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Reconstructing Sakhalin Taimen *Parahucho perryi* Historical Distribution and Identifying Causes for Local Extinctions

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ARTICLE

Reconstructing Sakhalin Taimen *Parahucho perryi* Historical Distribution and Identifying Causes for Local Extinctions

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Abstract
The Sakhalin taimen *Parahucho perryi* is an endangered salmonid with a natural range limited to the Russian Far East and Japan. We constructed a classification tree to determine the environmental factors shaping the historical global distribution of this species and then predicted its potential geographic range. The distribution was most strongly influenced by a spatial autocorrelation term, indicating that it is highly contiguous. Large drainage basins with low topographic relief and large floodplains had a higher probability of taimen occurrence. The boundary of the global distribution was delineated by mean monthly precipitation within the range of 54–96 mm. The presence of Sakhalin taimen was predicted in many drainage basins where it has never been recorded. We also modeled the status of 48 taimen populations in Japan, where it was possible to classify them into three categories: currently stable (7), endangered (5), and extinct (36). The most significant factor differentiating the 12 extant populations from the 36 extinct populations was mean annual air temperature, the extant populations being distributed exclusively in areas where the air temperature is below 5.2°C and agricultural development is minimal. The extant populations were found in drainages with significantly lower elevations and a smaller percentage of farmland compared with drainages where populations have been extirpated. The presence of lagoons was a common characteristic of the drainages with the 7 stable populations, suggesting that lagoons represent critical refugia for the species. The implications of this study for taimen conservation are discussed.

Identifying the geographical range of a species, potential threats to the species, its preferred habitats, and areas at risk of future exposure to these threats are crucial to the conservation of imperiled species (Richter et al. 1997; Gustafson et al. 2007; Williams et al. 2007). This has been poorly done for aquatic species, however, because the distributions are not easily observed and most local extirpations of such species have gone unnoticed by humans. Unless we understand the species' current and historical distributions and causes for past extirpations, we will be much less likely to achieve success in our conservation actions such as reintroduction of the species into currently unoccupied historical ranges (Williams et al. 2007).

Owing to their ability to adapt to changing conditions and migrate into nearby river systems through the marine environment,

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salmonids generally have vast global distributions, encompassing temperate to Arctic waters in the northern hemisphere (Groot and Margolis 1991; Augerot 2005). Detailed global distributions have been determined for most species, with a clear bias toward those that have economic importance. Noncommercial species inevitably have received less attention, and their global distributions are poorly described. Furthermore, widespread releases of nonnative salmonids for recreational fishing have increasingly made the species' original distributions difficult to delineate (Fausch et al. 2001).

Losses of salmonid populations worldwide are significant (Nehlsen et al. 1991; Slaney et al. 1996; Gustafson et al. 2007). Gustafson et al. (2007) estimated a 30% loss in Pacific salmon *Oncorhynchus* spp. populations since the beginning of European presence in the Pacific Northwest of the United States. Potential threats to salmonids include (but are not limited to) habitat loss caused by construction of dams (Morita and Yamamoto 2002; Fukushima et al. 2007), changes in land use (Cunjak 1996; Waite and Carpenter 2000; Pess et al. 2002), channelization (Brookes 1988; Wilcock and Essery 1991), logging activities (Bisson et al. 1992; Reeves et al. 1993), biological invasions and releases of hatchery-reared salmon (Hilborn and Eggers 2000; Fausch et al. 2001; Olden et al. 2006; Light and Marchetti 2007), and human exploitation, including poaching and bycatch (Zolotukhin et al. 2000; Vander Zanden et al. 2007).

Identifying specific causes for extirpation of imperiled species and populations is difficult for a number of reasons. First, species have usually become imperiled before baseline information has been established. Past disturbance history is also difficult to reconstruct (Schrott et al. 2005). Second, broad-scale and long-term data on population dynamics are rarely available unless the species was commercially or recreationally harvested (Augerot 2005). Third, species declines are usually driven by multiple anthropogenic factors that tend to covary (Light and Marchetti 2007). Furthermore, the influence of these factors can depend on spatial scales and environmental conditions surrounding the species (Lewis et al. 1996; Deschenes et al. 2007).

