Quantifying invasion pathways: fish introductions from the aquarium trade

Erin Gertzen, Oriana Familiar, and Brian Leung

Abstract: Introduced species can cause economic and environmental harm. Researchers have developed risk assessment models for exotic species based on biological characteristics. However, few have quantified propagule pressure despite its relevance for establishment. Both are needed to identify invasion risk. We focused on fishes introduced via the aquarium trade, because this pathway transports thousands of species throughout the world. We developed an approach to estimate propagule pressure by (*i*) identifying and quantifying aquarium fishes sold, (*ii*) determining fish owner behavior and disposal practices, and (*iii*) quantifying uncertainty. We used the St. Lawrence Seaway as our model system. Only one non-established species (*Tanichthys albonubes*, 117 per year) had the propagule pressure and environmental tolerances to likely invade this region. However, overall, more than 10 000 fishes were released annually from Montréal (Quebec, Canada) alone. The implication of the observed propagule pressures is that the aquarium trade should be a very important pathway in other warmer habitats and should be explicitly assessed. Knowledge of the numbers introduced of each species will be useful for population models to estimate the probability of establishment.

Résumé : Les espèces introduites peuvent causer des torts économiques et environnementaux. Des chercheurs ont mis au point des modèles d'évaluation des risques associés aux espèces exotiques basés sur les caractéristiques biologiques. Cependant, peu ont quantifié la pression des propagules malgré l'importance du phénomène pour l'établissement de l'espèce introduite. Les deux types de données sont nécessaires pour évaluer le risque d'invasion. Nous nous sommes intéressés aux poissons introduits par le commerce de l'aquariophilie, car cette voie entraîne le transport de milliers d'espèces partout dans le monde. Nous avons mis au point une méthodologie pour évaluer la pression des propagules (*i*) en identifiant et quantifiant les poissons d'aquarium vendus, (*ii*) en déterminant le comportement et les pratiques de mise au rebut des propriétaires de poissons et (*iii*) en quantifiant l'incertitude. Nous utilisons la voie maritime du Saint-Laurent comme système modèle. Seule une espèce non établie (*Tanichthys albonubes*, 117 par année) possède la pression des propagules et les tolérances environnementales nécessaires pour vraisemblablement envahir la région. Cependant, en totalité, plus de 10 000 sont libérés chaque année seulement à Montréal (Québec, Canada). Les conséquences découlant des pressions des propagules observées sont que le commerce de l'aquariophilie devrait être une voie très importante dans d'autres habitats plus chauds et devrait être évalué de façon explicite. Une connaissance des nombres de poissons introduits de chaque espèce devrait être très utile pour construire des modèles démographiques pour estimer les probabilités d'établissement.

[Traduit par la Rédaction]

Introduction

In a world increasingly dominated by international trade, many biological organisms have either intentionally or accidentally been spread beyond their natural range. Human activity has facilitated the spread of species and accelerated the rate of introduction of nonindigenous species (NIS) into new environments (Mills et al. 1992; Hochberg and Gotelli 2005). The consequences are serious and include economic damage (Levine and D'Antonio 2003; Pimentel 2005) as well as decline in ecosystem function and decrease in global biodiversity (Miller 1989; Pimentel 2005). In the United States, costs associated with NIS are estimated at 137 billion dollars (US) annually (Pimentel et al. 2000). Now NIS are considered to be one of the most important factors in the loss of global biodiversity, second only to habitat loss (Wilcove et al. 1998; Levine and D'Antonio 2003).

Quantifying the risk posed by NIS is of utmost importance for their proper management (Ricciardi and Rasmussen 1998). Overall, rigorous risk assessment requires the integration of knowledge from different steps in the invasion process: transport, introduction, establishment, spread, and impact (Kolar and Lodge 2001). Introduction is a necessary first step in the invasion process, without which establishment, spread, and impact are impossible (Kolar 2004). Propagule pressure, or numbers introduced, is one of the best indicators of invasion success (Williamson 1996), with the likelihood of successful invasion being directly corre-

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lated to the number introduced (Kolar and Lodge 2001). To date, rates of introduction have often been neglected in risk assessment models — previous studies mainly focus on risk assessment based on biological characteristics of species (Mandrak 1989; Kolar 2004; Copp et al. 2005) and previous invasion history (Ricciardi and Rasmussen 1998). Very few studies have attempted to quantify the numbers of each species being introduced (but see Rixon et al. 2005). Ideally, we should quantify propagule pressures and integrate this with information on biological characteristics that will affect the ability of a species to establish (e.g., broad environmental tolerances) and spread (e.g., rapid growth rates) to cause harm.

