# Simulated dispersal of exotic rainbow smelt (*Osmerus mordax*) in a northern Wisconsin lake district and implications for management

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**Abstract**: We simulated geographic dispersal of exotic rainbow smelt (*Osmerus mordax*) as a function of present introduction rates, the probability of invasion through stream connections among lakes and watersheds, and survival based on physical and chemical factors of lakes within a northern Wisconsin watershed. One fourth of the habitable lakes contained rainbow smelt after 1000 years if dispersal was restricted to stream corridors. In contrast, with present rates of human transport, half contained rainbow smelt after 200 years, three quarters after 300 years, and all after 1000 years. Simulated human introductions increased the number of epicenters for spread and were the most influential parameter in the model. Stream connections between lakes increased the number of lakes colonized; decreases in migration ability led to fewer invaded lakes. Although extinction was operating, human introductions outweighed extinction and led to a saturation of rainbow smelt across all habitable lakes within the watershed within 1000 years. Our results highlight the importance of human vectors in driving exotic fish dispersal, suggest that isolated lakes are important refuges for species negatively affected by rainbow smelt, and show that agencies interested in controlling the spread of exotic fishes need to strongly consider the human vector of transport.

**Résumé** : Nous avons simulé la dispersion géographique d'une espèce d'éperlan arc-en-ciel (*Osmerus mordax*) exotique en fonction des taux d'introduction actuels, de la probabilité d'invasion par les voies de communication entre les lacs et les bassins hydrographiques et de la survie fondée sur les facteurs physiques et chimiques des lacs d'un bassin hydrographique situé dans le nord de l'État du Wisconsin. Dans ce bassin, seul le quart des lacs habitables contenaient des éperlans arc-en-ciel après 1000 ans si la dispersion était limitée aux corridors des cours d'eau. Par contraste, avec les taux actuels de déplacement des êtres humains, la moitié des cours d'eau contenaient des éperlans arc-en-ciel après 200 ans, les trois quarts après 300 ans et tous en contenaient après 1000 ans. La simulation d'introductions par les êtres humains a augmenté le nombre d'épicentres de distribution et constituait le paramètre du modèle ayant la plus grande influence. Les voies de communication interlacustres ont augmenté le nombre de lacs colonisés; la diminution de la capacité de migration a entraîné l'invasion d'un moins grand nombre de lacs. Même si le phénomène d'extinction était actif, les introductions par l'être humain ont été supérieures à l'extinction et ont entraîné une saturation en éperlan arc-en-ciel de tous les lacs habitables du bassin hydrographique en moins de 1000 ans. Les résultats obtenus soulignent l'importance de vecteurs humains commandant la dispersion de poissons exotiques, ce qui laisse supposer que les lacs isolés constituent des refuges importants pour les espèces qui sont affectées négativement par la présence de l'éperlan arc-en-ciel et montrent que les organisations intéressées à contrôler la dispersion des poissons exotiques doivent prendre en compte sans réserve le vecteur du transport humain.

[Traduit par la Rédaction]

## Introduction

Introductions of exotic fishes are commonplace; exotics are spreading at a rapid rate worldwide (Moyle 1986; Lodge 1993*a*; Bruton 1995) and often cause negative impacts on native fauna and existing fisheries (Magnuson 1976; Moyle et al. 1986; Kaufman 1992; Lodge 1993*b*; Moyle and Moyle 1995). The addition of exotic species changes community composition and structure in many ecosystems as spread occurs across a landscape (Skellum 1951; Elton 1958; Mooney and Drake 1986).

The exotic rainbow smelt (*Osmerus mordax*) now exists in all of the Laurentian Great Lakes and is spreading secondarily to smaller, more isolated lakes within the Great Lakes region (Evans and Loftus 1987; Mayden et al. 1987; Franzin et al. 1994). Reproductive success of lake whitefish (*Coregonus clupeaformis*) and cisco (*Coregonus artedi*) has declined dramatically owing to predation by rainbow smelt on their larval stages (Loftus and Hulsman 1986; Hrabik et al. 1998). Predation by rainbow smelt has led to the rapid decline and probable extinction of cisco in Sparkling Lake, Wisconsin. The effects of competition by rainbow smelt on yellow perch (*Perca flavescens*) also have been observed in Crystal Lake, Wisconsin (Hrabik et al. 1998). Understanding processes governing the dispersal of rainbow smelt is of interest to fisheries managers, ecologists, and conservationists

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concerned with preserving the integrity of native fish communities.

