release events in a given period of time (propagule number) (Lockwood et al. 2005), and can be defined as an annual rate. A more crucial measure of propagule pressure, as it relates to population growth rates of introduced species and their probabilities of establishment, would explicitly represent the relationship between the impacted area and propagule size number. Such a measure of propagule pressure (Φ = absolute propagule pressure) is the number of non-native individuals introduced in a given area per year, or more specifically, Φ = number of individuals/m^2/y.

Without information about the number of release events through the most common vector, ballast water (Corkum et al. 2004), or information about the average number of round goby released in each event, it is challenging to separate the influence of natural survival and propagule pressure on our estimates of annual survival obtained from catch curves. Therefore, it is reasonable to assume that our estimates of adult survival are in fact a composite measure of natural survival and propagule pressure, such that $S_A = P_S + \Phi'$, where S_A is identified as "apparent adult survival", P_S is the natural annual survival rate and Φ' is a relative measure of propagule pressure, expressed in survival units that can be incorporated into a transition matrix:

$$\mathbf{N} = \begin{pmatrix} 0 & f_1(P_S+\Phi') & f_2(P_S+\Phi') & f_3(P_S+\Phi') & f_4(P_S+\Phi') \\ S_0 & 0 & 0 & 0 & 0 \\ 0 & P_S+\Phi' & 0 & 0 & 0 \\ 0 & 0 & P_S+\Phi' & 0 & 0 \\ 0 & 0 & 0 & P_S+\Phi' & 0 \end{pmatrix} \tag{7}$$

We estimated natural survival from the life history invariant $M/k = 1.65$ (Charnov 1993; Jensen 1996), where M is the mortality rate and k is the von Bertalanffy growth coefficient. Using a growth coefficient of 0.4, estimated for round goby from the upper Detroit River (www.fishbase.org), this procedure generated a natural survival rate of 0.52 that is consistent with previous estimates of round goby survival in Lake Erie (Bunnell et al. 2005). Variation in natural survival (P_S) was created artificially by increasing and decreasing its value by 20% (i.e., $P_S \pm 0.2\ P_S$) to analyze the influence that uncertainty in natural survival has on population dynamics. Relative propagule pressure (Φ') was computed for each sampling year and site as $S_A - P_S$ and incorporated into corresponding transition matrices (Eq. 7) to conduct an analysis of the sensitivity of round goby population growth rate to changes in the matrix elements S_0, P_S, Φ', and f_i (see next section).

Jerde and Lewis (2007), using a hierarchical approach to model the invasion process, arrived at a description of the probability of at least one individual remaining in the invaded area after one time step (γ) as a function of the probability of surviving in the new environment (P_S) and absolute propagule pressure (Φ):

$$\gamma = 1 - e^{-P_S \Phi} \tag{8}$$

Under this framework, Jerde and Lewis (2007) also calculated the probability of establishment ($P_{E(t)}$) at a given time (t) as:

$$P_{E(t)} = 1 - (1-\gamma)^t \tag{9}$$

Building on Eqs. 8 and 9, the relationship between the probability of establishment (P_E) and absolute propagule pressure (fish/m^2/year) necessary to establish at time T_E after arriving at time T_A was calculated as:

$$\Phi = \frac{\log\left[(1-P_E)^{1/(T_A - T_E)}\right]}{-P_S} \tag{10}$$

where $T_A - T_E$ represents the elapsed time between arrival and establishment.

We also applied Eq. 10 to estimate the absolute propagule pressure in terms of juvenile (age-0) fish, using S_0 instead of P_S in the computation and assuming the same home range for adults and juveniles, to obtain some insights into the levels of juvenile introduction needed for establishment. These computations were conducted for the range of juvenile survival values estimated in Hamilton Harbour during the study.

Prospective perturbation analysis

For projection matrices like $\mathbf{M}_t$ or $\mathbf{N}$, the influence of vital rates (i.e., survival and fecundity) on the population growth rate is indicated by the elasticities of matrix elements (ε_{ij}), which represent the partial derivatives of λ with respect to m_{ij}, the individual elements of the matrix. Multiplying the set of elasticities by λ produces a set of contributions which sum to λ, and the ε_{ij} themselves give the relative contribution of the different transitions to λ (de Kroon et al. 1986). Vital rates usually contribute to more than one matrix element and therefore the chain rule for differentiation was used to compute vital rate elasticities (Caswell 2001; Morris and Doak 2002). Vital rate elasticities represent how sensitive the population growth rate (λ) is to changes in individual vital rates.