Sakhalin taimen (also known as Japanese huchen) *Parahucho perryi*, while the only representative of its genus, is associated with a group of fishes in the genus *Hucho* that are remarkable given their biological characteristics and unusual life histories, including their primitive phylogenetic traits, slow growth, late age at maturity, long generation time, broad dietary habits, and threatened status (Holčík et al. 1988). The Sakhalin taimen was originally in the genus *Hucho*, but recent evidence based on mitochondrial DNA indicates that the species is distinct phylogenetically and should be categorized into a separate genus (Shed'ko et al. 1996). This species lives for more than 20 years, matures at late ages (6–8 years old), grows to at least 1.3 m in length and 24 kg in weight (Zolotukhin et al. 2000), exhibits limited anadromy (i.e., spawns in freshwater and later occupies brackish waters and coastal areas; Kawamula et al. 1983; Arai et al. 2004), and reproduces more than once in a lifetime (i.e., is iteroparous; Yamashiro 1965; Kimura 1966). Adult taimen prey primarily on fish and occasionally on small mammals (Kimura 1966; Gritsenko et al. 1974; Kawamula et al. 1983). The species is known to exist in the Russian Far East and northern Japan; its distribution in Japan is relatively well understood (Fukushima et al. 2008), but their distribution in Russia is largely unknown due to limited accessibility by researchers (Zolotukhin et al. 2000). Historical distribution of the species is also poorly understood compared with their present, already diminished distribution. Taimen population size in the Russian Far East is estimated to have declined more than 90% over the last three generations (42-year period), based on declining bycatch rates in commercial salmon fisheries (Rand 2006). This observed rate of decline led to the recent listing of the species as critically endangered in the International Union for the Conservation of Nature's (IUCN) Red List of Threatened Species. However, no investigation has been undertaken to identify causes for the drastic population decline of this important keystone species in the subarctic freshwater ecosystems of the Russian Far East and northern Japan.

Using classification trees, we reconstructed the historical global distribution of Sakhalin taimen based on a rangewide database of the species' occurrence and identified environmental determinants for their global distribution. We then identified possible causes for the extirpations based on the extant and extinct status of taimen populations in northern Japan, where more detailed information was available on the status of individual populations and disturbance history.

METHODS

Study area.—The known Sakhalin taimen distribution was classified into four broad regions: (1) the island of Sakhalin, (2) the continental Russian Far East (CRFE) along the coast of the Sea of Japan (i.e., the southern half of Khabarovsk Krai and Primorsky Krai), (3) northern Japan, including Hokkaido and a part of Honshu, and (4) the southern Kuril Islands (Figure 1). The study area comprised 2,493 drainage basins lying between 30°N and 58°N latitude and 125°E and 150°E longitude. We defined a drainage basin as the area of land drained by a river system with a single point of discharge into the ocean (with two exceptions described below).

Areas with known taimen populations range in annual mean air temperature from −1°C to 5°C and in annual precipitation from 600 to 1,200 mm, most of which falls from late August to September. The areas are mostly forested (60–80%) with broadleaf and coniferous trees. Although highest elevations are similar (1,600–1,800 m above sea level) among the four regions, topography is generally flat in Sakhalin and Hokkaido but hilly in the CRFE and the Kuril Islands. Wetlands are the dominant landscape in northern Sakhalin and central, northern, and eastern Hokkaido. In contrast, most rivers in the CRFE lack wetland habitat, have relatively steep channels, and originate from the Sikhote–Alin Mountain Range and drain straight to the Sea of Japan. Rivers in the southern Kuril Islands, a volcanic archipelago, are also generally steep. The four regions,