Spatially explicit population models can provide insight into the effects of alterations in landscape characteristics on spatial distribution of species (Dunning et al. 1995). Such models can characterize patch use by organisms, which is important for visualizing the effects of management strategies and determining the most important factors shaping distribution patterns (Turner et al. 1995). Currently, few models are available to predict or visualize the spread of exotic fishes across lake districts. Dispersal across a heterogeneous lake district is a slow process; lakes often are isolated to varying degrees by streams and land barriers (Magnuson et al. 1998). Because rainbow smelt dispersal is occurring within the Bear River watershed in northern Wisconsin and because it is reasonably well documented, we constructed a spatially explicit simulation model of dispersal to assess possible future rainbow smelt distributions over periods of time longer than practical through empirical measurement. We also evaluate potential methods of controlling the rates of dispersal within and across watershed boundaries through systematic manipulation of the model parameters and the time course for the persistence of lakes not invaded by rainbow smelt. We present data from field collections and reports documenting the spread of rainbow smelt in three adjacent watersheds in Vilas County, Wisconsin, and discuss the application of spatially explicit population models for use in management strategies to control the spread of exotic fishes.

## Methods

### Study area

Field studies were conducted in the Bear River and Manitowish River watersheds in western Vilas County. This 1556-ha area contains 507 lakes larger than 0.75 ha and has a maximum difference in elevation among lakes of 52 m (North Temperate Lakes Long-Term Ecological Research project (NTL-LTER) database). Of these lakes, 29% have stream outlets and or inlets (NTL-LTER database). The area was deglaciated 10 000 – 12 000 years ago and is characterized by noncalcareous soils composed of postglacial till, moraine, and outwash material and irregular topographic relief (Bowen 1978; Attig 1985). We constructed a simulation model of rainbow smelt dispersal within the Bear River watershed (Fig. 1), the only watershed for which we had information on both physical and chemical properties and approximate dates of rainbow smelt invasion of each lake to date.

### Field collections

We documented the dispersal and present distribution of rainbow smelt in lakes and streams through interviews and our own collections (Tables 1–3). We collected rainbow smelt during the spring spawning migrations in headwater streams and channels between lakes using a 12 × 1 m beach seine and long-handled dip nets. We collected rainbow smelt during the summer using five single-mesh, 4-m-wide vertical gill nets of 19-, 25-, 32-, 51-, and 64-mm stretch mesh that extended from the surface to the bottom (see Rudstam and Magnuson 1985). Personal communication with fisheries biologists from the Lac du Flambeau Natural Resource Department, the Wisconsin Department of Natural Resources, and local fishers who collected rainbow smelt during spring spawning migrations provided approximate dates of rainbow smelt invasions.

### Model and assumptions

The model was constructed to represent rainbow smelt dispersal among lakes in a low-gradient glacial outwash area containing small, low-gradient streams, lakes connected via streams, and lakes without stream connections. Assumptions related to the habitat characteristics suitable for rainbow smelt, the ability of rainbow smelt to move through connecting streams, and the habitability of lakes for rainbow smelt were estimated from characteristics of the lakes and the surrounding landscape.

The suitability of lakes for rainbow smelt habitation was estimated from physical and chemical characteristics of the lakes. In a study of 187 Canadian lakes that contained rainbow smelt, Evans and Loftus (1987) presented minimum and maximum values for pH, minimum depth, and minimum lake area. We used these values to constrain acceptable lake habitats for rainbow smelt. In our model, each of the three parameters had to lie within the minimum and maximum values to be considered acceptable. Physical and chemical data for most of the lakes in the watershed were available from the eastern lakes survey (Linthurst et al. 1986). Of about 114 lakes larger than 0.75 ha within the Bear River watershed, 41 met all three suitability criteria and 23 had stream outlets or inlets.

Stream connections between lakes were separated into their upstream and downstream components. Upstream movement to another lake is possible for adult rainbow smelt that migrate upstream through tributary streams during spring spawning migrations (Becker 1983; Nellbring 1989). Newly hatched rainbow smelt larvae can be washed out of the outlet downstream for several kilometres into downstream lakes (Naesje et al. 1987).