We used a stochastic approach, incorporating annual variation in vital rates and separating natural survival from relative propagule pressure as indicated by matrix $\mathbf{N}$ (see Table 1 for a summary of values), to conduct a perturbation analysis. This kind of analysis is designed to provide insights into the relative effects on round goby population growth rates from targeting different vital rates or propagule pressure in future control actions. For this model, we used computer simulations to generate 1000 random matrices with vital rate values drawn from various distributions. The beta distribution was used to simulate the variation in natural survival (P_S) and relative propagule pressure and parameterized with means and

Table 1 Mean, variance, minimum, and maximum values of population parameters used in stochastic simulations

Parameter	Symbol	Mean	Variance	Minimum	Maximum
Age-0 survival	S_0	0.0053	1.358E-05	0.0005	0.0087
Natural adult survival	P_S	0.52	0.010816	0.416	0.624
Propagule pressure	Φ'	0.158	0.0041	0.04	0.22
Apparent adult survival	S_A	0.678	0.0041	0.56	0.74
Age-1 fecundity	f_1	169.6	1353.3	134.0	225.2
Age-2 fecundity	f_2	221.5	2413.7	167.3	283.5
Age-3 fecundity	f_3	321.3	5230.5	250.1	427.3
Age-4 fecundity	f_4	503.3	12531.3	407.3	618.2

variances derived from rate values from all sampling years. This distribution is appropriate for binary events such as survival and produces random variables confined to the interval from 0 to 1. A uniform distribution was applied to age-0 survival (S_0) and parameterized with minimum and maximum values derived from all sampling years. The lognormal distribution was used to simulate age-specific fecundity values with mean and variance generated by age-specific rate values from all sampling years. This distribution produces only positive random variables bounded by zero and infinity, and is particularly appropriate for organisms with numerous offspring (e.g., Mertz and Myers 1996). Population growth rate (λ), elasticities of survival and fecundity rates, and the elasticity of propagule pressure were calculated for each matrix, and a parametric bootstrap was used to estimate mean stochastic elasticities and their 95% confidence intervals.

Results

Survival

Over the study period (2002–2008), 4590 adult round goby were sampled. Annual estimates of adult survival in Hamilton Harbour, derived from annual catch curves (i.e., apparent survival), ranged from 0.56 to 0.74. Inferred estimates of juvenile (age-0) survival for the same sampling period ranged from 0.0005 to 0.0087. There was a clear declining trend in survival with greater declines for age-0 (95% reduction) than for adult fish (22% reduction) (Fig. 3a).

Fecundity

Males were more abundant than females in all sampling years in Hamilton Harbour, with the proportion of females ranging from 0.28 to 0.39. Strong male bias has been observed in other studies (Corkum et al. 2004; Young et al. 2010) and been associated with territory and egg defence. These behavioural aspects have the potential to restrict the movement of adult males, thereby generating a male bias in capture probabilities (Young et al. 2010). Fecundity estimates in Hamilton Harbour ranged from 134 (age-1 fecundity for year 2006) to 618 (age-4 fecundity for year 2002). Age-4 females were not captured in 2003 and 2006. As 4 year olds are the oldest individuals captured in Hamilton Harbour, a small proportion of the population is expected to be comprised by age 4 females. The probabilistic nature of both survival and sampling makes it likely that the oldest age classes are not always sampled, which appears to have happened in 2003 and 2006. Further, apart from age-4 fecundity, which seemed to decline during the study period, age-specific fecundity was relatively constant throughout the study period (Fig. 3b).

Population growth and probabilities of habitat saturation

Estimates of annual population growth rate (λ_t) ranged from 0.56 to 1.75. Akaike weighs indicated a strong preference for the Ricker model (Table 2). Carrying capacities generated by this model were 7.4 and 22.3 fish/m^2 for low and high density estimates

