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ARTICLE

Simulating Effects of Nonintrogressive Hybridization with a Stocked Hatchery Strain of Rainbow Trout on the Sustainability and Recovery of Naturalized Steelhead Populations in Minnesota Waters of Lake Superior

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Abstract

A model was developed to explore the impacts of nonintrogressive hybridization with a stocked hatchery strain of rainbow trout *Oncorhynchus mykiss* (Kamloops strain [KAM]) on the sustainability and recovery of naturalized steelhead (anadromous rainbow trout) populations in Minnesota tributaries of Lake Superior. The model was used to assess the extinction risk of Lake Superior steelhead over a 50-year period based on multiple KAM stocking scenarios, initial population sizes, and levels of assortative mating. No extinctions occurred in simulated steelhead populations regardless of initial size after a one-time introduction of KAM; however, the risk of extinction due to nonintrogressive hybridization increased dramatically for scenarios involving annual stocking of KAM. The level of assortative mating among KAM and steelhead greatly influenced the risk of steelhead population decline or extinction for all scenarios. Results of the model support the contention that nonintrogressive hybridization could be an impediment to the sustainability and recovery of the steelhead population in Lake Superior.

Fish species have been historically introduced or routinely stocked into nonnative habitats (Nico and Fuller 1999), often resulting in hybridization between fish species that were once geographically isolated (Scribner et al. 2001). More than a quarter of documented hybridization events have been found to be a result of fish introductions (Scribner et al. 2001). Hybridization has received growing attention among fisheries managers (Busack and Currens 1995; Lassuy 1995; Allendorf et al. 2001; Utter 2003) as hybridization can increase the risk of extinction of native fish populations (Waples 1991; Lynch 1997). However, while previous research has primarily focused on the genetic perturbations associated with hybridization and its subsequent effects on the sustainability of fish populations (i.e., postzygotic effects; Dunham et al. 1992; Wirgin et al. 2005; Bennett and Kershner 2009), less attention has been devoted to the nongenetic impacts of hybridization, specifically the reproductive interference inherent with hybridization events.

Hybridization between divergent taxa commonly results in introgression, where the genes of one species become integrated into the genome of another (Scribner et al. 2001). Introgressive hybridization occurs when reproduction between species results in the production of viable and fertile hybrids (i.e., F_1 hybrids), which subsequently backcross with members of one or both of the original taxa to form advanced hybrids. The infusion of nonnative genes into the genome of a native fish population may compromise its sustainability by reducing

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interpopulation genetic diversity or by disrupting physical, behavioral, and biochemical adaptations to native environments (i.e., outbreeding depression; Busack and Currens 1995; Arnold 1997; Lynch 1997). If substantial, introgressive hybridization can ultimately result in the "genetic extinction" of one or both of the hybridizing taxa (e.g., type 5 hybridization; Allendorf et al. 2001), such that the "pure" genomes no longer exist (e.g., hybrid swarm; Lynch 1997; Epifanio and Philipp 2000; Scribner et al. 2001). The rate at which genetic extinction will occur is dependent on the initial composition, relative survival rates, and degree of assortative mating (i.e., mate choice) of the hybridizing taxa (Epifanio and Philipp 2000). The detrimental effects of introgressive hybridization between native and introduced nonnative fish on the long-term sustainability of native fish species and stocks have been well documented (e.g., Avise et al. 1997; Weigel et al. 2002; Porath and Nielsen 2003).

Less studied and less documented are the potential detrimental effects associated with nonintrogressive hybridization. Nonintrogressive hybridization occurs when the production of advanced hybrids is inhibited by the low survivability or infertility of F_1 hybrids (e.g., type 4 hybridization; Allendorf et al. 2001), thereby reducing the risk of genetic perturbations commonly associated with introgressive hybridization (e.g., genetic extinction; Epifanio and Philipp 2000). However, hybridization inherently results in a form of reproductive interference. Reproductive interference occurs when the interaction between groups results in the reduction or loss of the reproductive potential to produce genetically "pure" or viable offspring in one or both groups (Leary et al. 1995). In this case, hybridization with the Kamloops strain of rainbow trout *Oncorhynchus mykiss* (hereafter, KAM) interferes with the ability of Lake Superior steelhead (STT; anadromous rainbow trout) to mate with other STT and produce viable offspring. If nonintrogressive hybridization is prevalent, the loss in reproductive output over time may result in the inability of a fish population to sustain itself, particularly when survival and reproductive potential among hybridizing species differ greatly (Leary et al. 1995; Kanda et al. 2002). Wasted reproductive potential associated with nonintrogressive hybridization has been postulated as an impediment to the survival of a number of fish populations (Utter 2003). It has been suspected that nonintrogressive hybridization between wild STT and hatchery strains of rainbow trout within Minnesota tributaries of Lake Superior may have contributed to declines in STT numbers and subsequently inhibited population recovery.

Steelhead in Minnesota Waters of Lake Superior

Beginning in 1895 and continuing through the early 1900s, multiple strains of rainbow trout from a variety of sources throughout the Pacific Northwest (Krueger et al. 1994) were introduced into Minnesota tributaries of Lake Superior (Needham and Behnke 1962; MacCrimmon and Gots 1972). By the 1920s, self-sustaining populations of rainbow trout became established within multiple streams throughout Lake Superior (MacCrimmon and Gots 1972; Krueger et al. 1994) and were called Lake Superior STT. The Lake Superior STT retained migratory life history traits similar to those of anadromous populations from the Pacific Northwest. For example, Lake Superior STT migrate up tributaries to spawn in spring. Juveniles typically "smolt" at age 2 and spend 2–4 years in Lake Superior before returning to their natal streams for their maiden spawning run (i.e., a potamodromous life history; Negus et al. 2008).

By the mid-1900s, Lake Superior STT supported a popular recreational fishery. However, during the 1970s and early 1980s numbers of spawning Lake Superior STT and angler catch rates declined (Schreiner 2003). In response to declines in Lake Superior STT, two hatchery strains of potamodromous rainbow trout, the KAM and the Lake Michigan strain, were stocked into Minnesota tributaries of Lake Superior by the Minnesota Department of Natural Resources (MNDNR) in an effort to create additional fishing opportunities for anglers (Close and Hassinger 1981). Stocking of KAM was initiated in 1976, and stocking of the Lake Michigan strain began in 1981 (Schreiner 1992). In an effort to prevent further reductions in Lake Superior STT numbers and to rehabilitate populations, restrictive angler bag limits were implemented and hatchery supplementation programs were increased in the 1990s using wild Minnesota-strain STT (Schreiner 2003). In 1997, catch-and-release regulations were implemented for Lake Superior STT, and since that time the KAM program has provided the only harvestable rainbow trout fishery in Minnesota waters of Lake Superior (Schreiner et al. 2006).