Given these life history and dispersal characteristics, we developed equations to estimate the probability of rainbow smelt using each stream as a dispersal route. The stream connectivity parameters varied from 0 to 1 based on the equations

$$U_i = \left(\left(1 - \frac{\min(g_i, g_\mathrm{m})}{g_\mathrm{m}}\right)\left(1 - \frac{\min(l_i, l_\mathrm{m})}{l_\mathrm{m}}\right)\right)^{1/2}$$

$$D_i = \left(1 - \frac{\min(l_i, l_\mathrm{md})}{l_\mathrm{md}}\right)$$

where $U_i$ is the probability of rainbow smelt migrating upstream through a stream connection, $g_i$ is the gradient for each individual stream between two lakes estimated from topographic maps, $g_\mathrm{m}$ is the maximum gradient against which a rainbow smelt can migrate upstream, $l_i$ is the length of each individual stream between two lakes estimated from topographic maps, $l_\mathrm{md}$ is the maximum distance that rainbow smelt will wash downstream in the Bear River watershed, $l_\mathrm{m}$ is the maximum distance that rainbow smelt will migrate upstream in the Bear River watershed, and $D_i$ is the probability of rainbow smelt larvae being washed downstream to the next lake.

Streams in the Bear River watershed are small with discharges generally less than 75 $m^3$/s. Thus, we have not included a component that accounts for high-discharge events because the study area is characterized by stable and low flows. For application in large river systems, additional parameters accounting for increased downstream dispersal of larvae could be added by altering the downstream dispersal equation.

For baseline simulations, we used parameter values that were reasonable based on the known distribution of rainbow smelt and chronology of invasions in the Bear River watershed. Using this scenario, we were able to simulate an invasion into Fence Lake and the dispersal to connected lakes over 30 years (the duration since rainbow smelt were introduced into Fence Lake). The model consistently replicated what apparently happened naturally within the lakes connected to Fence Lake (Fig. 1). The rate of human intro-

**Fig. 1.** Map of the Bear River watershed in Vilas County, Wisconsin, showing (*a*) the present distribution of rainbow smelt in the watershed (lakes in black are those that contain rainbow smelt) and (*b* and *c*) the observed spread of rainbow smelt through connected lakes within the Fence Lake chain and the results of model simulations under baseline parameter settings where an introduction of rainbow smelt into Fence Lake and invasions of connected lakes are compared with what actually occurred.

