

# Risk analysis for species introductions: forecasting population growth of Eurasian ruffe (*Gymnocephalus cernuus*)

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**Abstract:** The North American distribution of the Eurasian ruffe (*Gymnocephalus cernuus*), an ecologically important and costly invasive fish, is presently limited to the Laurentian Great Lakes. Risk analyses for accidental introductions of ruffe to inland lakes should focus on the chance of establishment for small introductions such as those that would result from transporting ruffe as bait. Here I use Akaike's Information Criterion to select a population growth model for ruffe based on observed population dynamics during the invasion of Loch Lomond, Scotland. This population is regulated by a high carrying capacity and Allee effects were undetected. Parameter estimates obtained from this population forecast that the chance of establishment for possible introductions of ruffe to inland lakes in North America is high. A model for ruffe winter survival suggests that survivorship between introductions and spawning may be an important determinant of establishment success, but that the chance of establishment is high for introductions of only a few individuals. To prevent invasions of ruffe in inland waters, release of ruffe, whether intentional or accidental, should not be tolerated.

**Résumé :** La répartition nord-américaine du poisson eurasiatique, la grémille (*Gymnocephalus cernuus*), une espèce d'importance écologique et un envahisseur coûteux, se limite actuellement aux Grands Lacs laurentiens. Les analyses de risque d'introductions accidentelles dans les lacs de l'intérieur du continent devraient se concentrer sur la probabilité d'établissement de petites introductions, comme, par exemple, celles qui résulteraient du transport de grémilles pour servir d'appât. Le critère d'information d'Akaike permet de choisir un modèle de croissance pour la grémille d'après la dynamique de la population observée lors de l'invasion du Loch Lomond, Écosse. La population est contrôlée par un stock limite élevé et aucun effet Allee n'a été détecté. L'utilisation des estimations de paramètres obtenues dans cette étude pour prédire la probabilité d'un établissement lors d'introductions possibles de grémilles dans les lacs continentaux d'Amérique du Nord indique que la probabilité d'établissement est forte. Un modèle de la survie de la grémille à l'hiver indique que la survie entre l'introduction et la fraie peut être un important facteur déterminant du succès de l'établissement; cependant, la probabilité d'un établissement est forte même lors de l'introduction d'un petit nombre d'individus. Afin de prévenir l'invasion des eaux continentales par la grémille, on ne peut tolérer ni la libération volontaire, ni la libération accidentelle de grémilles.

[Traduit par la Rédaction]

## Introduction

Biological invasions of non-indigenous freshwater fishes, invertebrates, and plants have had considerable effects on the composition of North American freshwater ecosystems (Lodge 2001; Rahel 2002), are an important driver of declines in biodiversity (Sala et al. 2000), and impose considerable economic costs, for control and due to lost productivity (Leung et al. 2002). Risk-analysis methodology for intentional and unintentional introductions of non-indigenous species is therefore an important research frontier in applied ecology (National Research Council 2002).

The Eurasian ruffe (*Gymnocephalus cernuus*) was unintentionally introduced into the Great Lakes around 1986

(Pratt et al. 1992), probably in discharged ballast water, and has subsequently spread to other regions of the Great Lakes, including populations on the south and north shores of Lake Superior and at Thunder Bay River on Lake Huron (United States Geological Survey non-indigenous aquatic species database (available at <http://nas.er.usgs.gov>)). The ruffe is a demersal freshwater and brackish-water species that has been invasive in other parts of the world, including the United Kingdom and Eastern Europe (Froese and Pauly 2003). The distribution of ruffe in North America is presently limited to the Great Lakes, probably because vectors of dispersal to inland waters are primarily anthropogenic and because considerable effort has been invested in management of the ruffe since its discovery in North America. Eco-

Received 30 April 2004. Accepted 10 January 2005. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 20 May 2005.  
J18098