Determining high risk species and pathways will allow us to focus limited resources where they are most needed and will be most effective. Prevention is considered to be one of the most effective ways of managing NIS (Lodge et al. 2006). For prevention to be successful, we need to know which species and how many individuals are being introduced by different pathways (Ricciardi and Rasmussen 1998; Kolar and Lodge 2002; Kolar 2004). Failure to identify important pathways may negate other investments in prevention efforts. For instance, vectors of introduction such as ballast water (Ricciardi and Rasmussen 1998; Rixon et al. 2005) have been the focus of a great deal of research. This research has lead to current regulation requiring mid-oceanic exchange of ballast water as a management tool to control the influx of ballast NIS (Ricciardi and MacIsaac 2000). However, other introductory pathways, including aquarium release, escape from aquaculture facilities, the live food market, intentional introduction, and live bait release (Mills et al. 1992), need to also be considered. Intentional release from the aquarium trade is an important pathway for the spread of NIS (McDowall 2004), with species from the aquarium and ornamental trade being responsible for one-third of the world's aquatic NIS (Padilla and Williams 2004). Moreover, there is little regulation of the aquarium trade in terms of restricting potentially nuisance NIS (Ricciardi and Rasmussen 1998; McDowall 2004; Rixon et al. 2005).

Despite its clear relevance, quantitative estimates of propagule pressures via different pathways are typically lacking. The major difficulty is that it is likely impossible to directly measure propagule pressure. However, it should be feasible to quantify the steps leading to an introduction. For instance, for the aquarium trade, the steps are as follows: species need to be for sale in stores (Rixon et al. 2005), customers need to purchase the fishes and dispose live fishes, and the disposal pathway needs to be in connected waterways to water bodies of interest (e.g., the Great Lakes). The number of fishes released may be non-negligible, as some individuals consider live release to be the most humane method of disposal (Courtenay 1999; Severinghaus and Chi 1999). Of course, the actual propagule pressure will depend upon how many of each fish species is bought and what proportion of those fishes are released. Some fishes are more likely to be disposed of than others. For instance, becoming bored with a fish, the ability of a fish to grow to a large size, and aggressive behavior have been identified as factors that increase the probability of disposal (Duggan et al. 2006).

In our study, we focused on four aspects related to the aquarium trade: (*i*) identifying and quantifying the fish species sold to customers in the aquarium trade, (*ii*) determining fish owner behavior, (*iii*) quantifying the uncertainty in our empirical estimates, and (*iv*) integrating the empirical data and uncertainty into a model to quantify propagules pressure. We used Montréal and the St. Lawrence Seaway as our model system.

Materials and methods

Study system

We focused on Montréal and the St. Lawrence Seaway, given its importance as a major entry point of NIS into the Great Lakes through a series of built shipping canals and locks (Environment Canada 1996) and potentially into other areas of North America (Northeast–Midwest Institute and National Oceanic and Atmospheric Administration 2001). The Great Lakes themselves experience damages estimated at 5.7 billion dollars (US) annually in control measures and losses associated with depletions of commercial and sport fish stocks owing to nuisance NIS (Pimentel 2005). Introductions via the aquarium pathway may be very important for this region, with over 5000 fish species, most of which are non-native to the Great Lakes basin, traded internationally in aquarium trade, and brought into the region (Welcomme 1984; Chapman et al. 1997; McDowall 2004). We focused on the island of Montréal, Quebec, Canada (45°28′N, 73°45′W) — the major metropolitan center adjacent to the St. Lawrence Seaway. Quantification of propagule pressure from Montréal will likely provide the most important source of propagules from the aquarium trade to the St. Lawrence Seaway.

Data collection

We used a combination of social surveys and aquarium fish surveys to estimate propagule pressure.

Store inventories

In this step of our study, we extended work by Rixon et al. (2005), who use number of stores carrying a given fish species as a surrogate for propagule pressure. Here, we quantified the number of individuals of each species sold. We visited >75% of aquarium and pet stores (18 stores) carrying fishes in Montréal from February to May 2006. The remaining stores were either unwilling to participate or unable to provide us with the required information. The fish species present in these remaining stores were verified to ensure that no species would be missing from our comprehensive list of species present on the island of Montréal. The information collected in this section was used to estimate relative propagule pressures of fish species rather than absolute numbers, which was estimated using customer surveys described below. We are aware that intra-annual variability in sales exists (Chapman et al. 1997); however, currently this is the best data we have available. The 4-month sample period of our surveys will take into account some of this variability, and it improves on previous work that looked at a 1-day occurrence of species sold in aquarium and pet stores (Rixon et al. 2005).