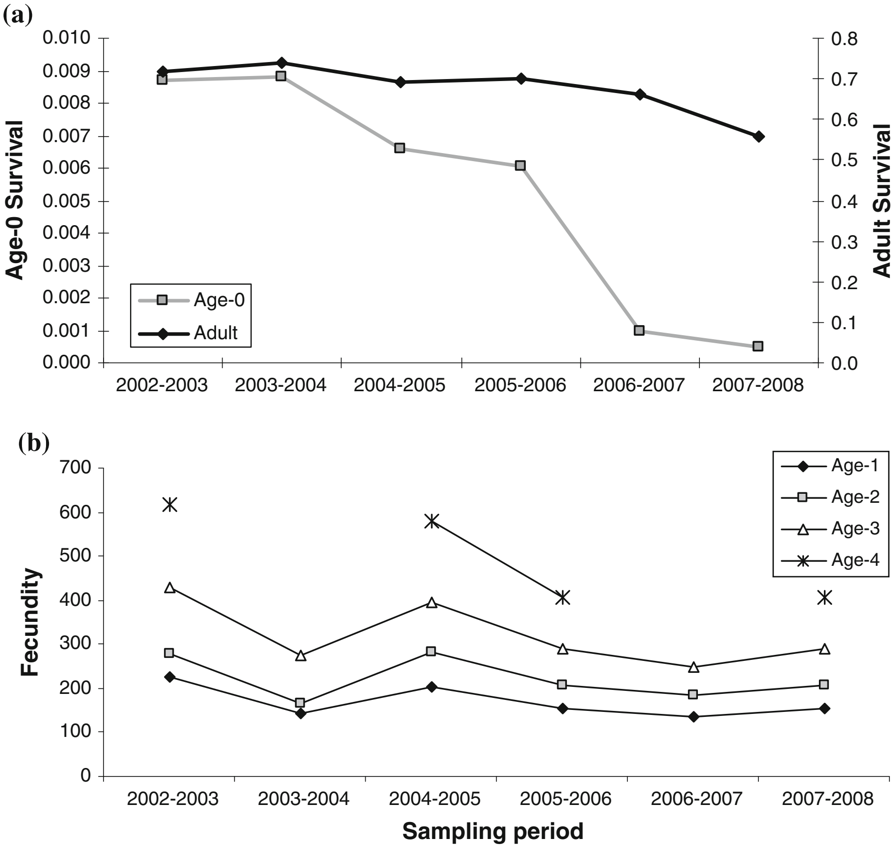

Fig. 3 Trends in apparent survival of age-0 and adult (**a**) and age-specific fecundity (**b**) for the study period 2002–2008. No age-4 females were collected in 2003 and 2006

and were exceeded by saturation densities of 11.62 and 34.87 fish/m^2, respectively, in 2006 (Fig. 2).

Arrival and establishment

Deterministic backcalculation of time of arrival and establishment indicated that round goby arrived at Hamilton Harbour in 1994–1995, 7–8 years prior to the beginning of the study. Establishment densities were apparently reached 3–4 years prior to the study (i.e., by 1998–1999). This produced an elapsed time of 3–4 years between arrival and establishment (Table 3). The deterministic backcalculations concur with the years in which round goby were first detected in the Great Lakes (1990; Jude et al. 1992) and in Hamilton Harbour (1999; Balshine et al. 2005). Our backcalculations indicate that round goby may have been present in the harbour up to 5 years before their detection. Low densities during the arrival phase most likely diminished the probabilities of detection.

Propagule pressure

Relative propagule pressure (Φ') averaged 0.16 and ranged from 0.04 to 0.22, representing between 7 and 30% of the value of apparent survival estimated from catch curve analyses in Hamilton Harbour. The probability of establishment increased convexly with absolute propagule pressure (Fig. 4). The probability of establishment for adult round goby was significant (>0.05) for an absolute propagule pressure of 0.02–0.03 fish/m^2/y. A 0.99 probability of establishment was reached at a propagule pressure of 2–3 adult fish/m^2/y (Fig. 4a).

In terms of juvenile (age-0) fish, the probability of establishment was significant (>0.05) for absolute

Table 2 Akaike information criterion (AIC) as a tool for model selection

Model	Density	Parameter estimates							
		r	K	θ	Vr	P	LLmax	AICc	AIC weight
Ricker	Low	0.782	7.4	–	0.10002	3	−1.606	21.212	0.5
	High	0.782	22.3	–	0.10002	3	−1.606	21.212	0.5
Theta logistic	Low	0.922	7.3	0.81	0.0998	4	−1.6	51.2	0
	High	0.922	21.9	0.81	0.0998	4	−1.6	51.2	0
Allee effect	Low	0.687	0.09	−0.21	0.09985	4	−1.601	51.202	0
	High	0.687	0.03	−0.63	0.09985	4	−1.601	51.202	0

Table includes data for population models using low and high densities resulting from lower and upper bounds in home range (see "Methods" for details)

r intrinsic rate of increase; *K* carrying capacity; θ theta parameter; *Vr* residual variance; *p* number of parameters; *LL*max maximum log likelihood

Table 3 Estimated time of arrival and establishment of round goby in Hamilton Harbour

	Home range	
	Low (2.65 m^2)	High (7.35 m^2)
Maximum estimated density (fish/m^2)	34.87	11.62
Minimum estimated density (fish/m^2)	6.71	2.24
Arrival (years prior to study)	8.22	6.62
Establishment (years prior to study)	3.74	3.44
Elapsed time between arrival and establishment (y)	4.48	3.18
Elapsed time between arrival and saturation (y)	12.22	10.62

Results are presented for density estimates derived from the low and high values of home range determined for round goby, which represent the range in home range reported by Ray and Corkum (2001)

propagule pressure ranging 1–32 juvenile fish/m^2/y (Fig. 4b). The variation in home range had a small influence on establishment probabilities relative to the influence of temporal variation in age-0 survival. Similarly, the probability of establishment reached a value of 0.99 at a propagule pressure of 118–2896 juvenile fish/m^2/y.