The KAM strain was initially believed to have originated from STT stocks within the Kamloops region of British Columbia; however, genetic analyses revealed that the strain is from an undetermined rainbow trout population from the West Coast of the United States (Krueger et al. 1994). The Lake Michigan strain was derived from annual gamete collections conducted by the Michigan Department of Natural Resources on the Little Manistee River (Krueger et al. 1994). Both the KAM and Lake Michigan strains have been found to differ genetically from Lake Superior STT (Krueger et al. 1994). Previous genetic analysis suggests that hybridization (introgressive hybridization) between Lake Superior STT and the Lake Michigan strain occurred and may have resulted in the loss of interpopulation genetic diversity (genetic homogenization) among a number of Lake Superior STT populations (Krueger et al. 1994). Consequently, stocking of the Lake Michigan strain was discontinued in 1992 (Schreiner 1992), and stocking rainbow trout from any nonlocal sources into Minnesota tributaries of Lake Superior has been questioned (Schreiner et al. 2006).

To date, no genetic evidence of introgressive hybridization between Lake Superior STT and KAM in Minnesota streams has been identified (Krueger et al. 1994). However, Lake Superior STT and KAM stocked in similar numbers within an experimental reach of a Lake Superior tributary were found to hybridize, suggesting that hybridization between Lake Superior STT and KAM may occur under conditions where the availability of suitable mates or spawning sites are limited (Close 1999)

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or where spawning sites overlap. Further, survival of hatchery-produced hybrids (F_1) of Lake Superior STT and KAM has been shown to be lower than that of Lake Superior STT (Negus 1999; Miller et al. 2004). Hybrids appear to be less tolerant of local stream temperature regimes and exhibit lower predator avoidance behavior, likely reducing their survivability and potential to backcross with pure-strain individuals (introgressive hybridization). Consequently, mating of Lake Superior STT and KAM may occur in the form of nonintrogressive hybridization, making hybridization difficult to detect by genetic analysis.

There is concern that reproductive interference associated with nonintrogressive hybridization between Lake Superior STT and KAM may be a current and future impediment to the recovery of Lake Superior STT populations in Minnesota (Schreiner 2003). Restoration of Lake Superior STT populations in Minnesota is important as fisheries based on natural production are more cost effective than those relying on artificial production. Lake Superior STT populations also provide additional fishing opportunities, and there is support among STT anglers for the preservation of the genetic integrity of the Lake Superior STT strain. To minimize the potential for hybridization between STT and KAM in Minnesota tributaries of Lake Superior, stocking of KAM has been restricted to three rivers in the extreme southwest end of the lake (Lester, Talmadge, and French rivers; Figure 1), all of which have limited or no spawning habitat accessible to potamodromous fish.

Weirs on the French and Knife rivers are maintained by the MNDNR to monitor annual spawner returns and collect gametes for hatchery production while also allowing biologists to limit KAM access to Lake Superior STT spawning sites. Straying of KAM has been documented and at times may comprise a small portion of rainbow trout spawning runs within a number of unstocked Minnesota tributaries (e.g., range = 6–35%, mean = 16% in the Knife River; MNDNR, unpublished data; Figure 1). Despite concerns, KAM stocking continues because it provides a very popular shore fishery, especially during winter when other species are unavailable. Harvest-oriented anglers continue to press for the expansion of KAM stocking to include all Lake Superior tributaries along the entire Minnesota shore.

The purpose of this study was to evaluate the possible impact of nonintrogressive hybridization with KAM on Lake Superior STT populations in KAM-stocked streams and adjacent streams along the Minnesota shore of Lake Superior. A model was developed using life history characteristics and survival rates from Minnesota populations to determine how different KAM stocking scenarios and levels of assortative mating influence Lake Superior STT abundance and associated population extinction risk over a 50-year period. This model could be used to evaluate the potential extinction risk of Lake Superior STT under the current management strategy of both creating a nearshore recreational KAM fishery and preserving and rehabilitating STT populations within Minnesota waters of Lake Superior. Further,

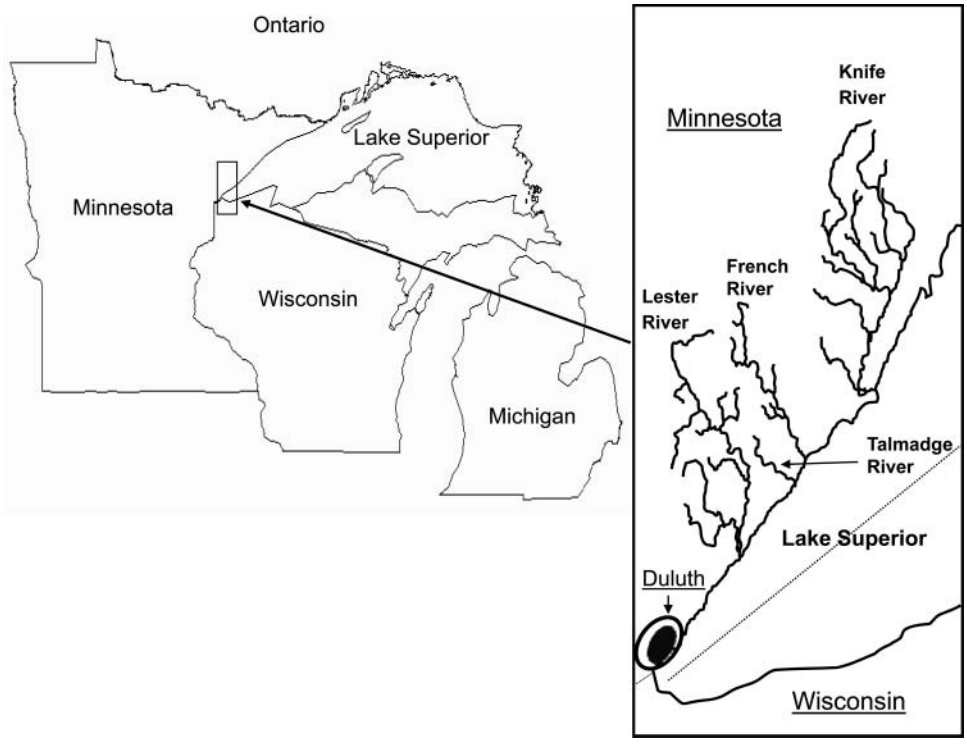

FIGURE 1. Map of a portion of Minnesota's Lake Superior shoreline, showing the locations of rivers where Kamloops-strain hatchery rainbow trout (KAM) were stocked (Lester, Talmadge, and French rivers) and where fish traps were installed to monitor KAM and Lake Superior steelhead populations (French and Knife rivers).