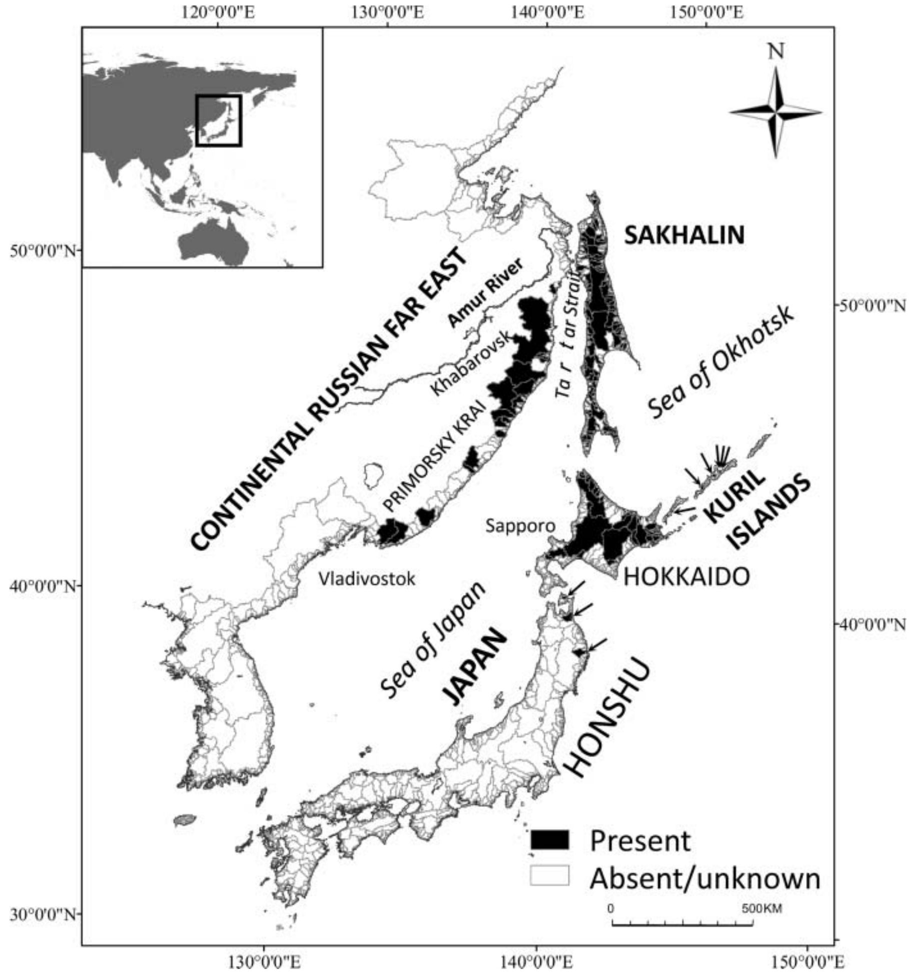

FIGURE 1. Areas of historically recorded Sakhalin taimen occurrence by drainage basin. Small drainages with historical taimen records in Honshu and the Kuril Islands are indicated by arrows.

especially the Russian Far East, are rich in natural resources with high oil, gas, timber, and fishery production (Newell 2004), potentially posing threats to Sakhalin taimen populations and habitats.

Sakhalin taimen data.—The observational data for Sakhalin taimen varied widely across the regions with respect to the accuracy of the recorded location and time and the availability of ancillary information. We summarized all the taimen data as the species' historical (and current) occurrence (presence or absence) for each drainage basin in the study area.

For Sakhalin Island, Russia, we tabulated the presence of Sakhalin taimen across the 203 major drainage basins based on the Sakhalin taimen red list assessment (Rand 2006) and Springmeyer et al. (2008). The latter source was based on the data from the Sakhalin Oblast Atlas Geography Outline Appendix, which represents a compilation of data from individual Sakhrybvod river assessments (Sakhalin Regional Book Publishing House 1994). We augmented the Sakhalin data set with information from the Pacific Rim Database (X. Augerot, Pangaea Environmental LLC, unpublished data).