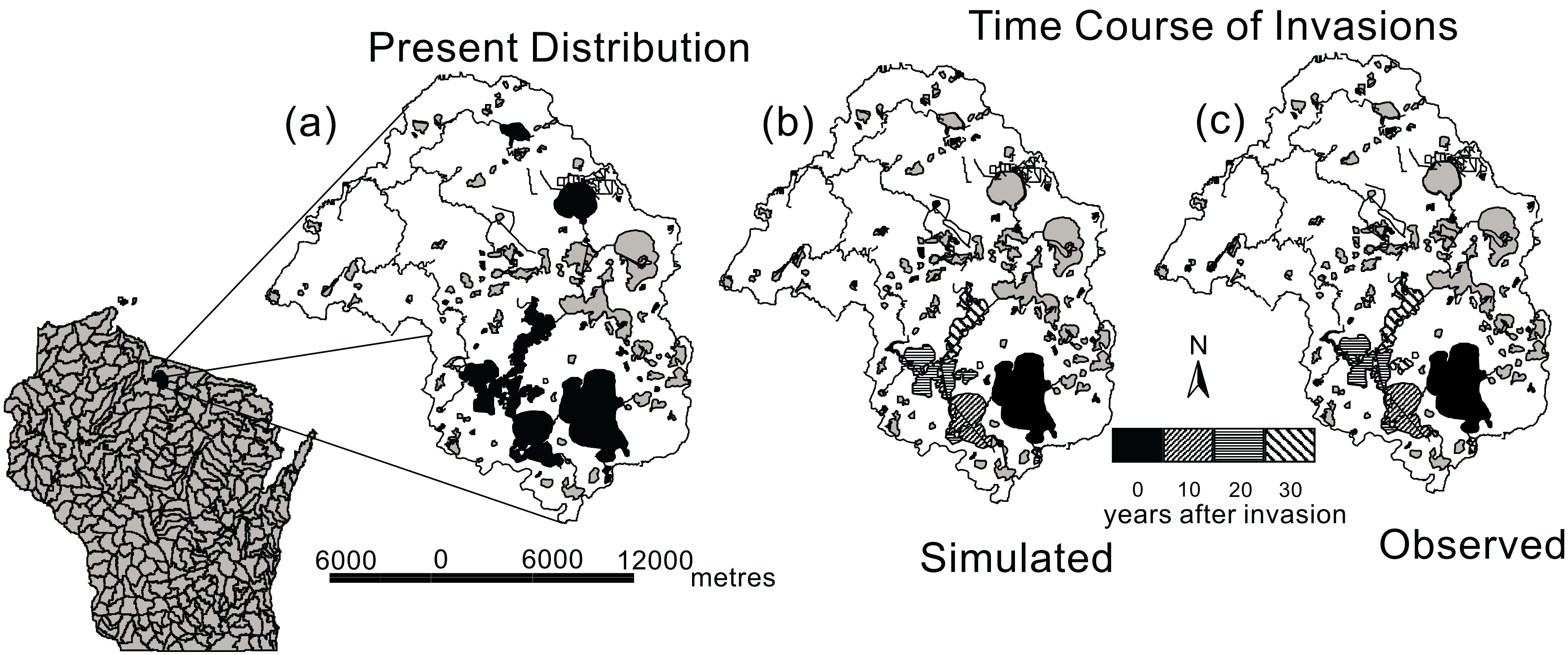


**Table 1.** Site, dates, and presence or absence of rainbow smelt at channel locations within the Bear River, Trout Lake, and Manitowish River watersheds sampled during field surveys.

| Lake or stream | Date | Rainbow smelt | Sampling gear |
|---|---|---|---|
| Long Interlaken/Big Crawling Stone Lake channel | April 23, 1996 | Yes | Beach seine |
| Flambeau/Pokegamma Lake channel | April 23, 1996 | Yes | Beach seine |
| Moss/Long Interlaken Lake channel | April 21, 1995 | Yes | Beach seine, dip net |
| Little Crawling Stone/Big Crawling Stone Lake channel | April 30, 1995 | Yes | Dip net |
| Bolton/Fence Lake stream | April 30, 1995 | Yes | Dip net |
| Bolton Creek (upstream from state highway 47) | April 30, 1995; April 23, 1996 | No | Beach seine, dip net |
| Fence/North Twin Placid Lake channel | April 24, 1996 | Yes | Dip net |
| Alder/Wild Rice Lake channel | April 24, 1996 | No | Dip net |
| Manitowish/Spider Lake channel | April 25, 1996 | No | Beach seine, dip net |

**Note**: The timing of sampling with beach seines and dip nets coincided with spawning runs of rainbow smelt in nearby lakes.

**Table 2.** Sites, dates, and presence or absence of rainbow smelt at locations within the Bear River, Trout Lake, and Manitowish River watersheds in northern Wisconsin during field sampling surveys.

| Lake | Date | Rainbow smelt | Sampling gear or data source |
|---|---|---|---|
| Fence Lake | July 21, 1993 | Yes | Vertical gill nets |
| Crawling Stone Lake | August 28, 1993 | Yes | Vertical gill nets |
| Manitowish Lake | June 24, 1996 | No | Vertical gill nets |
| Little Star Lake | July 10, 1996 | No | Vertical gill nets |
| Clear Lake | July 5, 1996; July 11, 1997 | No | Vertical gill nets |
| Dead Pike Lake | July 15, 1996 | Yes | Vertical gill nets |
| Big Lake | July 21, 1997 | No | Vertical gill nets |
| Sparkling Lake | 1982 to present | Yes | LTER database |
| Trout Lake | 1981 to present | No | LTER database |
| Allequash Lake | 1981 to present | No | LTER database |
| Big Muskellunge Lake | 1981 to present | No | LTER database |
| Crystal Lake | 1985 to present | Yes | LTER database |
| Papoose Lake | June 24, 1997 | No | Vertical gill nets |
| Little Trout Lake | May 1990 | Yes | L.Wawronowicz, personal communication |

**Note**: The timing of sampling with beach seines and dip nets coincided with spawning runs of rainbow smelt in nearby lakes. Sampling with gill nets occurred during thermal stratification in each lake.

**Table 3.** Approximate year that rainbow smelt were first noted in lakes within the Bear River watershed.

| Lake | Year | Source | Method of collection |
|---|---|---|---|
| Fence Lake | 1968 | Becker 1983 | Unknown |
| Big Crawling Stone Lake | 1975 | W. Wolfe, personal communication | Beach seine |
| Little Crawling Stone Lake | 1982 | T.R. Hrabik, personal observation | Dip net |
| Long Interlaken Lake | 1983 | T.R. Hrabik, personal observation | Beach seine |
| Moss Lake | 1989 | T.R. Hrabik, personal observation | Dip net |
| To To Tom Lake | 1990 | G. Fidiment, personal communication | Hook and line |
| North Twin Placid Lake | 1996 | T.R. Hrabik, field collection | Dip net |
| Pokegamma Lake | 1996 | T.R. Hrabik, field collection | Beach seine |

ductions within the watershed was estimated from the number of isolated lakes within the watershed containing rainbow smelt and was based on the following equation:

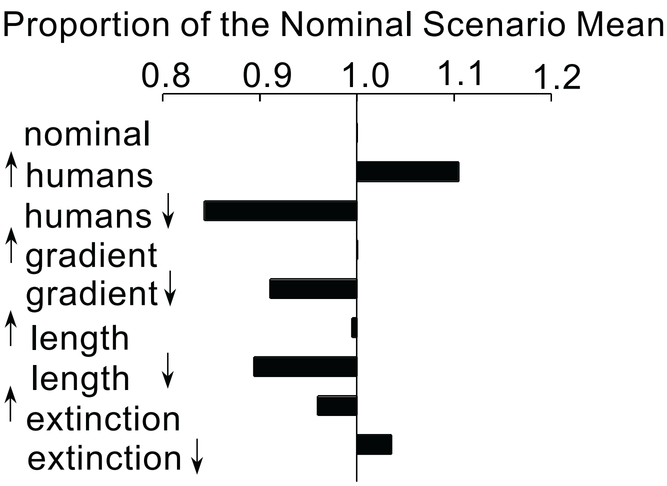
$$H = \frac{(L/L_t)}{T}$$

where $H$ is the rate of human introductions, $L$ is the number of lakes that were successfully invaded by rainbow smelt from human introductions, $L_t$ is the total number of habitable lakes within the watershed, and $T$ is number of years since the rainbow smelt were first introduced into the watershed.

The theory of island biogeography suggests that the extinction of a species is more likely on small islands than on large ones (MacArther 1972), and lakes can be considered as islands of water within the landscape (e.g., Magnuson 1976). We included an extinction function that fit this theory for the purpose of weighing its importance relative to other functions in the model. Based on this general contention, the probability of the extinction of rainbow smelt after an invasion had taken place in each lake was assumed to be inversely proportional to lake area and varied from 0 to 1 where extinction was equal to (lake area (ha))$^{-1.1}$.

Lakes that lacked stream connections to lakes containing rainbow smelt but still acquired rainbow smelt were assumed to have received introductions by humans. No observable lake characteristic seemed to make a lake more likely to receive rainbow smelt from human introductions, and no discernible pattern to these introductions was observed. Introductions might be expected to oc-

**Fig. 2.** Results of a sensitivity analysis from model simulations performed by changing each parameter by 20% while holding all others constant. Proportions shown are the mean number of lakes invaded from 100 simulations over 100 simulation years for each parameter setting divided by the mean number of lakes invaded under baseline parameter settings. Labels with upward pointing arrows represent scenarios with 20% increases in human introductions, rainbow smelt migration ability against gradient and length of streams, downstream dispersal ability, and increases in extinction rate. Labels with downward pointing arrows represent means from scenarios with a 20% decrease from each baseline setting.




cur in connection with sport fishing; rainbow smelt have a reputation as good forage for predatory fish (e.g., Jones et al. 1994). However, of the lakes in our study area that have received rainbow smelt introductions, 60% have been smaller than 70 ha. Thus, our model assumed that human introductions occurred randomly with respect to the size of the lake and that each lake had an equal probability of being invaded through human introductions at each time step. The probability of each event in the model was determined by drawing a random probability between 0 and 1 from a uniform distribution; if the random probability was less than the probability of an individual process (e.g., $U_i$, $D_i$, $H$) determined by the output of each model function, the process occurred.

Once rainbow smelt invade a lake, further dispersal from the lake may "lag" or be limited for several years by low abundance and the absence of mature adults. We simulated the lag by allowing rainbow smelt to disperse from a newly invaded lake after having been established for 6 model years. This represented about two generations: one to reproduce and the other to represent a cohort of spreading adults.

A sensitivity analysis was performed by individually varying $g_{\mathrm{m}}$, $l_{\mathrm{m}}$, $l_{\mathrm{md}}$, and $H$ by ±20% from the nominal parameter values. The response variable used for the analysis was the mean number of lakes invaded based on 100 simulations run for 100 years. The upstream and downstream dispersal components through streams were combined into a total stream dispersal component to be compared with the human dispersal and the extinction components in a systematic way.