TABLE 1. Life history parameter values for naturalized Lake Superior steelhead (STT); the values were used in a model evaluating the effects of nonintrogressive hybridization with Kamloops-strain hatchery rainbow trout on STT populations in Minnesota tributaries of Lake Superior. Parameters generate a starting (year-0) spawning population of 100, 350, and 1,000 adults (age ≥ 4) for the small, large, and recovered STT populations, respectively.

		Initial STT population size		
Life history parameter for STT	Value[a]	Small	Large	Recovered
Survival rates				
Egg[bc]	48.0%			
Fry to age 2	1.0% (0.002%)	46,400	162,400	464,000
Age 2	25.0% (0.050%)	464	1,624	16,240
Age 3	50.0% (0.050%)	116	406	4,060
Age 4	55.0%	58	203	2,030
Age 5	55.0%	42	148	1,480
Age 6	55.0%	24	84	840
Age 7	55.0%	17	60	600
Age 8	55.0%	8	28	280
Age 9	0.0%	6	21	210
Male: female sex ratio	1.0:1.5			
Fecundity (eggs/female)	3,450			
Maturation schedule[d]				
Age 4	28.5%			
Age 5	67.4%			
Age 6	100.0%			

[a]Values in parentheses are SDs.
[b]Egg survival rate distribution was a beta distribution ($\alpha = 7$, $\beta = 7$).
[c]Egg numbers were variable, and initial egg numbers were derived in the first iteration of the model.
[d]Percentage of STT at a given age that will spawn in each year of the model.

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the interactions between KAM and Lake Superior STT populations in Minnesota provide a unique opportunity for quantifying the potential risks of nonintrogressive hybridization with nonnative fish species or strains to the sustainability of native or naturalized fish populations in general.

METHODS

To evaluate the effects of nonintrogressive hybridization on the sustainability and recovery of STT populations within a hypothetical tributary of Lake Superior, we developed an age-structured spreadsheet model built using Microsoft Visual Basic for Applications within Microsoft Excel (contact K.S.P. for model details and availability). The model incorporates life history characteristics (e.g., egg production, survival rates, and maturity schedules) and abundances of Lake Superior STT and KAM (Table 1). The model calculated numbers of adult Lake Superior STT, KAM, and associated hybrids that would return to spawn annually over a 50-year period under multiple scenarios reflecting various KAM stocking rates and initial STT abundances. We differentiated between KAM produced in the hatchery and KAM produced in the wild as well as hybrid progeny derived from crosses where the maternal parent was a Lake Superior STT and those where the maternal parent was a KAM, as the survival rate of each was different. We performed 1,000 iterations of each scenario. The level of assortative mating (percent spawning only with members of the same strain) between Lake Superior STT and KAM for each iteration was assigned at random (values from 0% to 99%). Survival rates of early life stages for Lake Superior STT were allowed to fluctuate randomly across years. Survival of KAM and hybrids was calculated within the model by applying empirically and observationally derived relative survival rates (i.e., relative to Lake Superior STT). By using relative survival rates, the model was able to take advantage of previously measured differential survival rates (Negus 1999; Miller et al. 2004; Negus et al. 2008) and provide consistency in survival rates among rainbow trout strains over time (e.g., "poor" survival years for STT in Lake Superior were assumed to equate to poor survival years for stocked KAM). Details on the derivation of life history parameters and relative survival rates used in this model can be found in Appendix 1. For each iteration of the model, the status of the Lake Superior STT population after 50 years was classified as extinct, declining, stable, or growing. The risk of extinction for a STT population was evaluated based on the number of adult STT spawners remaining after 50 years and population trends.

Calculation of Lake Superior steelhead numbers.—At each year in the simulation, stage-specific survival rates for Lake Superior STT were first calculated by incorporating a stochastic element to the base survival rates, as described above. The age

TABLE 2. Relative survival rates of progeny produced from various crosses of naturalized Lake Superior steelhead (STT) and Kamloops-strain hatchery rainbow trout (KAM); relative survival rates are based on STT survival. Natural crosses refer to those potentially occurring in the wild, and hatchery crosses refer to KAM production in the hatchery. Relative survival of hybrids and naturally produced KAM from age 2 to age 9 was assumed to be 1.0.

Crosses[a]	Proportion female	Fecundity[b]	Maturation schedule[c]	Relative survival					
				Egg to fry[d]	Fry to age 2[e]	Ages 2–3	Ages 3–4	Ages 4–9	Overall survival
Natural Crosses									
Hybrid (*S*)	1.00	1.30	1.00; 1.00; 1.00	1.00	0.59	1.00	1.00	1.00	0.59
Hybrid (*K*)	1.00	1.30	1.00; 1.00; 1.00	0.80	0.37	1.00	1.00	1.00	0.30
KAM	1.00	1.70	1.00; 1.00; 1.00	0.67	0.21	1.00	1.00	1.00	0.14
Hatchery Production[f]									
KAM[g]			1.20; 0.94; 1.00			0.80	1.20	0.07	0.07

[a] S = STT female used in hybrid cross; K = KAM female used in hybrid cross.
[b] Strain fecundity based on hatchery observations.
[c] Relative percentages of fish spawning by age 4, age 5, and age 6, respectively.
[d] From Negus (1999).
[e] Modified from Miller et al. (2004).
[f] Relative survival rates of progeny produced by hatchery crosses were based on catch-curve analysis conducted by the Minnesota Department of Natural Resources.
[g] Because hatchery-produced KAM are stocked as yearlings and are equivalent in size and life stage to age-2 STT, the ages of these KAM are actually 1 year less than the ages stated in the column headings.