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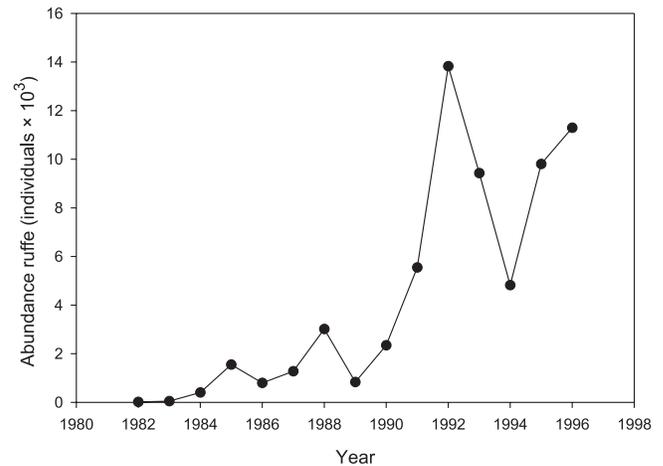
logical impacts of ruffe include predation on eggs of other fish species (Selgeby 1998) and competition with native fishes (Savino and Kolar 1996; Fullerton et al. 2000); ruffe could also impose high economic costs if its effect on the yellow perch (*Perca flavescens*) fishery is as severe as predicted (Leigh 1998). For these reasons, the prevention of future ruffe invasions in uninfested inland ecosystems is a current management objective. To accomplish this goal, prospective risk analyses for ruffe invasions should focus on the chance and rate of establishment of ruffe in inland lakes under different management scenarios.

As a preliminary assessment of the risk of establishment for small, unintentional introductions of ruffe, I conducted a demographic analysis based on the establishment and expansion of ruffe in Loch Lomond, Scotland (56°05'00"N, 004°36'00"W). Previous authors have suggested that stochastic population-growth models could be used to quantify establishment risk for intentional and unintentional introductions of non-indigenous species (Wilson 2000; National Research Council 2002), and similar techniques are already commonplace for assessing risk of extinction (Beissinger and McCullough 2002; Morris and Doak 2002). Although the ruffe population in the Great Lakes is likely beyond eradication, and possibly beyond control, invasion of other ecosystems, including many inland lakes, might still be avoided. In this paper I use a stochastic model of population growth to determine the chance of establishment for introductions of ruffe in such ecosystems as a function of the initial number of individuals introduced. I find no evidence for Allee effects and negligible effects of environmental variability, which suggests that ruffe are unlikely to exhibit long time lags between introduction and population growth. Survival between introduction and post-introduction spawning is therefore likely a crucial transition in ruffe invasions. To examine this transition, I develop a simple model for winter survival and find that establishment probability remains high for introductions of more than a few individuals. This finding is relatively insensitive to estimation error in adult mortality rate and sex ratio of the donor population.

## Methods

Adams and Maitland (1998) reported a time series for ruffe caught on screens at the Ross Priory Pumping Station on the south shore of Loch Lomond between 1982 and 1996. Although these data do not accurately reflect the relative abundances of different species in Loch Lomond because of different species-specific catch rates, they do accurately represent fluctuations within a species over time (Adams and Maitland 1998). These data (Fig. 1) exemplify the rapid population growth that is a common characteristic of the first phase of an invasion (Shigesada and Kawasaki 1997), but also vary considerably from year to year throughout the time series. This variability is important for two reasons. First, it obscures the predominant drivers of population growth, for instance whether or not the population is influenced by density-dependent factors. Second, it renders plausible the possibility that though the population might initially increase in abundance, it could eventually fail as a result of boom-and-bust cycles and (or) because the population fails to endure environmental fluctuations. Below, I consider the evi-

**Fig. 1.** Population dynamics of invasive Eurasian ruffe (*Gymnocephalus cernuus*) in Loch Lomond, Scotland. Data are from Adams and Maitland (1998).



dence from the observed dynamics of the Loch Lomond population for each of these hypotheses and quantify the chance of establishment for possible future introductions of ruffe in inland waters.