The trend of modeled invasions through time was well represented by an asymptotic function. The number of new lakes invaded by rainbow smelt was a function of time:

$$N_t = N_m\ (1 - \mathrm{e}^{-a(T)})$$

where $N_t$ is the number of lakes invaded at time $t$, $N_{\mathrm{m}}$ is asymptote parameter representing the maximum number of lakes to be invaded under current parameter settings, $T$ is time (years), and $a$ is a constant. The parameters in the model were estimated by fitting the function to the average number of lakes invaded at 50-year intervals for 100 simulations under the nominal parameter scenario. The fit resulted in an $r^2$ of 0.98 and parameter values of $N_{\mathrm{m}} = 43.3$ and $a = 0.004$ (Nonlin-Systat v.7, SPSS Inc.). This model also was fit to data from 100 individual simulations under the nominal parameter settings to observe the distribution and variability of estimates of $N_{\mathrm{m}}$ (see Results).

## Results

### Observed rainbow smelt distributions

Rainbow smelt were present in 6 of 9 creeks and channels sampled between lakes (Table 1). Rainbow smelt were numerous in the channels between Fence Lake and Big Crawling Stone Lake and between Big Crawling Stone Lake and Long Interlaken Lake, where they were observed in spawning masses. Rainbow smelt were present in 6 of 14 lakes sampled (Table 2). The chronology of the rainbow smelt invasions in each lake was estimated from personal communications with Lac du Flambeau tribal fisheries biologists (L. Wawronowicz) and Wisconsin Department of Natural Resources fisheries biologists (H. Carlson) and through interviews with local fishers who had caught rainbow smelt (Table 3).

### Simulated rainbow smelt invasions

The mean number of simulated invasions varied with changes in each model parameter. The largest variation in the number of invasions occurred due to changes in the human introduction rates (Fig. 2). Changes in the dispersal ability of rainbow smelt led to relatively smaller changes in the mean number of lakes invaded (Fig. 2). Changes in the extinction rate led to the smallest changes in the number of lakes invaded relative to either stream connections or human introductions (Fig. 2).

Model simulations in which human introductions and immigration parameters were changed concurrently led to the largest response in the number of lakes invaded (Fig. 3). The greatest number of lakes were invaded in simulations where human introduction rates and immigration parameters were increased, with the fewest invaded in simulations where human introduction rates and immigration parameters were concurrently decreased (Fig. 3). Changes in the human introduction rates affected the number of invaded lakes more dramatically than alterations of the connectivity parameters (Fig. 3). The importance of stream connections varied along the gradient of human introductions. At low levels of human introduction, stream invasions increased the number of lakes invaded. Increases in rainbow smelt migration ability at higher levels of human introduction rates had little additional effect (Fig. 3). Changing the level of human introductions was more important than changes in stream passability under several different levels of each parameter.

The rate of new invasions decreased over time, with the cumulative number of rainbow smelt lakes showing a curvilinear trend (Fig. 4). Under the nominal scenario, the model of invasions through time predicted that rainbow smelt would invade all of the habitable lakes after 1000 years

**Fig. 3.** Mean number of lakes invaded for 100 simulations over 100 years in response to (*a*) three levels of human introductions and (*b*) three levels of rainbow smelt migration ability showing the effect of concurrently varying each parameter. Hatched bars indicate results for a 20% reduction in human introduction rates and migration ability, solid bars indicate results for a nominal human introduction rate and migration ability, and open bars indicate results for a 20% increase in human introduction rates and migration ability.

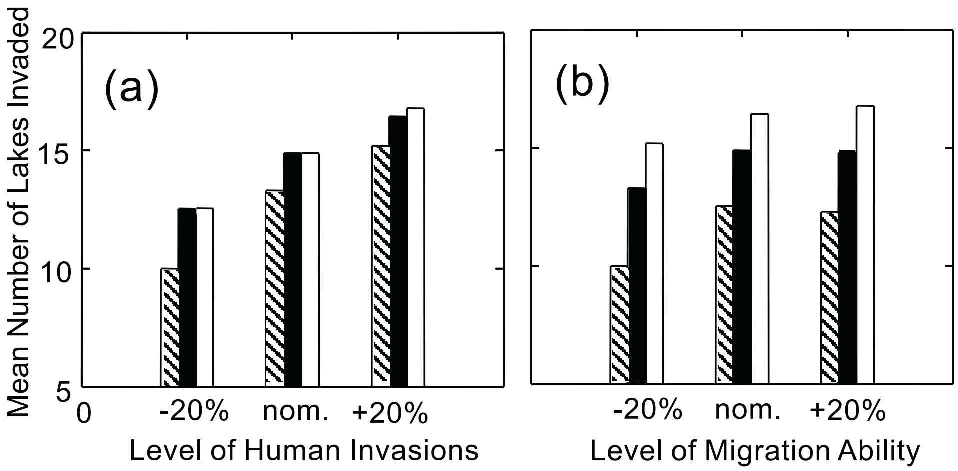



**Fig. 4.** Mean number of invasions for 100 simulations at 50-year intervals over 1100 years under the nominal parameter settings presented as a function of time. Error bars represent standard deviations of the mean. The curvilinear line represents a nonlinear model (see Methods) fit to output. The broken line indicates the number of habitable lakes within the watershed.