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structure in year t was then calculated as

$$N(a, t) = N(a - 1,\ t - 1) \cdot S(a - 1,\ t - 1) \text{ for } a > 1, \quad (1)$$

where a is age and S is the survival rate. The number of mature females was calculated as

$$\text{SST}(t) = \text{sum}[N(a,\ t) \cdot \theta(a)], \quad (2)$$

where θ is the proportion of females at age a. The number of STT oocytes can then be calculated as

$$N_{\text{oocytes}}(t) = \text{SST}(t) \cdot E, \quad (3)$$

where E is the average number of eggs per female. Next, the stage-specific survival rates for KAM were obtained by multiplying the STT survival rates by the relative survival values of KAM (Table 2). Updating of KAM age structure, number of mature females, and number of oocytes proceeded as described for Lake Superior STT. Stage-specific survival rates for hybrids were obtained by multiplying the STT survival rates by the hybrid relative survival values (Table 2), and updating of hybrid numbers proceeded as described for STT.

Given the assortative mating rate and with the numbers of mature male and female Lake Superior STT, KAM, and hybrids at hand, the expected proportion of matings with same-strain, other-strain, and hybrid lines could be calculated (as described under assortative mating rates). The number of oocytes was then assigned proportionately to calculate the number of zygotes produced ($N[a = 0, t]$) of each type (Lake Superior STT, KAM, hybrids, and backcrosses).

Scenarios.—We developed four sets of scenarios to evaluate the synergistic effects of nonintrogressive hybridization and stocking of KAM on the sustainability of STT populations in Minnesota waters of Lake Superior (Table 3). The first scenarios (1 and 2) were base scenarios that were run with no KAM stocking to estimate the intrinsic rate of population growth for Lake Superior STT. The second set of scenarios (3–11) was designed to estimate the response of the Lake Superior STT population to nonintrogressive hybridization after exposure to a one-time stocking of KAM (no annual stocking). The numbers of KAM yearlings introduced in year 1 of the model scenarios were 5,000, 25,000, and 50,000.

A third set of scenarios (12–20; Table 3) incorporated annual stocking of KAM beginning on year 1 of the model. Lake Superior STT spawner abundances were exposed to one of three annual KAM stocking rates (5,000, 25,000, and 50,000 yearlings/year). Although the numbers of KAM stocked were chosen arbitrarily, the greatest number of KAM stocked was similar to numbers previously stocked within the French and Lester rivers (Schreiner 2003; Figure 1).

Because KAM were known to stray from stocked streams (Schreiner 2003), we also modeled the impacts of KAM straying on unstocked streams (scenarios 21–23; Table 3). The model applied an annual straying rate into our hypothetical stream of 0.9%. While straying rates are often presented as the percent of the total spawning run, our straying rate represented the percent of KAM stocked into nearby streams and surviving to age 4 that subsequently strayed to our hypothetical stream. Survival of straying KAM from nearby streams paralleled annual variability in survival of Lake Superior STT in our hypothetical stream. Minnesota Department of Natural Resources management goals are to stock 92,500 KAM yearlings/year in the Minnesota waters of Lake Superior (35,000 yearlings/year in the French River; 32,500 yearlings/year in the Lester River; and 25,000 yearlings/year in the Talmadge River; Figure 1). The 0.9% straying

TABLE 3. Twenty-three modeling scenarios based on differing stocking frequencies, stocking numbers, and straying (annual straying rate = 0.9%) of Kamloops-strain hatchery rainbow trout (KAM); scenarios were used to evaluate the effects of nonintrogressive hybridization on the sustainability and recovery of small ($N = 100$ adults), large ($n = 350$ adults), and recovered ($n = 1{,}000$ adults) populations of naturalized steelhead (STT) within Minnesota tributaries to Lake Superior. For scenarios in which KAM were stocked once, stocking occurred at year 1 of the model.

Scenario	STT population size	KAM stocking	KAM number stocked (or presence of straying)
1	Small	None	None
2	Large	None	None
3	Small	Once	5,000
4	Small	Once	25,000
5	Small	Once	50,000
6	Large	Once	5,000
7	Large	Once	25,000
8	Large	Once	50,000
9	Recovered	Once	5,000
10	Recovered	Once	25,000
11	Recovered	Once	50,000
12	Small	Annual	5,000
13	Small	Annual	25,000
14	Small	Annual	50,000
15	Large	Annual	5,000
16	Large	Annual	25,000
17	Large	Annual	50,000
18	Recovered	Annual	5,000
19	Recovered	Annual	25,000
20	Recovered	Annual	50,000
21	Small	Annual	Straying
22	Large	Annual	Straying
23	Recovered	Annual	Straying

rate we used produced numbers of KAM strays ($N = 22$–120) similar to those observed in annual spawner assessments at the Knife River. Percentages of the Knife River spawning run comprising KAM strays from the French River (mean = 5.3%, range = 3–10%) appear typical for what has been documented among other hatchery-produced salmonids (Altukhov and Salmenkova 1994; McElhany et al. 2000; Schroeder et al. 2001).

Evaluation.—For each scenario, the sustainability and recovery of the Lake Superior STT population were evaluated based on the number of STT spawners remaining after 50 years. When the number of STT spawners was less than two fish after 50 years, the STT population was assumed to be extinct. Otherwise, we calculated the long-term population growth rate (r; Quinn and Deriso 1999; McClure et al. 2003) as

$$r = 1 + \frac{\left(\log_e N_{50} - \log_e N_0\right)}{t}, \quad (4)$$

where N_0 is the Lake Superior STT population size at year 1, N_{50} is the STT population size at year 50, and t is the number of years ($t = 50$). Growth rates greater than 1.0 represented an increasing population, growth rates equal to 1.0 represented a stable population, and growth rates less than 1.0 represented a declining population. Since the population size of Lake Superior STT is likely to be limited by factors such as available spawning habitat, we limited the STT population size to 1,000 spawners for the small population or 3,500 spawners for the large population. The proportion of iterations where the Lake Superior STT population went extinct, was in decline, was stable, or was growing was graphed for all scenarios and levels of assortative mating. Levels of assortative mating were grouped in 10% increments for analysis. Within a given level of assortative mating, we summed the proportion of iterations where the STT population went extinct or was in decline and defined this value as the "extinction risk." We arbitrarily designated scenarios where the extinction rate was 20% or higher as high risk. We also compared time to extinction (mean number of years) for populations that became extinct for each combination of assortative mating, level of KAM stocking, and initial STT abundance.