In each participating store, we determined the number of fishes sold over a month-long period, given by number sold in 30 days for species x = first count + sum of deliveries – final count. Because most stores simply record dollar value amounts and not species or quantities sold, we recorded standing stock populations in both the front and back rooms of the stores for every freshwater fish species at the beginning and end of the inventory period. To take into account new fishes that were delivered to the stores over the study period, we obtained copies of all relevant deliveries from store owners. Mortality was assumed to be of equal proportions between species and was not included in our analysis of relative species numbers. Several species were grouped together into genera (e.g., *Corydoras* spp.) or families (e.g., certain members of the Cichlidae family). This was necessary because we were limited owing to the fact that many of the deliveries simply stated "assorted corydoras," or "African cichlids."

Store owner surveys

We surveyed 20 aquarium and pet store owners and asked them to explain their policy on dealing with unsold fishes. The store owners surveyed included all stores where store inventories were conducted and two others. The aim of this component of the survey was to assess the likelihood of live release from aquarium and pet stores and to verify whether or not release directly from stores should be considered as a potential pathway contributing to the overall propagule pressure of aquarium fishes. We found that all fishes were either kept and put on sale until sold or returned to the distributor. Because none released fishes into the wild, store owners were not considered further.

Customer surveys

We conducted interviews with 86 customers outside 11 aquarium and pet stores in Montréal during October and November 2005. The purpose of the survey was to evaluate the history of behavior fish owners have had with their aquarium fishes. The survey instrument provided (*i*) the number of fishes owned in their lifetime and the time period over which they owned the fishes; (*ii*) the number of people who have released at least one fish in their lifetime; (*iii*) the proportion of fishes that had been released to the wild, returned to the store, given away, flushed down the toilet, or died in the aquarium; and (*iv*) the proportion of fishes released for a specific reason (aggressive behavior, large size, fish illness, rapid reproduction, becoming bored or annoyed with the fishes, not having time, or moving away). The survey was conducted in person and anonymously in efforts to ensure truthful and complete responses. From this data, we inferred the following: (*i*) the average number of fishes kept over a year (N), (*ii*) the probability that a person was a releaser ($P(I)$), (*iii*) the probability that a fish would be released given that the person owning it was a releaser ($P(R|I)$), and (*iv*) the relative probability that a fish was released, based on reasons for release (r_x). These variables were used in our model to generate propagule pressure.

Model for total propagule pressure

The total propagule pressure for all freshwater aquarium fishes from the aquarium trade is described by

$$\text{(1)} \qquad \text{overall propagule pressure} = M \cdot P(I) \cdot N \cdot P(R|I)$$

where M is the number of households that own fishes, $P(I)$ is the probability that a person is a releaser, N is the average number of fishes owned, and $P(R|I)$ is the probability that a fish is released given it is owned by a releaser.

The value for M was derived from existing literature (Chapman et al. 1997), whereas the values for $P(I)$, N, and $P(R|I)$ were calculated using data collected from customer surveys. We used a Bayesian statistical approach to assemble the components of the model for propagule pressure, taking into account uncertainty (i.e., extrapolating to the island of Montréal from our sample of 86 fish owners). A Bayesian approach was used to take into account the uncertainty of our data, given our sample size. Previous studies have not considered customer behavior as a factor affecting release, and we believe this is an important first attempt at doing so. Given we had no prior beliefs, we used an improper uniform prior such that the results obtained fully reflected our data. For example, if 7 out of 100 people sampled release fish, the most likely proportion of people releasing fishes in the population would be 0.07, given the data. However, there is a probability that the true population value was 0.06, and we observed 7 out of 100 people releasing fishes. We considered the probability of each true population value in our analysis, given the data observed. Probability distributions were generated for the components $P(I)$, N, and $P(R|I)$ (M was a constant). We multiplied the three distributions together — we considered all combinations of values for these three components and multiplied the probability that each value was correct, given the data, to create a joint probability distribution of our relative beliefs in numbers released. The joint probability distribution was our estimate, including uncertainty, of total propagule pressure of all fishes originating from aquarium and pet stores.

$P(I)$ is a binary variable; therefore, we used a binomial distribution. For the purpose of this study, a releaser is defined as a person who has released at least one fish into the wild over the time period in which he or she had kept aquarium fishes when interviewed. For the application of the model to the island of Montréal, we defined "wild" as the St. Lawrence Seaway. This assumption is justified because on the island of Montréal, the most likely water body in which a fish could be released in is the St. Lawrence Seaway. We recognize that it is possible that some fishes were released elsewhere on the island, such as in ponds; however, this is the best estimate we have.