Elasticities of population parameters

Mean elasticity for natural adult survival (P_S) had a value of 0.53 whereas an elasticity value of 0.16 was computed for relative propagule pressure (Φ'). The mean elasticities of both fecundity and age-0 survival were identical (0.31), as expected in age-structured models with maturation after the first year of life (Caswell 2001). Although in general the elasticity pattern in Hamilton Harbour suggested a greater sensitivity of population growth rates to changes in adult survival, a wide 95% confidence bar for fecundity indicated that under particular circumstances population responses to changes in this vital rate could be similar to those produced by fluctuations in adult survival (Fig. 5).

Perturbation analysis of elasticities indicated that a 20% reduction in individual demographic rates would, on average, reduce the population growth rate by 6.2% if fecundity rates or age-0 survival were reduced, 10.6% if adult survival were reduced, or 3.2% if propagule pressure were reduced. Based on an average population growth rate of 21% increase during the study period, 20% reductions in any individual vital rate would not significantly slow population growth during the establishment and spread phases. More specifically, annual population growth could still be 8 to 17% after reducing individual vital rates by 20%. Halting population growth and spread would have required a proactive, integrated pest management approach simultaneously reducing several vital rates. Our elasticity analysis indicated that for a scenario characterized by reductions in all demographic rates (i.e., vital rates and relative propagule pressure), reducing these rates by 13.2% could have halted round goby population growth rates. However, completely eliminating