RESULTS

Modeling the change in the Lake Superior STT spawning population where no KAM were stocked (base model), we found that the rate of growth for the small STT population ($N = 100$ adults) and large STT population ($N = 350$ adults) was 1.046. Therefore, the Lake Superior STT populations were expected to grow based on the life history parameters developed and no KAM stocking. Modeled scenarios evaluating changes in STT spawner abundance related to a one-time stocking of KAM (scenarios 3–11; Table 3) found that there was no risk of extinction due to nonintrogressive hybridization. The STT population was either growing or stable for scenarios involving a one-time stocking of KAM. Annual stocking of KAM (scenarios 12–20; Table 3) carried a much greater risk of extinction of STT populations. Although the proportions of iterations where STT populations went extinct or were declining, stable, or growing differed among KAM stocking rates and the initial STT population sizes, for most scenarios there was a high risk of extinction (i.e., scenarios where the STT spawner population was either extinct or declining after 50 years for at least 20% of iterations conducted) if assortative mating rates were less than 60% (Figure 2a–i). For the large STT population, there was a high risk of extinction if assortative mating rates were less than 50% when 5,000 KAM were annually stocked (Figure 2d). A notable reduction in extinction risk was observed for the "recovered" STT population ($n = 1{,}000$ adults) when KAM stocking was 5,000. The mean number of years to extinction decreased as the level of assortative mating and initial STT population size decreased and as the number of KAM stocked increased (Figure 3). In nearly all cases, the time to extinction was greater than 20 years, most cases being greater than 30 years. For modeled

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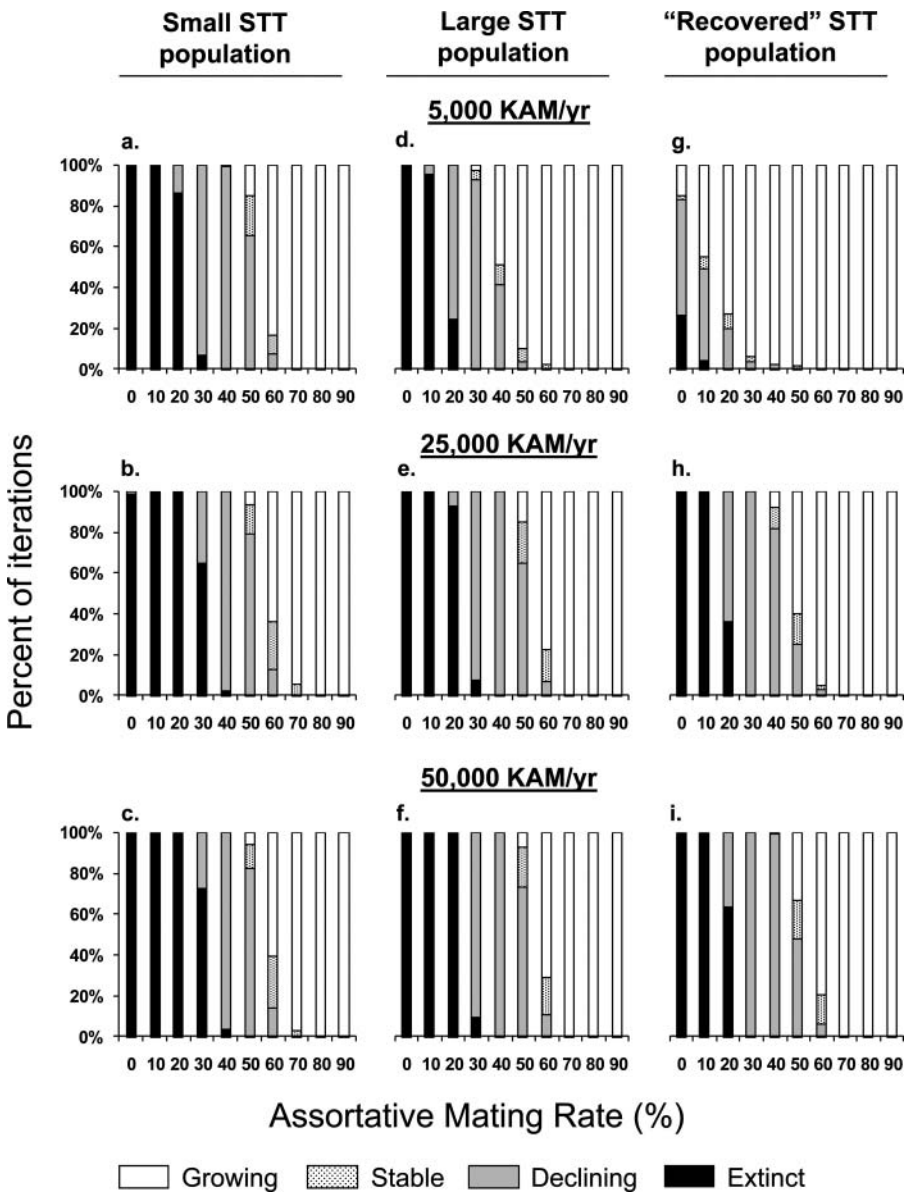

FIGURE 2. Proportion of model iterations, within a given level of assortative mating, in which a small ($n = 100$ adults), large ($n = 350$ adults), or "recovered" ($n = 1{,}000$ adults) population of Lake Superior steelhead (STT) was growing, stable, declining, or extinct after 50 years for three scenarios of Kamloops-strain hatchery rainbow trout (KAM) stocking.

scenarios involving the straying of KAM to our hypothetical stream (scenarios 21–23; Table 3), there was no risk of extinction found for the large and recovered STT populations and a high risk of extinction for the small STT population only if assortative mating rates were low (<30%).