$M{\cdot}P(I)$ gives the total number of releasers. To determine the number of fishes owned by releasers, we multiplied $M{\cdot}P(I)$ by N, which came from our survey data. We asked customers how many fishes they owned in their lifetime and the time period over which they owned these fishes. The nature of our surveys questioned people over their entire fish-owning history; thus, we took N as a yearly average of fish owned over the time people owned fish. We considered N as a yearly average over the fish-owning history of respondents and applied this average to Montréal's present population. Because of highly skewed data (most people owned few fishes and few people owned many fishes) ranging from 0 to 800, a lognormal distribution was used to describe the distribution of numbers of fishes owned.

With the use of data for $P(R|I)$, the equation was further broken down by the proportion of fishes released out of total number of fishes owned by releasers. $P(R|I)$ represents the proportion of fishes released given they are owned by a releaser. Along with asking the method in which fishes were disposed of (released to wild, put in the garbage, given away, etc.), we asked fish owners the number of fishes that they disposed of over their fish-owning life and converted this into a yearly proportion. Possible values for $P(R|I)$ ranged from 0 to 1; therefore, we used the beta distribution to describe the distribution of $P(R|I)$ across releasers (i.e., we did not expect all individuals to release the same proportion of their fish). The multiplication of all these elements, $M{\cdot}P(I){\cdot}N{\cdot}P(R|I)$, generated an estimate of total propagule pressure for all freshwater aquarium fishes from the island of Montréal.

Model for species-specific propagule pressure

The basic model for propagule pressure (eq. 1) was further broken down to estimate the propagule pressure of individual species of fishes by taking into account specific characteristics and population size:

(2) species-specific propagule pressure

$$= M \cdot P(I) \cdot N \cdot P(R|I) \cdot r_x \cdot c \cdot s_x$$

where r_x is the relative rate of release, depending on specific characteristics, c is a correction factor, and s_x is the relative proportion of fishes belonging to a certain species. We estimated s_x using the total sold for a given species, summed across all stores during a standardized time period of 30 days.

Based on customer survey results, probability of release was adjusted for characteristics that affect this probability of release. Two characteristics, large size (defined as able to grow to 20 cm and over) and aggressive behavior, were common responses as reasons for fish release. Aggressiveness and maximum size of fishes were determined using www.fishbase.org/home.htm (Froese and Pauly 2005). All fish species were divided into four exhaustive and mutually exclusive categories, based on the two characteristics.

The variable r_x describes the relative increase in probability of release due to unwanted characteristics compared with reasons independent of fish characteristics (base rate = 1). We can calculate r, r_{as}, r_s, and r_a for different characteristics, based on T, T_{as}, T_s, and T_a, which are the proportion of fishes released for base reasons, aggressiveness or size or base reasons, size or base reasons, and aggressiveness or base reasons, respectively. The equations used to calculate the relative increase in rates of release due to undesired characteristics are as follows:

(3) base rate of release (nonaggressive and non-large species) : $r = T/T$

(4) relative increase in rate of release for species that can be both aggressive and large : $r_{as} = (T + T_a + T_s)/T$

(5) relative increase in rate of release for species than can be large but not aggressive : $r_s = (T + T_s)/T$

(6) relative increase in rate of release for species that can be aggressive but not large : $r_a = (T + T_a)/T$

These only provide relative rates of release. To determine the actual rates of release, a correction factor (c) was required such that summing species-specific propagule pressures (eq. 2) across all fish species would be equal to the total number of fishes released (eq. 1). To calculate c, we had to consider release rates based on species-specific characteristics (r_x) as well as total relative sales (F, F_{as}, F_s, F_a) of each category of fishes (none, both aggressive and large, large, and aggressive, respectively):

$$(7)\quad c = \frac{1}{(F \cdot r) + (F_{as} \cdot r_{as}) + (F_s \cdot r_s) + (F_a \cdot r_a)}$$

Once $r_x{\cdot}c$ for the four categories was determined, the adjusted relative rates of release were multiplied by each s_x. According to its characteristics and relative population size, the propagule pressure of each fish species was calculated using the model with the appropriate r_x and s_x values for that species (eq. 2).

Results

Store inventories

Store inventories revealed that 252 species and a total of 46 722 fishes were sold over a 30-day period in the 18 stores we sampled. The top five species sold (Table 1) were goldfish (*Carassius auratus*), guppies (*Poecilia reticulata*), assorted platyfishes (*Xiphophorus* spp.), neon tetras (*Paracheirodon innesi*), and mollies (*Poecilia sphenops*). Goldfish, neon tetras, and Siamese fighting fish (*Betta splendens*) were the only species present in 100% of stores (frequencies of occurrence); however, sales of goldfish (23.2% of total sales) were much higher than sales of neon tetras (8.5%) and Siamese fighting fish (2.4%).