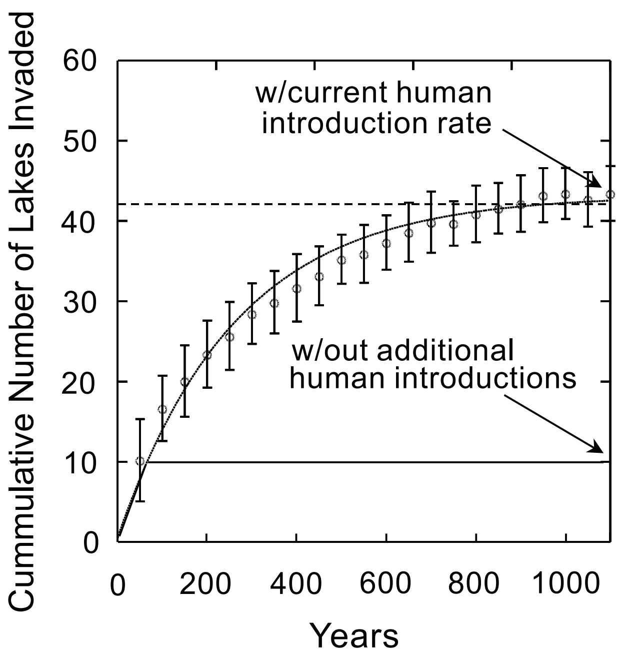
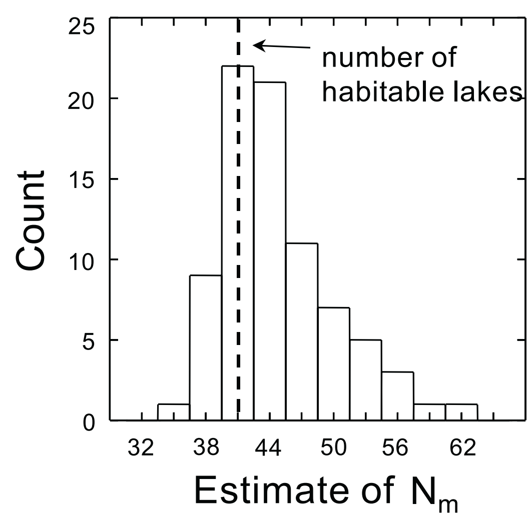



**Fig. 5.** Distribution of estimated asymptote values for 100 individual simulations run for 1100 years. The broken line indicates the total number of habitable lakes within the watershed.




(Fig. 4). If no other human invasions had occurred within the model watershed after Fence Lake was invaded, less than 25% of the lakes would have been invaded by rainbow smelt over 1000 years (Fig. 4). The distribution of maximum number of lakes invaded ($N_m$) from 100 simulations under nominal parameter settings over 1100 years of invasion suggests that extinction may occur but that the lakes often are reinvaded via humans or streams after an extinction takes place (Fig. 5).

## Discussion

Rainbow smelt dispersal across isolated lakes depends primarily on transport and introductions by humans. In the Bear River watershed, only one fourth of the habitable lakes contained rainbow smelt after 1000 years if dispersal was restricted to stream corridors. In contrast, with the present rates of human transport, half contained rainbow smelt after 200 years, three quarters after 300 years, and all after 1000 years. This suggests that lakes isolated from humans will be the only refuge for fishes negatively influenced by rainbow smelt and that they should be managed as such; little can be done once rainbow smelt are in a lake. Human transport creates new epicenters for rainbow smelt to reach new sets of lakes by stream corridors or further human transport and is the only way for rainbow smelt to be dispersed to lakes without stream connections. Clearly, the first priority in the management of exotic rainbow smelt is to eliminate or reduce random dispersal by humans through education of humans about potential vectors.