DISCUSSION

Our model has shown that unless assortative mating rates are very high, nonintrogressive hybridization with KAM may negatively impact the long-term sustainability of STT populations in Lake Superior tributaries if KAM are stocked annually. The rate of KAM stocking and level of assortative mating greatly influence the extent of nonintrogressive hybridization, Lake Superior STT population size, and probability of extinction. There was little evidence that a one-time stocking of KAM (5,000, 25,000, or 50,000) would impact the long-term sustainability of Lake Superior STT populations at any level of assortative mating. Resiliency of modeled STT populations after a one-time stocking of KAM was likely related to the lower long-term survivability of KAM and hybrids relative to Lake Superior STT (Table 2; Negus 1999; Miller et al. 2004). Even though KAM females were 1.7 times more fecund than Lake Superior STT, relative survival of stocked KAM from ages 3 to 8 (0.07) and the

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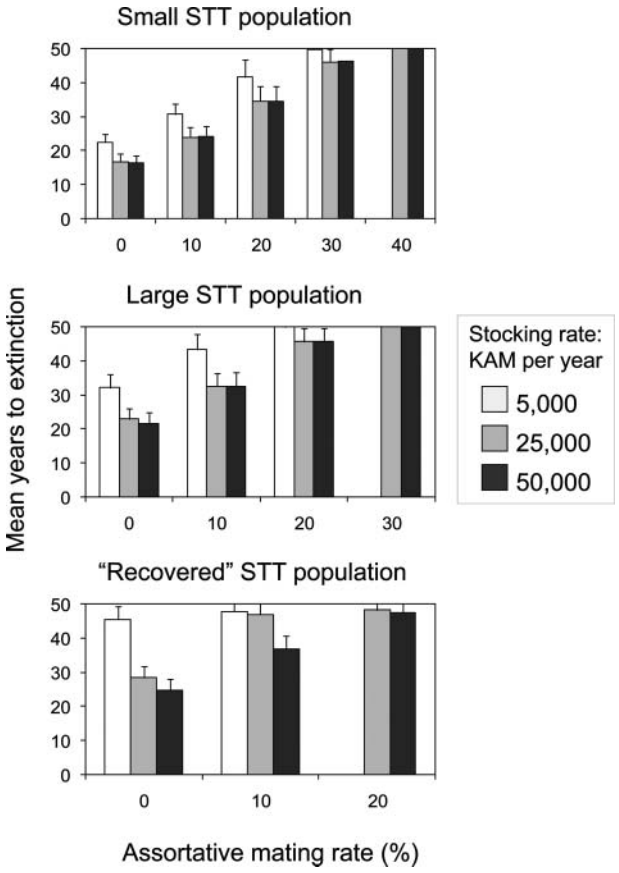

FIGURE 3. Mean (+SE) number of years to extinction of simulated Lake Superior steelhead (STT) populations as related to initial STT population size and annual stocking rates of Kamloops-strain hatchery rainbow trout (KAM) yearlings.

subsequent relative survival of naturally produced KAM from egg to age 2 (0.14) were low. Consequently, lower long-term survivability relative to Lake Superior STT prevented KAM from perpetuating over the time frame of the model (50 years), limiting the potential for nonintrogressive hybridization to impact the sustainability of Lake Superior STT populations. However, the model also showed that STT numbers tend to decline precipitously during the first 10–20 years after a one-time stocking of KAM before rebounding, resulting in the potential short-term risk of extinction due to a catastrophic event or disease.

Annual KAM stocking resulted in a large and consistent number of KAM hybridizing with Lake Superior STT over the entire time frame of the model, reducing the long-term reproductive potential of STT and greatly increasing the risk of extinction of Lake Superior STT populations. In another model evaluating introgressive hybridization, Epifanio and Philipp (2000) found that differential survivability among hybridizing taxa had a dramatic influence on the rate at which introgressive hybridization resulted in the genetic extinction of parental lineages. Within the Bitterroot River system of Montana, a combination of disproportionate reproductive fitness and nonintrogressive hybridization was suspected of contributing to the replacement of native populations of bull trout *Salvelinus confluentus* by introduced brook trout *S. fontinalis* (Leary et al. 1995). Intuitively, the annual stocking of KAM in our model resulted in an increase in the population size of KAM relative to Lake Superior STT. This increases the rate at which STT indiscriminately spawn with KAM and thereby reduces the per capita production of pure STT embryos.

The risk of extinction of Lake Superior STT populations from nonintrogressive hybridization will ultimately depend on the level of assortative mating between STT and KAM. The potential for strongly assortative spawning may be reduced where access to spawning areas is limited. Most Lake Superior tributaries in Minnesota are generally small and possess limited spawning habitat, and upstream migration is inhibited by waterfalls that occur within a kilometer of the lake (Hassinger et al. 1974; Negus 2003). Hybridization between naturalized and hatchery-produced STT in other Great Lakes has been documented (Bartron and Scribner 2004). Also, hybridization between taxa can be exacerbated through environmental or anthropogenic perturbations (Scribner et al. 2001), such as a reduction or degradation of spawning habitat. These disturbances result in increased competition for quality spawning sites, compromising previously established temporal and spatial isolation barriers. Further, hybridization between highly divergent salmonids, which can possess stronger ecological, physical, and behavioral reproductive barriers when compared with Lake Superior STT and KAM, is a common occurrence (Hubbs 1955; Scribner et al. 2001). In addition, and particularly pertinent to this study given the large numbers of KAM stocked relative to the number of Lake Superior STT, the relative proportion of each strain of rainbow trout within a system may influence the potential for hybridization (e.g., difficulty in locating mates; Scribner et al. 2001). Therefore, although the actual rate of assortative mating between Lake Superior STT and KAM is not known, it likely occurs to some extent and varies among streams and conditions.

The time to extinction for the Lake Superior STT populations that went extinct in our model was as little as 16 years, suggesting that extinction may occur quickly if assortative mating is low. Given that no Lake Superior STT population actually went extinct during the 20–30 years after initial declines, assortative mating may be greater than the lowest levels of assortative mating evaluated (e.g., <20–30%). However, where STT populations were declining at higher levels of assortative mating in our model, extinction would be expected to occur beyond the 50 years. Knife River trap data and creel data from many streams show that KAM generally do not move upstream as far, or surmount small barriers as successfully as Lake Superior STT (MNDNR, unpublished data), which would suggest that assortative mating is relatively high. More research into the extent of reproductive isolation between Lake Superior STT and KAM is needed.