Customer surveys

Customer surveys revealed that 6 out of 86 respondents (6.98%; $P(I)$) reported having released at least one fish (Table 2). The average number of fishes owned per year was five, based on the lognormal distribution. The average percentage of fishes released, derived from customer survey data on numbers released given numbers owned by a releaser, was 5.1% ($P(R|I)$).

The reasons for which fishes were unwanted were used to determine the differential rates of release for the four mutually exclusive categories of fish (large size, aggressive, both large size and aggressive, and none). Customer surveys

Table 1. Relative numbers sold, propagule pressure (with and without characteristics of large size and aggressive behavior taken into account), temperature tolerances, and behaviors for the 30 most popular freshwater aquarium fish species.

		Population		Propagule pressure				
Common name	Scientific name	Relative size	With character adjustment	Based on relative population size	With character adjustment	Lower temperature tolerance (°C)*	Aggressive*	Large size*
Goldfish	*Carassius auratus*	0.2317	0.2537	2340.5	2562.8	0		X
Guppy	*Poecilia reticulata*	0.0849	0.0799	857.3	807.5	18		
Assorted platyfishes	*Xiphophorus* spp.†	0.0499	0.0511	519.7	489.5	18	X	
Neon tetra	*Paracheirodon innesi*	0.0514	0.0485	503.7	515.9	20	X	
Molly	*Poecilia sphenops*	0.0353	0.0332	356.2	335.5	18		X
Zebra danio	*Danio rario*	0.0295	0.0278	298.3	281	18		X
Assorted swordtails	*Xiphophorus* spp.†	0.0285	0.0292	287.7	294.7	22		
Siamese fighting fish	*Betta splendens*	0.0239	0.0245	241.6	247.5	24	X	
Tiger barb	*Puntius tetrazona*	0.0227	0.0213	228.9	215.6	20	X	
Assorted plecostomus	*Pterygoplichthys* spp.	0.0127	0.0139	228.8	209.9	18	X	
Coolie loach	*Pangio kuhlii*	0.0184	0.0173	185.4	174.6	24		
Cardinal tetra	*Paracheirodon axelrodi*	0.018	0.017	181.9	171.3	23		X
Corydoras catfish	*Corydoras* spp.	0.0177	0.0167	179.3	168.8	18	X	
Angelfish	*Pterophyllum scalare*	0.0177	0.0167	178.9	168.5	15.5		
Black neon tetra	*Hyphessobrycon herbertaxelrodi*	0.0151	0.0142	152.3	143.5	23		
Harlequin rasbora	*Trigonostigma heteromorpha*	0.0138	0.013	128.1	140.2	22	X	X
White cloud mountain minnow	*Tanichthys albonubes*	0.0123	0.0115	123.8	116.7	5		
Dwarf gourami	*Colisa lalia*	0.0102	0.0096	103.1	97.1	22		
Chinese algae-eater	*Gyrinocheilus aymonieri*	0.0087	0.0095	100.2	94.4	22		
Danio burmese glowlight	*Danio choprai*	0.0099	0.0093	97.8	92.1	20		
Norman's lampeye	*Aplocheilichthys normani*	0.0097	0.0091	87.7	82.6	22		X
Clown loach	*Botia macracanthus*	0.0075	0.0089	87.5	95.8	24	X	
Lemon tetra	*Hyphessobrycon pulchripinnis*	0.0087	0.0082	80.4	75.7	22.5		
Black phantom tetra	*Megalamphodus megalopterus*	0.008	0.0075	77.8	73.3	22		X
Bloodfin tetra	*Aphyocharax anisitsi*	0.0077	0.0073	76.2	89.7	18		
Glowlight tetra	*Hemigrammus erythrozonus*	0.0072	0.0068	72.9	68.7	24		
Blackline penguinfish	*Thayeria boehlkei*	0.0067	0.0064	68.2	64.2	22		
Jewel tetra	*Hyphessobrycon eques*	0.0064	0.0066	66.3	64.7	22	X	X
Golden otocinclus	*Otocinclus affinis*	0.0064	0.006	64.7	61	20		
Firehead tetra	*Hemigrammus bleheri*	0.0063	0.0059	63.6	59.9	23		

*Based on Froese and Pauly (2005).

†*Xiphophorus* spp. is used for platyfishes and swordtails to describe two groups of visibly distinguishable assortments of species.

Table 2. Responses to customer survey questions (n = 86).