Random fluctuations in population-growth rate are usually represented as the combination of two interacting stochastic processes. Demographic stochasticity refers to the effect of variation in individual fitness on population dynamics and results from growth of a population of discrete individuals (Engen et al. 1998; Lande et al. 2003). In contrast, environmental stochasticity refers to random fluctuations in population vital rates over time (Engen et al. 1998; Lande et al. 2003). Below, I assume that effects of demographic stochasticity and random variation in sex ratio on long-term population dynamics (i.e., persistence) are negligible. For most fish species, including the ruffe, this assumption is justified because high individual fertilities overwhelm the effects of individual variation in fertility. Measured fecundities of ruffe range from tens to hundreds of thousands of eggs per individual, depending on size (Kolomin 1977; Ogle 1998). The estimated average annual fecundity of ruffe in North America (~45 000) is consistent with this range (Selgeby and Ogle 1992). Similarly, highly predictable, long life-spans (7–11 years; Kolomin 1977) result in relatively low variation in survival rates of mature individuals. For this reason, larval survival rate is a much more important determinant of long-term population growth in species such as the ruffe. At this developmental stage, however, there are sufficient individuals (even if only one female has spawned) that individual variation in survival is overwhelmed by fluctuations in average survival from year to year, i.e., demographic stochasticity is overwhelmed by environmental variation. This phenomenon is well known in fisheries research and is captured in the concept of year-class strength. Thus, the first model developed below focuses on environmental stochasticity, but shows that these fluctuations are unlikely to have an important effect on establishment probability; a second model is developed to study effects of individual variation and sex ratio on winter survival.

**Model for long-term persistence**

Population dynamics of seasonally reproducing species in a fluctuating environment can be represented by the stochastic difference equation

$$(1) \quad N_{t+1} = f(N_t) + \varepsilon$$

where  $N_t$  is the population size at time  $t$ ,  $\varepsilon$  is a random perturbation due to environmental variability, and  $f(N_t)$  is a continuously differentiable, possibly density-dependent model for the mean change in population size. An approximation to eq. 1 is the diffusion process characterized by an infinitesimal mean,  $\mu$ , and variance,  $\sigma^2$  (Dennis et al. 1991). This modeling framework commonly serves as a basis for inference and for forecasting extinction dynamics, on the assumption that the growth of small populations will be nearly exponential. After testing for Allee effects, it is assumed that this approximation holds for invading populations of ruffe.

Following the convention of log-transforming models and data so that exponential growth is more simply represented as a linear autoregressive process and residuals exhibit constant variance (Lande and Orzack 1988; Dennis et al. 1991; Morris and Doak 2002), a model was selected by fitting the observed data to the following common population-dynamical models: constant population growth rate (exponential population growth), Ricker model, theta-logistic model, and an Allee effect model (Table 1). Assuming that environmental variation in the transformed time series is distributed normally, maximum-likelihood estimates of parameter values are obtained by fitting least squares (Morris and Doak 2002). Parameter estimation was conducted with PROC NLIN in SAS version 8.2 (SAS Institute Inc. 1999). Model selection was determined by the smallest Akaike's Information Criterion (AIC) adjusted for small data sets (AIC<sub>c</sub>; Burnham and Anderson 2002). AIC selects the model that minimizes the expected Kullback–Leibler distance between a complete representation of the data-generating process and its approximate representation by a parameterized model (Burnham and Anderson 2002). This can be conceptualized as a formalized procedure for selecting the most likely model (in terms of posterior likelihood) with a penalty to correct for bias caused by model complexity. Using this procedure, I determined that the Ricker model provided the best fit to the observed data.