The initial size of the Lake Superior STT population had little impact on the risk of extinction for most scenarios

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evaluated. Within a given level of assortative mating, the proportion of iterations where a STT population either went extinct or was declining typically increased as the stocking rate of KAM increased. However, overall trends in the risk of extinction were fairly consistent across stocking rates for all STT populations modeled, particularly for KAM stocking rates of 25,000 and 50,000. This was surprising given that the large STT population was 3.5 times greater than the small STT population and the recovered population was 10 times greater than the small population. Previous models have shown initial relative abundance of hybridizing taxa had an appreciable effect on the rate of introgressive hybridization (Epifanio and Philipp 2000). We speculate that the numbers of STT, particularly for the small and large populations, may not differ enough (in relation to the large numbers of KAM stocked) to promote an appreciable difference in the risk of extinction. Because the small and large STT population sizes modeled reflected the range of STT population sizes found within Minnesota tributaries to Lake Superior, STT populations in Minnesota tributaries might possess similar risks of extinction if large numbers of KAM are stocked in the same vicinity and if the limited spawning habitat is accessible to both strains. Notably, extinction risk was greatly reduced for the recovered population when KAM stocking was 5,000, suggesting that Lake Superior STT numbers may have to be substantially high or KAM stocking may have to be very low to greatly reduce the risk of extinction. Further modeling to identify whether there is a threshold in Lake Superior STT population size at which the risk of extinction dramatically declines and how that population size relates to restoration goals would be useful.

Model Limitations

The complexity of our model has advantages and disadvantages. By using actual Lake Superior STT life history data from Minnesota waters, results of the model will be more comprehensive and realistic. However, by doing so, we were required to make a number of important assumptions regarding relative survival rates, assortative mating, spawning behavior, and environmental influences on the two strains. For example, we assumed that adult hybrids (age ≥ 4) would have the same survivability as Lake Superior STT. This may be an overestimation given that survival rates of hybrids at earlier life history stages are low compared with Lake Superior STT. However, given the lower relative survival of hybrids from eggs to age 4, very few survived to maturity and mated with STT in our model, resulting in little influence by hybrids on the overall results. In addition, the extinction risk for Lake Superior STT could differ from that observed due to density-dependent forces differentially limiting the numbers of STT and KAM. Lake Superior STT production in Minnesota streams is limited by stream morphology (e.g., limited spawning and nursery habitat) and productivity, and competition for a limited forage base in Lake Superior may limit both STT and KAM survival. Further, assortative mating rates may change relative to population size. That is, as the abundance of Lake Superior STT declines relative to KAM over time and as mates become scarce, the level of assortative mating may decrease, thereby accelerating the time to extinction.

Management Implications

The results of this model suggest that nonintrogressive hybridization coupled with unrestricted annual stocking of KAM may impede the sustainability and rehabilitation of STT populations within Minnesota waters of Lake Superior. However, the KAM fishery maintains substantial angler interest and support as KAM are the only strain of rainbow trout that may be harvested within Minnesota waters of Lake Superior. In the Lake Superior spring shorewide creel from 1992 through 2008, 44.9% of anglers targeting rainbow trout indicated they were targeting KAM. Consequently, to achieve the goals of conserving Lake Superior STT and providing additional angling opportunities, KAM stocking and STT restoration efforts are both required. We recommend no expansion of the stocking of KAM or any other hatchery strain of rainbow trout. Current management practices that restrict KAM stocking to a limited number of streams (with little or no accessible spawning habitat) near the City of Duluth (i.e., closer to anglers) should be maintained. Although we did not find KAM straying to be an appreciable risk to the sustainability of Lake Superior STT at current straying rates, efforts to reduce straying of KAM and to monitor the extent of straying should continue in order to assess the potential risks to Lake Superior STT populations. Concomitantly, efforts to enhance the fidelity of KAM to stocking sites (e.g., stock at earlier life stages) should also continue (Schreiner 2003). In addition, Lake Superior STT abundance should be monitored closely. Even if Lake Superior STT populations were to remain stable or grow in spite of hybridization with KAM, STT numbers may still not be large enough to prevent losses in genetic or behavioral diversity (Allendorf and Ryman 1987; Lande and Barrowclough 1987; Rieman and Allendorf 2001), and smaller populations may be more vulnerable to environmental perturbations such as drought or disease.

In conclusion, our model evaluated the effects of hybridization on a fish population in a context rarely considered within fish management. Previous research on the effects of hybridization has focused primarily on the extent and impacts of introgressive hybridization on fish populations, where extensive introgressive hybridization results in the disruption of genetic, physical, and behavioral adaptations, potentially reducing the long-term sustainability of fish populations. Our model focused on an extreme end of the introgressive hybridization continuum—nonintrogressive hybridization—and found that hybridization may continue to inhibit the sustainability of fish populations even when introgression does not occur. Although limited in scope to population and life history characteristics of STT within Minnesota tributaries to Lake Superior, our model may be used as a frame of inference for the management of other STT populations throughout the Great Lakes. For example, there is concern that hybridization with hatchery-produced strains may negatively impact STT populations within Michigan tributaries to

Lake Michigan (Bartron et al. 2004; Bartron and Scribner 2004). Our model may help to conceptualize and quantify the potential negative impacts that nonintrogressive hybridization may have on naturalized or native species or strains, particularly among conspecifics (Allendorf 1991; Allendorf et al. 2001). Periodic stocking of introduced fish may exacerbate the risks associated with nonintrogressive hybridization by diminishing or negating intrinsic competitive advantages in survival or reproductive potential of native or naturalized fish.

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Appendix 1: Model Life History Parameters and Relative Survival Rates

INITIAL LAKE SUPERIOR STEELHEAD ABUNDANCE

The mean annual numbers of adult Lake Superior STT returning to spawn in the French River (mean $\sim$ 100; range = 35–235) and the Knife River (mean $\sim$ 350; range = 87–594) were used to represent small and large STT populations, respectively, along the Minnesota shore of Lake Superior. These data were collected during annual spawner assessments by MNDNR staff from 1996 to 2008 on the Knife River and from 1993 to 2008 on the French River. Although spawner trap catches were not equivalent to the total size of the Lake Superior STT population in each respective river, fisheries managers use spawner abundance as an index of the sustainability of a STT population over time; therefore, spawner trap catches are used as a surrogate measure of population size within our model. A Lake Superior STT abundance of 1,000 was used to estimate the impacts of hybridization on a recovered STT population. However, it should be noted that this value does not necessarily reflect any specific management goals and may be impractical for many STT populations due to limited spawning habitat. It should also be noted that hatchery supplementation of Lake Superior STT does occur within a limited number of systems. However, supplemental stocking of STT was not incorporated within the model as this is a stopgap measure designed to support and restore STT populations until they are self-sustaining, and the inclusion of STT stocking would confound our ability to identify underlying limitations in Lake Superior STT survival.