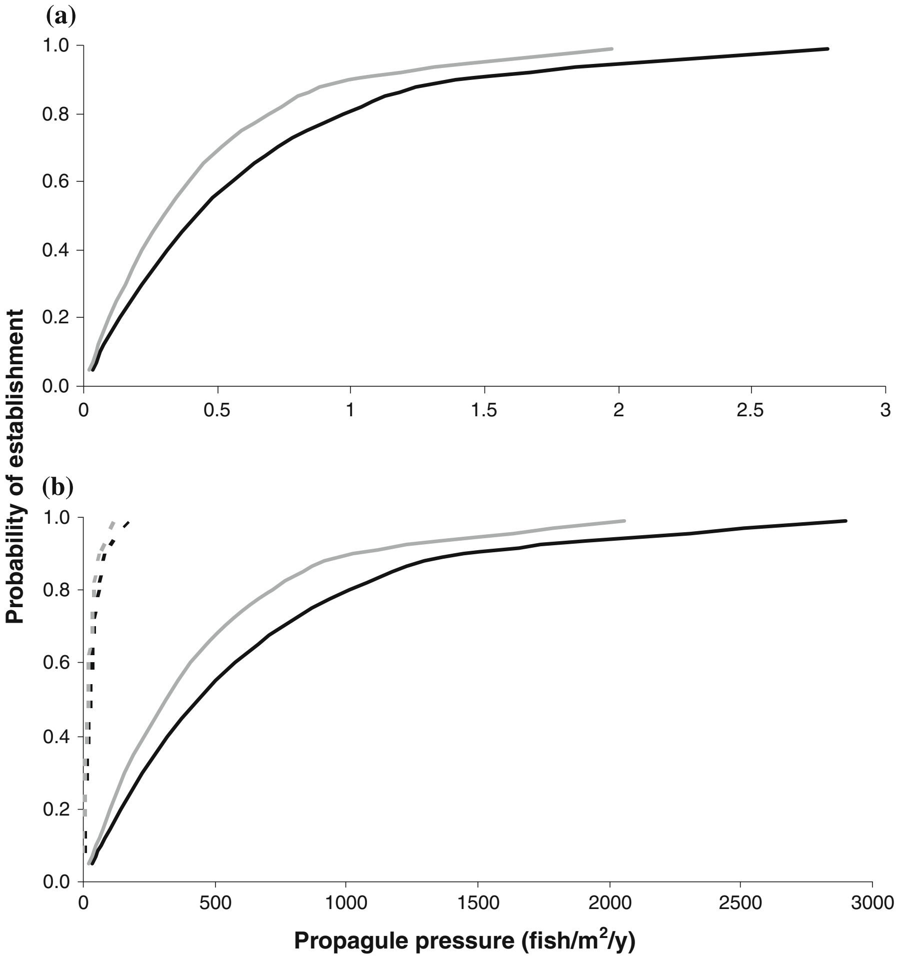

Fig. 4 Probability of establishment as a function of absolute propagule pressure and elapsed time between arrival and establishment determined from low (*grey lines*) and high (*black lines*) home range estimates. **a** Propagule pressure measured as adult fish/m^2/y. **b** Propagule pressure measured as age-0 fish/m^2/y and establishment probability influenced by minimum (*solid lines*) and maximum (*dashed lines*) age-0 survival rates in Hamilton Harbour. Note the change of scale on the *x*-axis between panels a and b

propagule pressure after establishment would not have produced equilibrium, still allowing a 2% annual population growth rate.

Discussion

Five major conclusions emerge from our modelling analyses. First, round goby populations in Hamilton Harbour reached saturation densities approximately one decade after arrival (2006) with densities 55–56% greater than the carrying capacities. The existence of density-dependent processes explained the decline in survival rates of age-0 and adult round goby. After reaching saturation densities, strong inter-specific competition for food and space resources, and perhaps increased predation rates associated with high round goby densities, may have triggered the declines in survival. Second, round goby population dynamics during the first phases of invasion seem to reflect deterministic processes characterized by high propagule pressure and quick transitions from arrival to establishment (3–4 years). Third, significant probabilities of establishment can be reached at low absolute propagule densities of 0.02–0.03 adults/m^2/y. Absolute propagule pressure

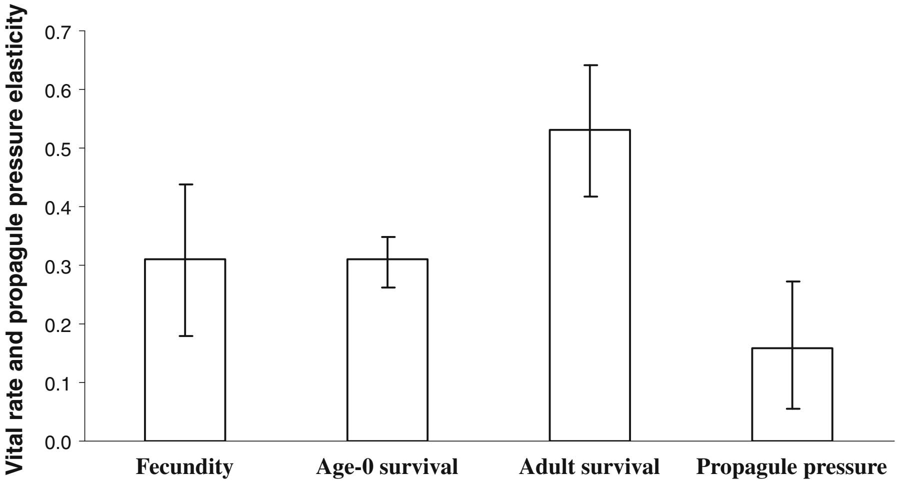

Fig. 5 Vital rate and propagule pressure elasticities for round goby in Hamilton Harbour. Bars indicate 95% confidence intervals

in the form of juvenile introductions would have to be two to three orders of magnitude larger than adult introductions to produce significant probabilities of establishment. In addition, large temporal variability in survival during the first year of life increases uncertainty in the establishment probabilities of juveniles, for which a string of several favourable years would be required to produce a significant probability of establishment. Fourth, the time from establishment to saturation could be twice as long as the time from arrival to establishment. Fifth, an aggressive integrated management approach is necessary to generate long-term population declines or reduce equilibrium densities after establishment. Perturbation analysis showed that simultaneous (i.e., additive) reductions greater than 13% in juvenile survival, adult survival, fecundity, and relative propagule pressure (Φ') would have been necessary to produce continuous population declines. Further, these analyses showed that without a proactive approach sustained population declines could not be achieved after establishment even if propagule pressure were completely removed.

Our study showed that once adult density was greater than one fish/m^2, population density rapidly increased to saturation densities, abruptly declining after reaching peak densities in 2006. Maximum densities estimated by other studies in the Great Lakes (e.g., 50 fish/m^2, Charlebois et al. 1997; 40 fish/m^2, Vanderploeg et al. 2002; 50 fish/m^3, Miner and Farver 2004) were greater than the carrying capacity values (K) generated by the Ricker model but they were similar to saturation densities in our study. Although density values reported by Miner and Farver (2004) are given in cubic meters, the difference between a two-dimensional and a three-dimensional metric of density may be small given the benthic behaviour of round goby, particularly adults and large juveniles, which rarely swim in the water column (Hoover et al. 2003). It is worth noting however, that newly hatched round goby are pelagic (Hensler and Jude 2007).