Question	Percentage of respondents
Percentage releasing fish ($P(I)$)	6.98
Percentage released by releasers ($P(R\|I)$)	5.10
Reason for disposal	
Aggressive behavior	7.04
Large size	13.03
Frequent illness	15.14
Rapid reproduction	1.06
Other	63.73

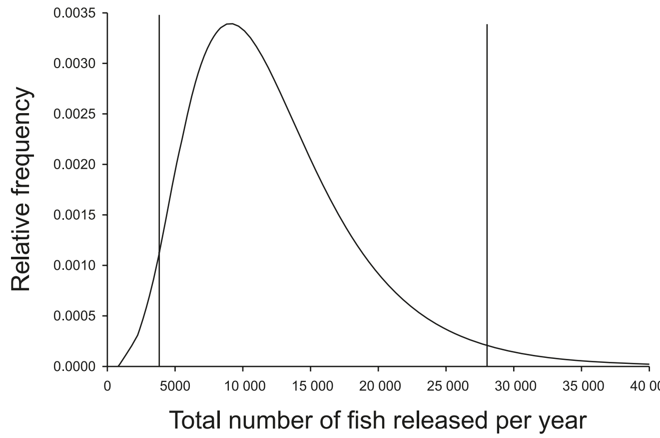
showed that 15% of unwanted fishes were unwanted because of fish illness, 13% because of large size, 7.0% because of aggressive behavior, and 1.0% because of rapid reproduction. The rest of the fishes were unwanted for reasons other than the characteristics of the fishes, including becoming bored with fishes or moving. Other reasons for release (e.g., fish illness and rapid reproduction) were considered as the base rate of release (r). Fish illness was incorporated into the base rate because illness is often dependent on the environment in which the fish lives (size of tank, cleanliness of water, density of fishes, etc.), more so than the characteristics of the fish species itself, and these fishes would likely die in the new environment if already unhealthy. Reproduction was likewise not included because they accounted for only 1% of release and because of the lack of data available on reproductive rates for the majority of aquarium fish species. The base rate accounted for 80% of total unwanted fishes. Fishes that have the ability to grow to a large size and aggressive behavior were assigned greater probabilities of release, based on their importance revealed in survey data. Using eqs. 3, 4, 5, and 6, $r = 1$, $r_{as} = 1.25$, $r_s = 1.1625$, and $r_a = 1.088$.

Model for total propagule pressure

The framework developed here was used to find the propagule pressure of all fishes being released from the island of Montréal (eq. 1). The distributions were multiplied together, as well as by M applied to the present population of Montréal; the population of households on the island of Montréal (805 820; Statistics Canada 2001) was multiplied by 10.6% (percentage of North American households that own fishes; Chapman et al. 1997) and 96% (percentage of aquarium fishes of freshwater origin; Chapman et al. 1997) to give the total number of households that keep freshwater aquarium fishes — 82 002 households. These published figures were used to estimate M because we believe their universality provides better data of the number of households that own freshwater aquarium fishes than a simple snapshot of the population of freshwater aquarium fish owners in Montréal in one time period.

Our study was broken into two sections and data was obtained from each section: total number of fish owned (N) from customer surveys and proportion of fish species sold (s_x) from store inventories. We used customer survey data to estimate absolute numbers of fish owned, because we were more confident in these estimates than in estimates of total number of fishes sold in stores because of the seasonality issue.

Fig. 1. Relative probability distribution of propagule pressure of all fish from the island of Montréal. The mode of the distribution is 10 103.6, with a 95% certainty that more than 4600 fish are released per year.



We multiplied together the three posterior distributions, all from customer survey data (N, $P(R|I)$, $P(I)$), to give us total propagule pressure and the uncertainty around our data. The most likely propagule pressure was 10 103.6 fishes released per year. Based on the uncertainty associated with the data, there is a 95% chance that the true propagule pressure was at least as great as 3800 fish per year and lower than 27 900 fish per year (Fig. 1).