For forecasting population establishment, I used a density-independent model of population growth in a variable environment (Dennis et al. 1991). This model assumes that Allee effects, carrying capacity, random fluctuations in sex ratio, and demographic stochasticity are negligible (see Møller and Legendre 2001; Dennis 2002; Engen et al. 2003). Data were not available to estimate fluctuations in sex ratio or demographic stochasticity, so these phenomena were studied in an exploratory way using a second model. The following observations justify the decision to use a density-independent model for long-term forecasts.

First, the success or failure of the introduced population depends primarily on population growth during the years immediately following introduction, i.e., during the exponential-growth phase of the approach to carrying capacity. If recruitment during such years is poor as a consequence of environmental fluctuations, then the invasion may

**Table 1.** Models used to forecast the chance of establishment for introductions of Eurasian ruffe (*Gymnocephalus cernuus*) to inland lakes in North America. AIC = Akaike's Information Criterion.

Model	Parameter		Model fit			Reference	
	$r$	$\kappa$	$\theta$	SSE <sup>a</sup>	df <sup>b</sup>		AIC <sub>c</sub>
Exponential: $\ln(N_{t+1}/N_t) = r$	0.4642			11.2733	14	41.79	Dennis et al. 1991
Ricker <sup>c</sup> : $\ln(N_{t+1}/N_t) = r(1 - N_t/\kappa)$	0.8817	8104.5		8.3834	14	40.95	Morris and Doak 2002
Theta-logistic: $\ln(N_{t+1}/N_t) = r[1 - (N_t/\kappa)^\theta]$	2.9687	6189.1	0.1337	6.8673	14	42.20	Morris and Doak 2002
Allee effect: $\ln(N_{t+1}/N_t) = \ln(N_t) - \ln(\theta + N_t) + r - \kappa N_t$	0.8817	$1.09 \times 10^{-4}$	$1.09 \times 10^{-4}$	8.3834	14	45.00	Morris and Doak 2002

<sup>a</sup>Sum of squared errors.

<sup>b</sup>Uncorrected total degrees of freedom.

<sup>c</sup>Best fit overall.

fail. Linearizing the Ricker model around  $N_0 = 0$  yields  $\ln(N_{t+1}/N_t) = r$ , indicating that exponential growth is a good approximation to the Ricker model during this phase of invasion. Second, population estimates for ruffe in Loch Lomond are relative (depending on the sampling rate) and are not absolute measures of abundance. Since the sampling rate is unknown, one cannot determine the true carrying capacity of Loch Lomond. Furthermore, the carrying capacity of the Great Lakes (or even of just Lake Superior) is likewise unknown. However, it certainly is very large, and standard results (e.g., Tier and Hanson 1981) indicate that it will therefore have a negligible effect on the chance of extinction within ecological time scales. Even for introductions to smaller inland lakes, carrying capacity is unlikely to affect the chance of establishment, as ruffe populations likely can attain high densities without adverse effects on individuals.

The population growth rate,  $r$ , was obtained from the best fit (Ricker) model (Table 1). Observe that the Ricker model can be rescaled by defining  $N_t^* = N_t/\kappa$ , resulting in the two-parameter model  $\ln(N_{t+1}^*/N_t^*) = r(1 - N_t^*)$ , leaving the value of  $r$  unchanged. The mean of the diffusion process is approximately this value less the variance divided by 2 (Dennis et al. 1991). The variance was estimated by mean squared error of the best fit model (Morris and Doak 2002). Uncertainty in parameter estimates was propagated throughout these estimates using estimators derived by Dennis et al. (1991).

Finally, I considered two additional models. First, I supposed that population dynamics might exhibit density-dependent time lags, which can be modeled as autoregressive processes (Turchin 2003). Time lags are important because, when coupled with demographic stochasticity and environmental variability, they can result in non-negligible probabilities of extinction even at population sizes near carrying capacity (Belovsky et al. 1999). Additionally, density-dependent time lags are the most likely mechanism for the boom-and-bust cycles commonly observed in biological invasions. I used the partial rate correlation function (PRCF) as a probe for density-dependent time lags in population growth and sequential-blocks cross-validation (validation block size of one data point) as described by Turchin (2003) for selection of autoregressive models.