We included presence data for Sakhalin taimen in CRFE and the Kuril Islands based on data compiled from a number of sources (Zolotukhin et al. 2000; Rand 2006). We excluded the Amur River, the ninth longest river in the world, from this study because of its disproportionately large drainage size compared with the other drainages. This river supports a related species, the Siberian taimen (also known as simply taimen) *Hucho taimen*, but not Sakhalin taimen (Zolotukhin et al. 2000). Siberian taimen grow larger and have many more scales along their lateral line and fewer spots on their head compared with Sakhalin taimen (Holčík et al. 1988). We assumed that the occurrence of Sakhalin taimen is unknown for all other drainages within the range boundary in Russia described in Rand (2006) due to inadequate sampling effort.

We derived taimen presence–absence data for Japan from a data set compiled by Fukushima et al. (2007). This data set includes more than 78,000 freshwater fish records (one fish species captured at a specific site and date represents one record) based on more than 1,300 mostly published reports and articles over the last half century.

TABLE 1. Numbers of drainage basins categorized as present, absent, and unknown with respect to Sakhalin taimen occurrence in the four geographical regions (CRFE = Continental Russian Far East). The drainages in which taimen were known to be present and absent were used to construct the historical distribution model; the drainages with unknown occurrence were used only for prediction.

Occurrence	Sakhalin	CRFE	Japan	Kuril Islands	Total
Present	110	20	46	6	182
Absent	93	640	794	0	1,527
Unknown	177	218	303	86	784
Total	380	878	1,143	92	2,493

We treated drainages just outside of the known global range as unknown with respect to the occurrence of Sakhalin taimen. We added more distant drainages to the north (in Khabarovsk Krai) and the south (including the Korean Peninsula) and characterized taimen occurrence in each of these basins as absent.

Overall, we identified 182 rivers where Sakhalin taimen are present and 1,527 rivers where they are absent (Table 1). Taimen occurrence was unknown for the remaining 784 rivers. A total of 110 rivers were reported to have the species in Sakhalin. Only 20 rivers supported the species in the CRFE. Forty-six rivers had historical records of the species in Japan. Six taimen rivers were recorded in the southern Kuril Islands.

Status of Sakhalin taimen populations in Japan.—According to Edo (2007) and Fukushima et al. (2008), 7 Sakhalin taimen populations are currently stable, 5 are endangered, and 36 are extinct in Japan (Figure 2). We adopted these categories for our analysis. The Ishikari River, the largest taimen river in Hokkaido, now supports two stable but landlocked taimen populations above two impassable dams on major tributaries. However, the species has been extirpated from the rest of the basin below the dams. Therefore, in our database we document the presence of two extant (stable) populations and one extinct population within a single basin of the Ishikari River. The seven stable populations tend to be distributed in the northern part of Hokkaido, whereas the endangered populations are located mainly in the eastern region. The current distribution of the species (pooling stable and endangered populations) now represents only 23% of their historical range in Japan. When