Human behavior and rainbow smelt spawning habits may be the most important factors contributing to the regional spread of rainbow smelt. Rainbow smelt are caught recreationally each year in the tributaries of the Great Lakes (Becker 1983). They also are caught by the growing numbers of people fishing for them in streams and channels within the Bear River watershed and other watersheds (T.R. Hrabik, personal observation). Rainbow smelt caught during spawning runs are sexually mature adults that contain gametes that, when mixed, may lead to thousands of viable zygotes. After cleaning their catch, people often discard rainbow smelt viscera by tossing them into a nearby waterbody. Introductions from dumping, the use of ripe rainbow smelt as bait, intentional introductions, and accidental introductions all are enhanced by the gathering of the rainbow smelt in shallow tributaries and channels used as spawning habitat by adult rainbow smelt.

Increasing the maximum stream length and gradient through which rainbow smelt migrate during spawning runs did little to influence the simulated dispersal of rainbow smelt through the Bear River watershed, but decreasing each did reduce the average number of lakes invaded. Gradient and stream length may be important considerations in areas with higher topographic relief and longer streams between lakes. In our simulations, the change in number of lakes invaded caused by altering migratory ability was less than that caused by altering human introduction rates. This suggests that the dispersal of rainbow smelt through streams is highly efficient and happens quickly in lake districts where the gradient is slight and stream length between lakes is less than a few kilometres. In large river systems that experience much higher discharge and flooding, downstream dispersal may occur even more rapidly and efficiently over much greater distances (see Mayden et al. 1987; Franzin et al. 1994).

The lakes suitable for habitation by rainbow smelt may be invaded repeatedly over several hundred years through human introduction and from connected lakes. Increasing the rate of introductions by humans led to a proportionately smaller change in the number of new lakes invaded than a decrease in the rate, suggesting a saturation effect at high human introduction rates. Through time, the rate of invasions to new lakes or lakes that had experienced an extinction also decreased. However, based on model output, estimates of the total number of new lakes invaded often exceed the number of habitable lakes (Fig. 5), suggesting that the extinctions were occurring and that lakes were subsequently reinvaded. Given that little is known about the rate of extinctions in rainbow smelt populations, we used estimates that may have overestimated actual rates. Even so, the mode of the asymptote distribution (see Fig. 5) of the number of invaded lakes after 1000 years is roughly equal to the habitable lakes within the Bear River watershed. This suggests that at current rates of human introductions, lakes with suitable habitat that experience an extinction of rainbow smelt will likely be repeatedly reinvaded over longer time scales. In effect, even moderate rates of human introduction may lead to a relatively rapid "saturation" of watersheds. Saturation is likely to occur more quickly under a combination of high human introductions and efficient spread through stream connections and be maintained as long as human introduction rates continue unchecked.

In watersheds like the Bear River watershed, dispersal could be slowed if temporary physical barriers such as low head dams could be placed in areas likely to experience rainbow smelt swimming upstream during spring spawning migrations. At the risk of prohibiting migration of native species that spawn at the same time, these barriers could be maintained for the short duration of rainbow smelt spawning runs and subsequently removed, allowing subsequent runs of native fish to use the streams for spawning habitat. For example, a simple flume with a removable face capable of holding a head of water 3 ft high would likely stop the upstream movement of rainbow smelt in regions that do not experience floods. Downstream movement by larvae will be the most difficult aspect of rainbow smelt dispersal to control because larvae are small, eurythermal, and abundant. Downstream spread is likely responsible for the rapidity of rainbow smelt spread throughout the Missouri, Mississippi (Mayden et al. 1987), English (Campell et al. 1991; Franzin et al. 1994), and Nelson rivers (Remnant et al. 1997).

Assessment and prediction of the most important factors influencing the spread of exotic fishes will continue to be an important aspect of fisheries ecology and fisheries management. Most studies on exotic species focus on how the exotic influences the native biota or ecosystem dynamics. However, conservation and management strategies must focus on reducing the spread of harmful exotics. Observing how spatially explicit population models represent fish dispersal can be used as a method to systematically vary and weigh each parameter and examine the importance of potential factors governing the spread of an exotic species. This method is useful because equations and parameter settings can be altered to simulate dispersal of different species or the same species in very different types of lake districts, making the approach more generally applicable. This approach makes possible projections of potential distributions and the planning of management scenarios prior to likely invasions taking place. Knowing how dispersal of a harmful exotic is represented by a model may help set conservation priorities for vulnerable species in lakes less likely to be invaded and preserve species and populations that might otherwise be locally lost. Accurate prediction of likely invasions may allow unique populations to be conserved through management, a more productive activity than observing the negative effects of rainbow smelt on yet another lake.

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