Second, Adams and Maitland (1998) suggest that the Loch Lomond population grew exponentially (constant growth rate) during the period 1982–1992 and stabilized thereafter. Although I found more support for the Ricker (density-dependent) model than for the exponential-growth model, it does not follow that this is the best two-parameter model for density dependence. Alternatively, the growth of ruffe populations is perhaps better characterized by a “ceiling” model in which the population grows exponentially until it reaches a ceiling, at which time it abruptly ceases to increase (Foley 1994). The Ricker model considered above might fit such a model quite poorly. Therefore, to test for this possibility I compared the observed log-transformed interannual population-growth rates given by  $X_t = \ln(N_t/N_{t-1})$ , where  $N_t$  is the population size at time  $t$ , before and after 1993, with a two-tailed  $t$  test for populations with unequal variances.

## Model for winter survival

The model considered above reflects the effect of fluctuating environments on long-term persistence of an introduced population, conditional on persistence to spawning in the first year following introduction. Importantly, because the number of initially introduced individuals is small, demographic stochasticity and random fluctuations in sex ratio could have a profound effect on persistence at this phase of establishment. Some insight into this process can be obtained by considering an introduction of individuals that is a random sample of a donor population, after the spring spawning and before winter mortality occurs. Ignoring the possibilities of a late-season spawn (Fedorova and Vetkasov 1974; Kolomin 1977) and hermaphroditism (Butskaya 1976), the probability of successful spawning is determined by the chance that at least one male and one female survive through the winter. Representing winter mortality by  $\delta$  with a subscript to indicate sex, the chance that at least one female survives is  $(1 - \delta_F^F)$  and the chance that at least one male survives is  $(1 - \delta_M^M)$ , where  $F$  is the number of females and  $M$  is the number of males. Here we assume that adult mortality is not age-dependent, though extending this model to include age structure would be straightforward. For  $F$  females and  $M$  males, the joint probability of at least one male and one female surviving is

$$(2) \quad (P_{\text{mate}} | M, F) = (1 - \delta_F^F)(1 - \delta_M^M)$$

The total chance of mating, conditional on  $N$  and assuming no Allee effects, is given by

$$(3) \quad (P_{\text{mate}} | N) = (P_{\text{mate}} | M, F)(P_{M,F} | N)$$

If the  $N$  introduced individuals are drawn from a population with sex ratio of  $\phi$  males per female, the probability of  $M$  males and  $F$  females is given by the binomial distribution with parameter  $p = (1 + \phi)^{-1}$ . Since  $M = N - F$ , the total chance of mating, given an introduction of  $N$  individuals of unknown sex is

$$(4) \quad (P_{\text{mate}} | N) = \sum_{F=1}^N (1 - \delta_F^F)(1 - \delta_{M=N-F}^{N-F}) \binom{N}{F} p^F (1-p)^{N-F}$$

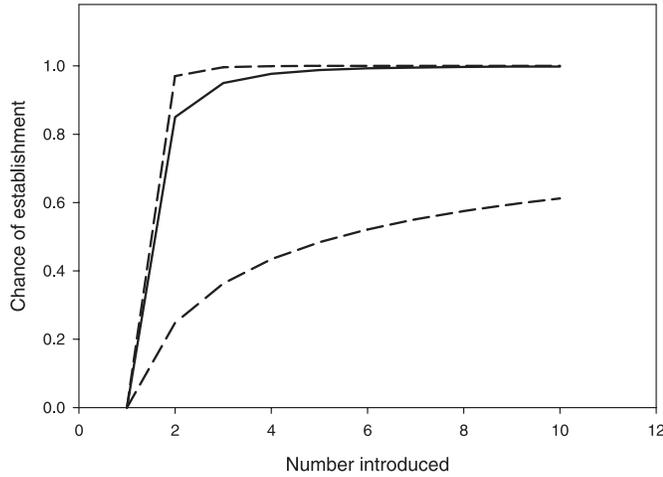
Holding all other parameters constant, this formula takes its maximum value at  $p = 0.5$ , i.e., where the sex ratio is equal to 1.