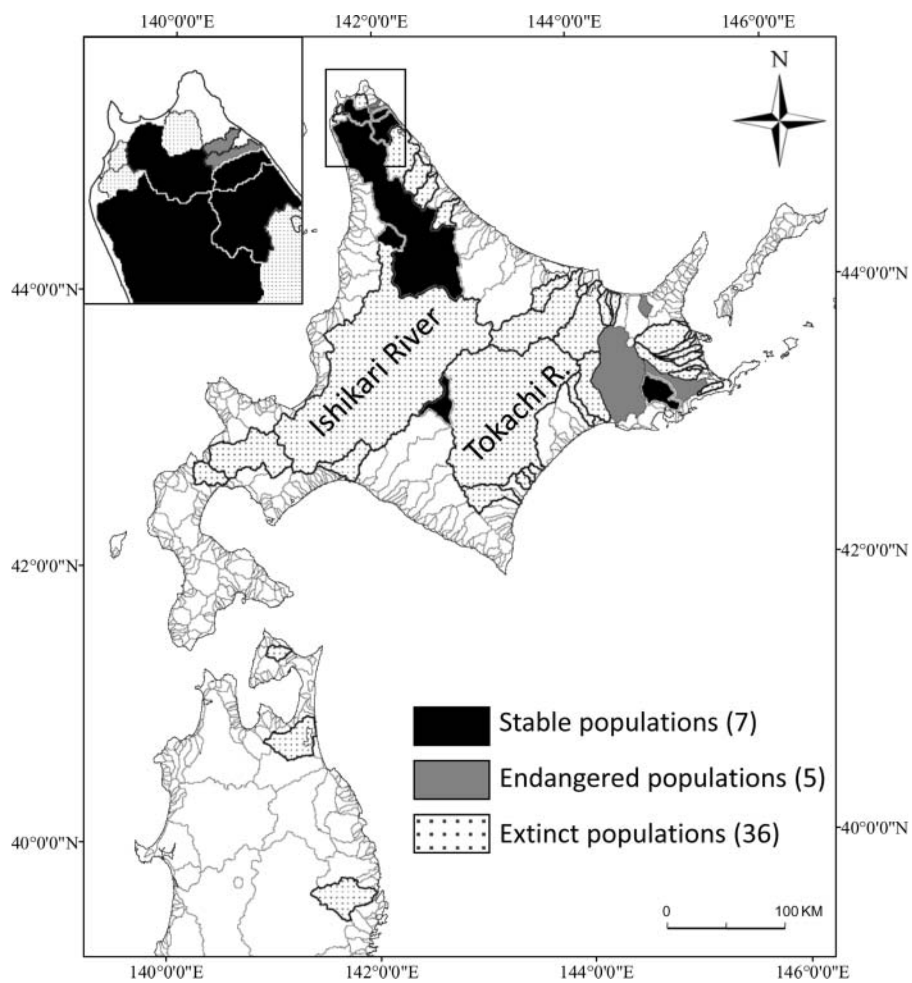

FIGURE 2. Extant–extinct status of Sakhalin taimen for each drainage basin in northern Japan showing 7 stable, 5 endangered, and 36 extinct populations. Population status was based on Edo (2007) and Fukushima et al. (2008).

considering only the stable populations, the range reduction is 16% of the historical range. Sakhalin taimen populations in northern Honshu are considered to have been extinct by the 1960s (Fukushima et al. 2008).

Model.—We used classification trees to model both the rangewide historical distribution of Sakhalin taimen (hereafter referred to as the historical distribution model) and local extirpations of the taimen populations within Japan.

The historical distribution model was fit to 1,709 data points (182 basins where taimen are or were present and 1,527 basins where taimen have never been recorded) as a training data set to construct a classification tree with which to predict taimen occurrence for the remaining 784 basins throughout the entire study area in Russia and Japan (Table 1).

To model the local extirpations, we focused on 48 Sakhalin taimen populations in 46 drainage basins in Japan where taimen exist or historically have existed (note that one basin, Ishikari, supported three populations; Figure 2). We prepared two different training data sets for two submodels depending on how we categorized the data. For the first submodel, we combined the 7 stable and 5 endangered populations (i.e., 12 extant populations) and contrasted them to the 36 extinct populations (hereafter referred to as the "extant" population model). For the second submodel, we contrasted the stable populations with a combined category including the endangered and extinct populations (hereafter referred to as the "stable" population model).

We prepared 14 natural environmental variables to model the historical distribution and an additional 8 anthropogenic variables to model the extant and stable populations (Table 2). Based on a HydroSHEDS database originally derived from the elevation data of the Shuttle Radar Topography Mission at 15-arc-second resolution (Lehner 2005), we delineated the drainage basins using a geographical information system as a spatial unit for the compilation of the natural and anthropogenic environmental variables.