Our approach to estimating initial establishment conditions via the extrapolation of population dynamics at large population sizes excluded the demographic influences of important small population processes such as Allee effects and demographic stochasticity (Leung et al. 2004). However, an elapsed time of 3–4 years between arrival and establishment suggests that dynamics were largely deterministic and the influence of Allee effects and demographic stochasticity were likely overwhelmed by high propagule pressure and low natural mortality of introduced adults. In other words, the ecological resistance to biological invasion was overwhelmed by high propagule pressure (Von Holle and Simberloff 2005). Jerde and Lewis (2007) also report that with high propagule pressure, invasion dynamics become essentially deterministic, swamping the influences of stochastic processes. Courtship and spawning in round goby is mediated by the release of sex pheromones (Corkum et al. 2006). Such long distance attraction substances would considerably improve the probability of finding a mate even when densities are low.

The demographic contribution of propagule pressure to the invasion process varied depending on the invasion phase. Our results indicate that levels of propagule pressure in the form of adult introductions as low as 0.02–0.03 fish/m^2/y was sufficient to produce significant probabilities of establishment. This finding mirrors that of Drake (2005) for the Eurasian ruffe (*Gymnocephalus cernuus*) invasion of Loch Lomond, Scotland, where the introduction of only a few mature adults produced a considerable risk of invasion. However, once the spread phase is initiated, propagule pressure had little influence and eliminating propagule pressure could not halt population growth and further spread. In contrast, our analysis of propagule pressure in the form of juvenile introductions showed that high concentrations of juveniles would have to be released annually to escape the negative effects of environmental stochasticity on survival rates and to represent a significant risk of invasion.

The short time lag between arrival and establishment suggests some important management implications. First, corrective management strategies or a learning period after detection is not the best approach to controlling round goby invasion. Second, control efforts should focus on preventive measurements. To control future establishment, spread, and ecological and economic impacts of round goby in new locations, strong emphasis should be placed in eliminating or minimizing propagule pressure. This study suggests that determining the relative contributions of different dispersal vectors (e.g., ballast water or live bait) facilitating round goby invasion, and identifying ways to reduce propagule pressure, should be central themes in future investigations. The combined application of gravity models, which allow the estimation of long-distance dispersal between discrete points in heterogeneous landscapes (Thomas and Hugget 1980; Bossenbroek et al. 2001), and our demographic indices of relative contribution to establishment and population growth could reveal critical levels of propagule pressure, generating risk profiles for different locations. Alternatively, the analytical approach introduced in our study for estimating absolute propagule pressure (Eq. 10) can be used to infer these critical levels in different aquatic environments.

We acknowledge that although our deterministic backcalculations of time of arrival and establishment are consistent with the first round goby detections in the Great Lakes and in Hamilton Harbour, our approach has some limitations that need to be addressed. Among these limitations, the estimated area of influence of a single minnow trap played a major role in determining densities. However, our results showed that using either the lower or the upper limit of home range had only a minor to moderate influence on the elapsed times between arrival, establishment, and habitat saturation. Density also had limited influence on the relationship between propagule pressure and probability of establishment. Our analyses were limited by a relatively short time series; additional years of round goby sampling would provide better resolution of the population dynamics. Even with these limitations, our analyses provided important insights into the invasion dynamics of round goby despite some unavoidable uncertainties with respect to density and home range. Circumstantially, the study period included the time period when saturation densities were achieved, producing an unambiguous preference for the Ricker density-dependent model.

Finally, our analyses revealed that proactive and integrated management actions, such as the application of simultaneous control strategies targeting reductions in propagule pressure, survival, and reproductive success, would be needed to halt population growth after a round goby population has established. Even a complete elimination of propagule pressure after the establishment phase of the invasion process would be unlikely to halt population growth or reduce equilibrium densities. These findings suggest that preventative measures would be the most effective management options available to reduce the risk of future invasions. The use of electric barriers (Savino et al. 2001) and the application of piscicides (Dawson et al. 1998) have been explored as methods to prevent the spread of round goby in the Great Lakes. However, given the relative importance of propagule pressure during the establishment phase, introduction vectors such as ballast water (Ricciardi and MacIsaac 2000) should be strongly curtailed and the use of round goby as live bait should be discontinued (UOT 2010).