## Results

### Model selection

Goodness-of-fit statistics ( $AIC_c$ ) for the log-transformed linear, Ricker, theta-logistic, and Allee effect models are given in Table 1. The Ricker model provided the best fit to these data (Table 1). Model selection was based on the lowest  $AIC_c$  value. The difference between the estimated  $AIC_c$  value for the Ricker model and the next best model (exponential population growth) was 0.837, indicating that support for the Ricker model against the exponential-growth model was only about 2.3 to 1. The PRCF showed a significant negative spike ( $\text{PRCF} \leq 2/\sqrt{t}$ , where  $t$  is the number of data points; Turchin 2003) at a time lag of 1 year, indicating dependence only on the population size in the previous year.

**Fig. 2.** Estimated chance of establishment for small introductions of ruffe determined from stochastic population-growth models (solid line) with 95% confidence intervals (broken lines).



Sequential-block cross-validation showed that higher order (lagged) models were not warranted by these data. Additionally, there was insufficient evidence for the ceiling model ( $P = 0.131$ ), though it is interesting that the average  $X$  value from 1993 to 1996 was not significantly different from zero ( $P = 0.879$ ), which is consistent with the carrying capacity implicit in the Ricker model having been reached. The lack of first-order autocorrelation among the residuals ( $P = 0.989$ ) confirms that observations were independent, thus satisfying the assumptions of the model (Dennis et al. 1991).

**Forecasting long-term persistence**

The maximum-likelihood estimate of the population-growth parameter,  $r$ , in the Ricker model is 0.8817 (95% confidence interval 0.2207, 1.5426). Maximum and minimum observed values for  $X_t$  were 2.156 and -1.284, respectively. The maximum-likelihood estimate for environmental variation,  $\sigma_e$ , is 0.599. The chance of establishment,  $\pi_{est}$ , defined as the complement of the chance of extinction, is given by the equation (Dennis et al. 1991)

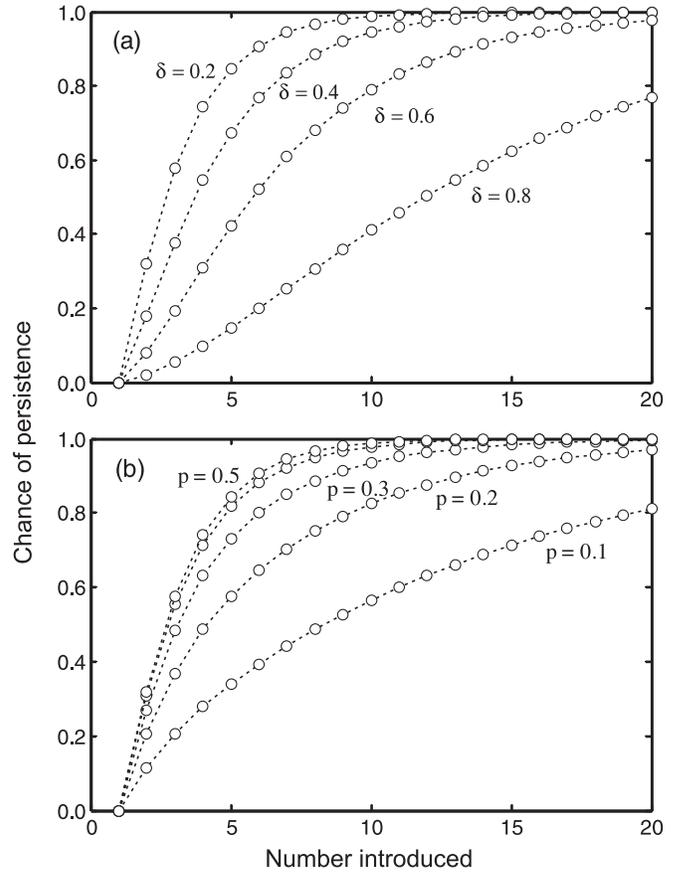
$$(5) \quad \pi_{est} = \begin{cases} 0 & \mu \leq 0 \\ 1 - \exp[-2\mu \ln(N_0)/\sigma^2] & \mu > 0 \end{cases}$$