For the historical distribution model, we calculated minimum, mean, and maximum annual air temperature and mean monthly precipitation for each drainage basin within the study area based on the CRU TS 2.1 Global Climate Database (Mitchell and Jones 2005). As the spatial resolution of this database was relatively coarse (0.5°), we first intersected the drainage polygons with the grid-based climate data and merged the intersected polygons back into the original drainages to make the climate data numerically better represent each basin. Although recent climate has probably been affected by global warming, we used the recent 20-year (1981–2000) data set because of its potentially higher accuracy due to the larger number of meteorological stations. For the extant and stable population models, however, we used air temperature and precipitation data with a finer spatial resolution (30 × 45 s for latitude and longitude) only available for Japan (MLITT 2010).

Because the occurrence of Sakhalin taimen has often been associated with the presence of wetland and lagoon habitats in a basin (Yamashiro 1965; Kimura 1966; Fukushima et al. 2008), we included several variables representing these geographic characteristics in our analysis. We calculated the percentage of drainage area below 10, 20, and 30 m in elevation; we identified and calculated occurrence, number of lagoons, and the total area of each lagoon (>1 km along the longest axis) by digitizing either topographical maps, LANDSAT images, or both.

As the Ishikari River has taimen populations only in subbasins above reservoirs higher in altitude, we calculated the elevations for these populations relative to the water level of the reservoirs (i.e., the reservoir elevation was subtracted from elevations in upstream basins). Also, we treated these reservoirs as a surrogate for lagoons and defined their surface area as lagoon area.

Spatial autocorrelation has been identified as one of the most important ecological factors determining the distributions of organisms (Legendre 1993). Disregarding this correlation in statistical analyses, especially in statistical modeling, can seriously distort the true mechanisms underlying species–environment relationships. We expected the species distribution to be highly contiguous. This would be expressed as a strong correlation in

TABLE 2. Candidates predictor variables for the historical distribution and extant–stable population models showing the specific number of variables and those supported by the classification trees.

Variable	Number of variables	Historical distribution model	Extant – stable population models
Drainage area (km^2)	1	X	X
Air temperature (°C)	3	X	X
Precipitation (mm)	1	X	X
Elevation (m)	1	X	X
Area below 10, 20, and 30 m (%)	3	X	X
Lagoon presence, number, and area (km^2)	3	X	X
Spatial autocorrelation	1	X	
Geographical region	1	X	
Farmland (%)	1		X
Forest (%)	1		X
Human population and density (per km^2)	2		X
Nonnative species richness	1		X
Rainbow trout occurrence	1		X
Dam number and density (per km^2)	2		X
Total	22	14	20

species occurrence among contiguous watersheds, particularly those whose river mouths are in close proximity, creating a migratory link between river systems. To better represent such a spatial linkage, we prepared a spatial autocorrelation term for each drainage basin by summing the inverse of distances from the basin's river mouth to river mouths of all the other basins with taimen within the study area. We calculated the distance between any two river mouths as the length of the shortest path measured along a triangulated irregular network (TIN) formed by connecting a set of points of river mouths and coastline vertices so that the connecting path lies only within coastal marine waters. We then transformed the autocorrelation term to range between zero and one. A categorical variable of the geographical region (i.e., Sakhalin, CRFE, Japan, and the Kuril Islands) was also included.

The anthropogenic variables included land-cover types (farmland and forest), human population and population density from the National Census of Japan, nonnative fish species richness, occurrence of introduced rainbow trout *Oncorhynchus mykiss*, and the number and density of dams (>15 m high) for each drainage basin. We prepared farmland data by combining the MODIS-satellite-based land-cover categories (MOD12) of woody savanna, grassland, cropland, and cropland–natural vegetation mosaic and prepared forest data by combining the categories of evergreen needle-leaf forest, evergreen broadleaf forest, deciduous needle-leaf forest, deciduous broadleaf forest, and mixed forest (Belward et al. 1999; Scepan 1999). Such reclassification of the original MOD12 categories resulted in more realistic land cover data for Japan (MLITT 2010). The nonnative rainbow trout were first introduced into Japan in the late 19th century from the United States. This species is a salmonid in the same subfamily as Sakhalin taimen and also spawns at a similar time as taimen, serving as a possible disturbance to Sakhalin taimen through redd superimposition (Aoyama et al. 1999).