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References

Andersen MC, Adams H, Hope B, Powel M (2004) Risk assessment of invasive species. Risk Anal 24:787–793

Arim M, Abades SR, Neill PE, Lima M, Marquet PA (2006) Spread dynamics of invasive species. Proc Nat Acad Sci 103:374–378

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

Bolger T, Connolly PL (1989) The selection of suitable indices for the measurement and analysis of fish condition. J Fish Biol 34:171–182

Bossenbroek JM, Nekola JC, Kraft CE (2001) Prediction of long-distance dispersal using gravity models: zebra mussel invasion of inland lakes. Ecol Appl 11:1778–1788

Bunnell DB, Johnson TB, Knight CT (2005) The impact of introduced round gobies (*Neogobius melanostomus*) on phosphorus cycling in central Lake Erie. Can J Fish Aquat Sci 62:15–29

Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer, New York

Caswell H (2001) Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts

Chant V (2002) Reproductive ecology and potential impacts of the invasive round goby (*Neogobius melanostomus*) in Hamilton Harbour. B. Sc. Dissertation. McMaster University, Hamilton, ON, Canada

Chapman DG, Robson DS (1960) The analysis of a catch curve. Biometrics 16:354–368

Charlebois PM, Marsden JE, Goettel RG, Wolfe RK, Jude DJ, Rudnika S (1997) The round goby, *Neogobius melanostomus* (Pallas). A review of European and North American literature. Illinois-Indiana Sea Grant Program and Illinois Natural History Survey, Illinois. INHs Special Publication No. 20

Charnov EL (1993) Life history invariants. Oxford University Press, Oxford

Chotkowski MA, Marsden JE (1999) Round goby and mottled sculpin predation on lake trout eggs and fry: field predictions from laboratory experiments. J Great Lakes Res 25:26–35

Corkum LD, Sapota MR, Skora KE (2004) The round goby, *Neogobius melanostomus*, an invader on both sides of the Atlantic. Biol Invasions 6:173–181

Corkum LD, Arbuckle WJ, Belanger AJ, Gammon DB, Li W, Scott AP, Zielinski B (2006) Evidence of a male pheromone in the round goby (*Neogobius melanostomus*). Biol Invasions 8:105–112

Dawson VK, Boogaard MA, Bills TD (1998) Evaluation of piscicides for controlling range expansion of round goby (*Neogobius melanostomus*) and ruffe (*Gymnocephalus cernuus*). United States Geological Survey, Biological Resources Division

de Kroon H, Plaisier A, Groenendael JV, Caswell H (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427–1431

Drake JM (2004) Allee effects and the risk of biological invasions. Risk Anal 24:795–802

Drake JM (2005) Risk analysis for species introductions: forecasting population growth of Eurasian ruffe (*Gymnocephalus cernuus*). Can J Fish Aquat Sci 62:1053–1059

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

Eshenroder RL, Burnham-Curtis MK (1999) Species succession and sustainability of the Great Lakes fish community. In: Taylor WW, Ferreri CP (eds) Great lakes fisheries policy and management: a binational perspective. Michigan State University Press, East Lansing, pp 145–184

Fretwell SD, Lucas HL (1970) On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor 19:16–36

Haccou P, Iwasa Y (1996) Establishment probability in fluctuating environments: a branching process model. Theor Popul Biol 50:254–280

Hensler SR, Jude DJ (2007) Diel vertical migration of round goby larvae in the Great Lakes. J Great Lakes Res 33:295–302

Hoover JJ, Adams SR, Killgore KJ (2003) Can hydraulic barriers stop the spread of the round goby? ANSRP Technical Notes Collection (TN ANSRP-03-1), U.S. Army Engineer Research and Development Center, Vicksburg, MS. www.wes.army.mil/el/ansrp

Janssen J, Jude DJ (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 27:319–328

Jensen AL (1996) Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Can J Fish Aquat Sci 53:820–822

Jerde CL, Lewis MA (2007) Waiting for invasions: a framework for the arrival of nonindigenous species. Am Nat 170:1–9

Jude DJ (2001) Round and tubenose gobies: 10 years with the latest Great Lakes phantom menace. Dreissena 11(4):1–14

Jude DJ, Reider RH, Smith GR (1992) Establishment of Gobiidae in the Great Lakes Basin. Can J Fish Aquat Sci 49:416–421

Kuhns LA, Berg MB (1999) Benthic invertebrate community responses to round goby (*Neogobius melanostomus*) and zebra mussel (*Dreissena polymorpha*) invasion in southern Lake Michigan. J Great Lakes Res 25:910–917