where  $\mu = r - \sigma^2/2$  and  $N_0$  is the initial number of females introduced (assuming an adequate number of males is introduced for fertilization to occur). This result is presented with approximate 95% confidence intervals reflecting uncertainty in the parameter estimates (Fig. 2; Dennis et al. 1991).

**Winter survival**

To understand the effects of changes in mortality and sex ratio on the chance of persistence to first spawning, I evaluated eq. 4 for different values of the parameters  $\delta$  and  $p$ . The effect of increasing mortality while holding sex ratio constant is to diminish the chance of persistence for an introduction of a given size, consistent with intuition (Fig. 3a). However, even for very high levels of winter mortality, the chance that one male and one female survive is unacceptably high even for very small introductions (e.g., 30% chance of

**Fig. 3.** Estimated chance of winter survival and reproduction for small introductions of ruffe. Results are relatively insensitive to (a) adult mortality and (b) sex ratio. Estimates in a were obtained by evaluating eq. 4 at different values of  $\delta_M = \delta_F = \delta$ , holding sex ratio constant ( $\phi = 1$ ). Estimates in b were obtained by evaluating eq. 4 at different values of  $p$ , holding adult mortality constant ( $\delta = 0.2$ ).



persistence for an introduction of eight individuals). A skewed sex ratio in the donor population had a less pronounced effect on the chance of persistence than did winter mortality (Fig. 3b). The uppermost line (Fig. 3b) represents introduction from a population with a sex ratio of  $\phi = 1$ , showing that the chance of mating is highest when males and females are in equal proportions. However, to vastly change this result, highly skewed sex ratios are required, as represented by the bottom two lines, which correspond to  $\phi = 4$  and  $\phi = 9$ , respectively. Since the processes underlying Figs. 2 and 3 are independent, these probabilities can be multiplied to obtain a joint probability of persistence. Clearly, the phase represented by Fig. 3 (winter mortality and biased sex ratio in the donor population) will overwhelm the joint probability for most introduced populations.

**Discussion**

The results of this study support the tentative conclusion of Adams and Maitland (1998) that the ruffe population in Loch Lomond is density regulated and moreover that is has approximately stabilized. However, according to model forecasts, lakes with even small introductions are at considerable

risk for invasion. The estimated chance of long-term persistence for an introduction of just two females prior to spawning (assuming that a male is also introduced, to ensure reproduction) is 0.85. If introduction occurs after spawning so that winter survival is the crucial factor determining establishment success, the chance of persistence is diminished but still unacceptably high for introductions of even modest size (e.g., 30% chance of establishment for  $N_0 = 8$ ). While zero tolerance to introductions of non-indigenous species is probably not generally feasible, if invasions of ruffe are to be prevented, introductions of any size should not be tolerated. If during model fit it had been assumed that the Loch Lomond population was not regulated (i.e., if an exponential model had been assumed), the chance of establishment would have been estimated as even higher and would have been overestimated.

As with all modeling exercises, the results obtained here depend on assumptions that are approximations of the real data-generating process. I suggest that taken together the two models studied here provide a reasonably robust framework for understanding the effect of size of the introduced population on the chance of establishment for ruffe. In particular, even under a management policy with high tolerance for invasions (the opposite of a risk-averse or precautionary policy) the most severe models estimate that the chance of establishment is unacceptably high for even very small introductions. Including additional biological details is unlikely to affect this outcome for the following reasons.