ASSORTATIVE MATING RATES

To assess the influence of assortative mating on the effects of nonintrogressive hybridization, the model applied an assortative mating rate of between 0% and 99% to Lake Superior STT and to all KAM (naturally and hatchery produced). As an example, if the assortative mating was set to 60%, we assumed that 60% of the spawning STT and KAM would spawn exclusively with their own strain. The remaining 40% of the spawning STT were assumed to spawn indiscriminately and proportionately with a pool of potential mates consisting of all STT, all hybrids (F_1 and beyond), and 40% of the KAM. The pool of potential mates for indiscriminately spawning KAM was calculated similarly. It should be noted that the range of assortative mating rates we used likely exceeds what may be biologically realistic; however, comparative or empirical information on assortative mating rates among STT or other salmonids appears to be lacking.

SURVIVAL RATES

Average number of eggs produced per STT and KAM female was based on long-term hatchery data, and the number of eggs produced by hybrid females was assumed to be the average of the numbers produced by Lake Superior STT and KAM females (MNDNR, unpublished data; Table 2). Based on data collected during spawner assessments, we used a 1.0:1.5 male-to-female ratio to estimate the number of male and female progeny produced. We employed data from the hatchery (e.g., percent egg hatch; Negus 1999), data collected at smolt and adult spawner traps (French and Knife rivers; Figure 1), and catch-curve analyses (ages $\geq$ 3) to estimate Lake Superior STT survival from hatch to age 9 within the model. Because the survival rates of early life stages of STT are highly variable, we developed a distribution of survival rates for each early life stage: hatch, fry to age 2, age 2 to age 3, and age 3 to age 4 (adulthood). The model randomly selected survival rates independently from each distribution and then multiplied the individual survival rates to calculate an overall survival rate for juvenile STT (hatch to age 4; Table 1). Within a hatchery environment, mean egg to fry survival for French River STT averaged 75% (range = 16–97%) under ambient river water temperatures (Negus 1999). Although the mean egg-to-fry survival rate can vary greatly, for modeling purposes we used a median survival rate of 48% (MNDNR, unpublished data). We assumed a beta distribution ($\alpha = 7$, $\beta = 7$) for STT egg to fry survival because natural conditions (e.g., highly variable flow rates, temperature, and sedimentation) within Minnesota promote lower hatch rates than those observed in the hatchery. The distribution encompassed both

minimum (20%) and maximum (90%) estimates of survival observed in the hatchery (Negus 1999). Survival rates of STT life stages from fry to age 4 were assumed to be normally distributed because ranges of observed survival rates for these life stages were narrow. Data collected from the smolt trap on the French River (1994–2008) suggest that the mean survival rate of fry to age 2 was 1% (SD = 0.002). French River data suggest that survival from age 2 to spawning is about 10%. In this model, we used a survival rate of 25% (SD = 0.050) for STT from age 2 to age 3 and a survival rate of 50% (SD = 0.050) for STT from age 3 to age 4. Survival rates of STT in Lake Superior between age 2 and age 4 have not been directly evaluated but were estimated based on the number of STT collected annually at the French River (1993–2008) and Knife River (1996–2008) spawner traps. Based on catch-curve analyses from Knife River spawner assessments, we assigned an annual STT survival rate of 55% for all STT from age 4 to age 9. We assumed based on catch-curve data that no STT survived past age 9.

Survival of naturally produced KAM and hybrids from hatch to age 2 was derived from relative survival rates (i.e., relative to STT) developed by Negus (1999) and Miller et al. (2004), while relative survival of naturally produced KAM and hybrids older than age 4 was assumed to be 1.0. Although relative survival rate estimates from Miller et al. (2004) were calculated from fry up to age 1+ ($\sim$13.5 months), we applied them to fry through age 2, a probable overestimate of survival for this period. We assumed that the survival of all progeny developed from all backcrosses was zero. We believe that this is a reasonable assumption given that genetic analysis has found no hybridization between Lake Superior STT and KAM, while hybridization between Lake Superior STT and other strains has been extensive. Furthermore, research has shown that fitness of Lake Superior STT $\times$ KAM hybrids is substantially lower than that of Lake Superior STT.

Relative survival of stocked KAM was estimated based on data collected from catch-curve analyses and spawner assessments at the French River (1993–2008). The KAM are stocked as yearling smolts that have been reared at an accelerated rate in the hatchery to a similar size and life stage as those of age-2 wild STT smolts. Survival estimates for KAM of ages 1–3 were derived based on the number of KAM sampled at the French River spawner trap. The survival of yearling KAM to age 2 was selected as 20% (we assumed an SD of 0.050), or 0.8 times the survival of age-2 STT to age 3 (all comparisons of stocked KAM with wild STT are offset by 1 year due to the accelerated development of KAM in their first year of life; Table 2). Survival of stocked KAM at age 2 was 60%, or 1.2 times the survival of comparably sized age-3 STT. Survival of stocked KAM was estimated to be 55% at age 3 and 28% annually for ages 4 and older. Note that the survival rate for adult KAM (identifiable by a clipped adipose fin and subject to harvest) was lower than that of adult Lake Superior STT (for which harvest is prohibited).

Since STT mature at different ages, we derived a maturation schedule (28.5% at age 4; 67.4% at age 5; and 100% at age 6) based on spawner assessment data and consistent with the estimated age composition of STT maiden spawners (age 4: 48%; age 5: 36%; age 6: 16%; MNDNR, unpublished data) and with our estimated survival rates. For KAM, we used a maturation schedule (34.8% at age 4; 63.4% at age 5; and 100% at age 6) that was consistent with the age composition of KAM maiden spawners (age 4: 62%; age 5: 28%; age 6: 10%).

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