Leung B, Drake JM, Lodge DM (2004) Predicting invasions: propagule pressure and the gravity of Allee effects. Ecology 85:1651–1660

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends Ecol Evol 20:223–228

MacInnis AJ (1997) Aspects of the life history of the round goby, *Neogobius melanostomus* (Perciformes: Gobiidae) in the Detroit River. M.Sc. Dissertation, University of Windsor, Windsor, Ontario

MacInnis AJ, Corkum LD (2000a) Age and growth of round goby *Neogobius melanostomus* in the Upper Detroit River. Trans Am Fish Soc 129:852–858

MacInnis AJ, Corkum LD (2000b) Fecundity and reproductive season of the round goby *Neogobius melanostomus* in the Upper Detroit River. Trans Am Fish Soc 129:136–144

Mertz G, Myers RA (1996) Influence of fecundity on recruitment variability of marine fish. Can J Fish Aquat Sci 53:1618–1625

Miner JG, Farver JR (2004) Quantifying round goby dispersal mechanisms: impacts on mitigation efforts. Final Report for Lake Erie Protection Fund Grant, Sea Grant 185-02

Morris WF, Doak DF (2002) Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates Inc, Sunderland, MA

Morrison HA, Whittle DM, Haffner GD (2000) The relative importance of species invasions and sediment disturbance in regulating chemical dynamics in western Lake Erie. Ecol Model 125:279–294

Nichols SJ, Kennedy G, Crawford E, Allen J, French J III, Black G, Blouin M, Hickey J, Chernyak S, Haas R, Thomas M (2003) Assessment of Lake Sturgeon (*Acipenser fulvescens*) spawning efforts in the lower St. Clair River, Michigan. J Great Lakes Res 29:383–391

Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs of nonindigenous species in the Unite States. Bioscience 50:53–65

Ray WR, Corkum LD (2001) Habitat and site affinity of round goby. J Great Lakes Res 27:329–334

Ricciardi A, MacIsaac HJ (2000) Recent mass invasion of the North American Great Lakes by Ponto Caspian species. Trends Ecol Evol 15(2):62–65

Roman J, Darling JA (2007) Paradox lost: genetic diversity and the success of aquatic invasions. Trends Ecol Evol 22:454–464

Roy R, Legendre P, Knowles R, Charlton MN (1994) Denitrification and methane production in sediment of Hamilton Harbour (Canada). Microb Ecol 27:123–141

Savino JF, Jude DJ, Kostich MJ (2001) Use of electrical barriers to deter movement of round goby. Am Fish Soc Symp 26:171–182

Shigesada N, Kawasaki K (1997) Biological invasions: theory and practice. Oxford University Press, Oxford

Simberloff D (2003) How much information on population biology is needed to manage introduced species? Conserv Biol 17:83–92

Stepien CA, Tumeo MA (2006) Invasion genetics of Ponto-Caspian gobies in the Great Lakes: a ‘cryptic’ species, absence of founder effects, and comparative risk analysis. Biol Invasions 8:61–78

Taylor CM, Norris R (2007) Predicting conditions for migration: effects of density dependence and habitat quality. Biol Lett 3:280–283

Thomas RW, Hugget RJ (1980) Modeling in geography. Barnes and Noble Books, Totowa, New Jersey

UOT (2010) Alarming invasion of round goby into Great Lakes tributaries: impact on endangered fishes. University of Toronto, ScienceDaily 7 September 2009. 24 April 2010 <http://www.sciencedaily.com—/releases/2009/08/090811143727.htm

Vanderploeg HA, Nalepa TF, Jude DJ, Mills EL, Holeck KT, Liebig JR, Grigorovich IA, Ojaveer H (2002) Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Can J Fish Aquati Sci 59:1209–1228

Vatland S, Budy P (2007) Predicting the invasion success of an introduced omnivore in a large, heterogeneous reservoir. Can J Fish Aquat Sci 64:1329–1345

Vermeij GJ (1996) An agenda for invasion biology. Biol Conserv 78:3–9

Von Holle B, Simberloff D (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology 86:3212–3218

Williamson MH, Fitter A (1996) The varying success of invaders. Ecology 77:1661–1666

Wolfe RK, Marsden JE (1998) Tagging methods for the round goby (*Neogobius melanostomus*). J Great Lakes Res 24:731–735

Young JAM, Marentette JR, Gross C, McDonald JI, Verma A, Marsh-Rollo SE, McDonald PDM, Earn DJD, Balshine S (2010) Demography and substrate affinity of the round goby (*Neogobius melanostomus*) in Hamilton Harbour. J Great Lakes Res 36:115–122