Factors not considered by the model for long-term persistence are Allee effects (which were tested for but not detected and for which the power to detect is probably low), demographic stochasticity, and fluctuations in sex ratio. I have argued that for species like ruffe and other fishes with per-capita annual fecundities in the tens of thousands, environmental stochasticity in larval survival will overwhelm demographic stochasticity and fluctuations in sex ratio (cf. Engen et al. 2003). This life history contrasts with the life histories of other groups, particularly birds, for which much of the recent theory about demographic stochasticity and fluctuating sex ratio was developed (Sæther et al. 1998; Engen et al. 2003), and is consistent with the idea that fluctuating environments will affect species differently depending on life history. Detection, estimation, and analysis of Allee effects present a much more challenging problem. In Lake Superior, aggregation during spawning probably removes any effect of mate limitation. It remains to be determined if ruffe are regulated by Allee effects from other sources. The failure to detect Allee effects in this analysis is consistent with a Bayesian meta-analysis, which yielded little evidence for depensation in four other taxonomic groups of fish (salmonids, gadiforms, clupeiforms, and pleuronectiforms; Liermann and Hilborn 1997), suggesting that Allee effects may be rare in fish species generally. How often and under what conditions Allee effects occur in fish are important topics for future research.

In contrast to the model for long-term persistence, the model for winter survival explicitly considers effects of demographic stochasticity (individual heterogeneity in winter survival) and sex ratio, but does not consider environmental variability. Here, the major limitations are ignorance of the correct model structure and uncertainty in parameter esti-

mates. For these reasons this model should be viewed as a thought experiment rather than as a representation of this particular system. Interpreted this way, this model shows that either a severely biased sex ratio in the donor population or extremely high winter mortality is required for demographic stochasticity and fluctuations in sex ratio to greatly influence the chance of establishment. Despite limitations, these models support relatively strong inferences from the perspective of potential policy. Considered together, they suggest that even under extreme conditions, the chance of establishment is around 10% for an introduction of just four individuals.

Additionally, these results rely on the premise that data from ruffe populations in Loch Lomond and within the species' native range are representative of demography in North America. Unfortunately, long-term data from other invaded ecosystems are not available to compare ruffe demography in different regions and to assess heterogeneity among lakes. In the absence of better data, it is not unreasonable to consider Loch Lomond a surrogate for North American lakes. Loch Lomond is monomictic and has average depth of 37 m. Minimum and maximum temperatures from biweekly sampling over 5 years (1996–2001) are  $5.5 \pm 1.2$  and  $16.5 \pm 0.75$  °C (mean  $\pm$  standard deviation (SD)), respectively; Adams and Maitland 2001). While minor differences among lakes are inevitable even within a region, these characteristics are broadly consistent with the features of many North American lakes and differences are unlikely to greatly affect population dynamics.

Future analyses of invasion risk should focus on characterizing uncertainty in forecasts, estimates of which should accompany recommendations for management. More importantly, an outstanding problem in invasion biology is why so many introduced populations fail to establish, especially when many exhibit high population-growth rates (Williamson 1996). Clearly the phenomena modeled here (small population sizes and environmental variation) are not sufficient to explain the low rates of establishment commonly observed. It follows, therefore, that without further understanding of the biological mechanisms that limit population establishment, model projections cannot be expected to provide reliable estimates of invasion risk. In this respect the estimates obtained here should be interpreted as an upper bound on invasion risk for ruffe. Until lower bounds are determined, these are also our best estimates.

## Acknowledgements

I thank K.L.S. Drury, D.M. Lodge, and two anonymous reviewers for comments on an earlier version of the manuscript. This work was funded by grants from the US Environmental Protection Agency's Science to Achieve Results program (USEPA STAR) (to David Lodge), a USEPA STAR Graduate Research Fellowship (to John Drake), and a University of Notre Dame Schmitt Research Fellowship (to John Drake).

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