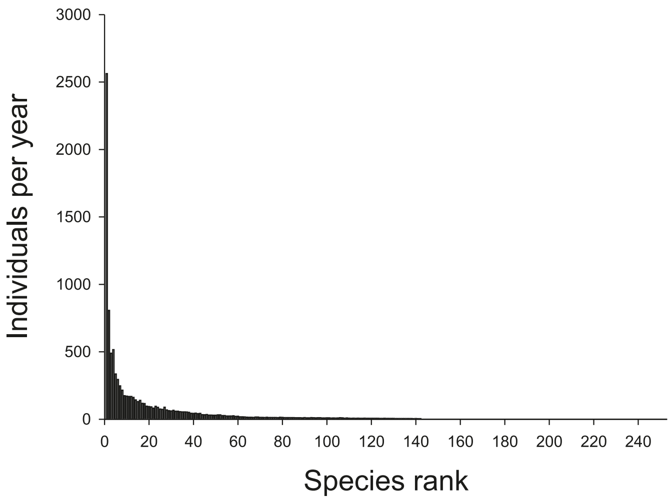
Propagule pressure by species

To generate propagule pressure by species, the outcome of the basic model was multiplied by $r_x \cdot c \cdot s_x$. Of all fishes sold, the proportion that were aggressive was 0.1267 (F_a), whereas 0.2970 could grow to be too large (F_s), 0.0092 were both aggressive and too large (F_{as}), and 0.5670 were neither aggressive nor grew to be too large (F). These values of F_a, F_s, F_{as}, and F were used in the equation to determine c, the scaling factor for relative rates of release (0.9419). The values for s_x, the relative population of all species, came directly from store inventory data. For example, $s_{goldfish}$ was 0.23 and s_{guppy} was 0.085 (Table 1). Using the model, we found that goldfish, a species that can grow to be large, has a propagule pressure of 2563 when we take into account characteristics and 2340 when we do not take into account characteristics. A histogram of release rates for all 252 aquarium fish species was created (Fig. 2). Rare and unpopular species have negligible propagule pressure (<1). This shows us that most fish species have low propagule pressure, whereas a few popular species have high propagule pressure.

Discussion

The knowledge acquired from risk assessment and propagule pressure models help us better understand and manage the introduction, establishment, and spread of potentially nuisance NIS. Understanding the importance of different pathways of introduction helps us to focus limited resources. Popular aquarium and ornamental trade species (e.g., goldfish and koi carp (i.e., domesticated varieties of the common carp, *Cyprinus carpio*)) have already established populations in the Great Lakes – St. Lawrence Seaway region (Mills et

Fig. 2. Rank – propagule pressure curve for all fish species sold in Montréal aquarium and pet stores over the study period. The histogram shows that most species have low propagule pressure and few species have large propagule pressure.



al. 1992), suggesting that further investigation into the importance of the aquarium trade in importing potentially nuisance NIS may be merited.

The implications of propagule pressure are great. Propagule pressure is highly related to establishment success (Kolar and Lodge 2001). Organisms must enter a new environment in numbers great enough for reproduction and spread to occur. Moyle and Marchetti (2006) suggest that a propagule pressure of greater than 100 individuals for Californian lakes and streams is adequate for establishment. In our study, we observed that 18 species had propagule pressures exceeding 100, and 42 species had propagule pressures exceeding 40, but only two of these species (goldfish and koi carp) are known to have established populations in the St. Lawrence Seaway. Nevertheless, the number of colonizers required will depend on other factors affecting establishment. Propagule pressure required for establishment will vary depending on the size of the habitat area, frequency versus dose of introductions, and Allee effects (Leung et al. 2004). For example, for a population to establish, individuals must be able to find mates and reproduce. In a large system such as the St. Lawrence Seaway, it is likely that this would occur less than in smaller systems. Determining the required propagule pressures for individual species would require population dynamics models, which in turn would relate to species characteristics such as reproductive rate and mortality given physical and chemical conditions in the new habitat.

The establishment of most aquarium species in the St. Lawrence Seaway is likely mainly limited by extreme physical conditions, namely cold temperate waters. Most aquarium species are tropical in origin and have poor cold tolerance (see Table 1 for cold tolerance of top 30 species; Mandrak 1989; McDowall 2004; Duggan et al. 2006). Of all species sold, five non-native species (one native species was excluded) can survive at low temperatures (<5.5 °C; temperature requirement for the Great Lakes – St. Lawrence Seaway region, as defined by Rixon et al. 2005), two of which are already established. The other nonestablished, cold-tolerant NIS are the white cloud mountain minnow (*Tanichthys albonubes*), weatherfish (*Misgurnus fossilis*), and hogchoker (*Trinectes maculatus*); however, the weatherfish and hogchoker have very low propagule pressures (6 and 1 individuals per year, respectively). In our data, the white cloud mountain minnow was reported with a propagule pressure in the top 20, at 117 per year, highlighting the potential high risk associated with this species. Thus, based on our findings, we can greatly focus our research and management efforts in the St. Lawrence Seaway. The quantitative estimates of propagule pressure that we provide in this study will be useful for population dynamics models should researchers decide that further research is important. Specifically, while preliminary evidence from other systems suggests that 100 individuals per year should be regarded as high risk, we recommend that for white cloud mountain minnow, a population model explicitly including demographic and environmental stochasticity, Allee effects, mortality rates, and reproductive rates should be built to determine whether 117 fish introductions per year is sufficient for establishment in this system.

More generally, for the St. Lawrence Seaway, researchers and managers can focus their efforts on other pathways. However, the implications of the magnitude of overall propagule pressure observed in this study (over 10 000 individual fish), with 42 species having propagule pressures greater than 40, is that the aquarium trade should be important for other regions with different environmental conditions (i.e., the moderate waters of western Canada or the warm waters of Florida; McDowall 2004; Padilla and Williams 2004) and that propagule pressures should be quantified in other areas. For example, assuming similar numbers and species sold, in a warmer west coast city such as Vancouver (winter water temperature of 8 °C; Fisheries and Oceans Canada 2006), nine species could potentially establish. In a warmer southerly city such as Miami (winter water temperature of Lake Okeechobee = 19.4 °C; International Lake Environment Committee 2001), at least 55 species could potentially establish.

Although we believe that we provide the best current estimates of propagule pressure for aquarium species, the full story remains incomplete. This study focuses on one pathway of introduction into a major system (St. Lawrence – Great Lakes basin). A full analysis of invasion risk for this region would expand to look at all species and all pathways of introduction. Our study identifies a simple method to quantify propagule pressure, which can be applied both to other pathways (i.e., live bait or live food market) in the St. Lawrence Seaway and to the aquarium trade in other regions of the world that may be more susceptible to potentially nuisance NIS from the aquarium trade.

Our work extends previous work by providing quantitative estimates of numbers introduced. Previous studies suggest the importance of popularity, as estimated by frequency of stores selling a species, in determining propagule pressure (Rixon et al. 2005; Duggan et al. 2006). We extended these studies by determining the actual numbers sold and integrating that with other information available to quantify propagule pressure. Previous studies also suggest that large size and aggressive behavior are important factors determining the likelihood of aquarium release (Courtenay

1999; Duggan et al. 2006). We investigated this further and were able to quantify their importance. Although 7% of releases were due to large size and 13% were due to aggressive behavior, these characteristics did not greatly alter species-specific propagule pressure (see Table 1 for propagule pressure before and after release rates were adjusted for these characteristics).

Further, our study focused on the fate of aquarium fishes that are sold in aquariums and pet stores. Although the overall number of fish introductions was based on the customer surveys and would remain unaffected, other factors could result in a higher propagule pressure for specific species than estimated in this study. One such area is reproductive rate. This focus excluded fishes originating from other means such as the Internet or breeding by hobbyists (Padilla and Williams 2004). For example, water hyacinth (*Eichhornia crassipes*), a nuisance aquatic plant that is banned in aquarium and pet stores in many regions, is still available on the Internet for only $4 (Padilla and Williams 2004). The potential impact of the Internet trade on imported species may be substantial and should be investigated along with more traditional avenues of trade in aquarium fishes. Similarly, our study did not cover the extent to which fishes are bred and distributed by hobbyists. Aquarium societies, growing in popularity, have fish auctions at which they sell fishes they have bred at home or that they can no longer take care of. Finally, we considered a 4-month period to represent an average sales amount for the year overall. Generally, this should be a good estimate of the relative numbers of fish sold. However, there may be intra-annual variation due to factors such as population dynamics of individual species, seasons, and religious holidays (Chapman et al. 1997; Severinghaus and Chi 1999) that were not considered. Further, differential mortality in stores may also cause errors in the estimates of fish sold.

Nevertheless, we advance the field by focusing on the behavior of fish owners as a major determinant of propagule pressure because it is ultimately humans who determine the rate at which aquarium fishes are entering our waterways. Fisheries and Oceans Canada states that the most effective method of controlling NIS is to regulate the pathway of introduction (Fisheries and Oceans Canada 2004). Therefore, modifying human behavior is the key to reducing the potential ecological and economic impacts of live aquarium release. Indeed, more educated people are less likely to participate in religious releases of fishes (Severinghaus and Chi 1999). Educational tools such as the Habitattitude campaign (www.habitattitude.net) already exist and should be implemented on a wider scale. Education of the general public could reduce overall rates of introduction and possibly lead to the mitigation of the damaging consequences of NIS.

In conclusion, our study provides an important first step into looking at how human behavior and fish popularity affect rates of introduction. We found that over 10 000 fishes are released annually from the Montréal aquarium trade to the St. Lawrence Seaway, with fish characteristics of aggressiveness and large size minimally affecting release rates. Although the establishment of most aquarium species is limited in this region owing to environmental tolerances, the framework and empirical data provided here can be used to estimate propagule pressure and invasion risk in other regions that may be more susceptible to invasions from the aquarium trade. Further research should attempt to combine studies on propagule pressure of aquarium fishes with risk assessment models based on biological characteristics and population dynamics to obtain a more rigorous estimate of invasion risk as a means to better focus management efforts.

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