Classification trees provide an alternative to linear and additive logistic models for classification problems. The models are fitted by binary recursive partitioning whereby a data set is successively split into increasingly homogeneous subsets until it is no longer feasible to continue (Clark and Pregibon 1991). Classification trees are effective when handling nonlinear relationships between response and predictor variables and complex interactions between the predictors. Processes of species extinctions or extirpations are often context dependent, and a priori specification of functional relationships is rarely possible, a situation better suited to classification trees.

Using the historical distribution model, we predicted the global Sakhalin taimen distribution by calculating the probability of the species' occurrence for each drainage basin in the study area, including drainages categorized as unknown for taimen occurrence. However, we did not attempt to predict the extant–extinct status of Sakhalin taimen because of the small number of observations available to construct the extant and stable population models. Rather, we focused on explaining the extinction processes of Sakhalin taimen populations in Japan.

We determined the best classification tree for the historical distribution model based on the 10-fold cross-validation technique (Clark and Pregibon 1991). This technique first divides the original training data set into 10 mutually exclusive sets. We used nine sets to grow the tree and tested it on the tenth. Misclassifications from each set are accumulated as a function of node size. We repeated this whole process 10 times and calculated the mean and SE of misclassifications. We selected a model with the smallest node size with the smallest error rate according to Breiman et al.'s (1984) one SE rule.

RESULTS

Historical Global Distribution Model

The best Sakhalin taimen historical distribution model retained eight terminal nodes in the classification tree consisting of the following five predictor variables: spatial autocorrelation, drainage area, mean elevation, mean air temperature, and mean monthly precipitation (Figure 3). Assuming that taimen are or were present where predicted, occurrence probability exceeded 0.5; 156 out of the 182 rivers in which Sakhalin taimen were present were predicted to have a taimen population (sensitivity = 0.86), whereas 1,484 out of the 1,527 rivers without taimen were predicted not to have a population (specificity = 0.97). The overall resubstitution error rate (i.e., the errors committed by the model when it was applied to the same data set as that

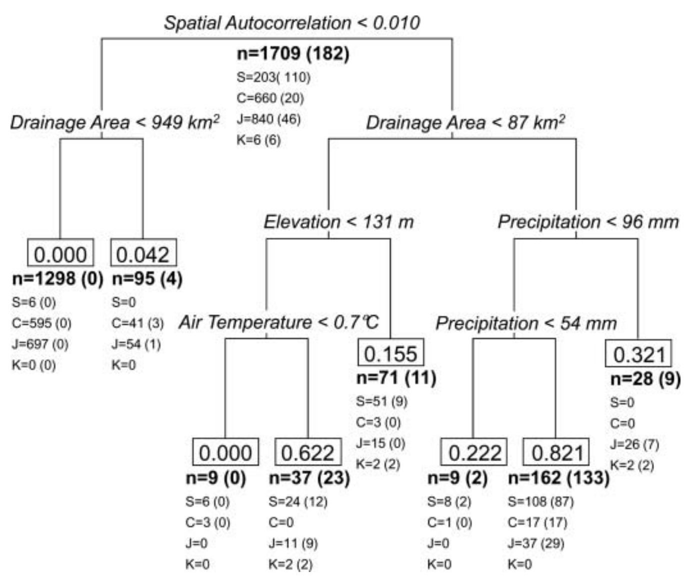

FIGURE 3. Classification tree for the historical distribution model of Sakhalin taimen. Successive partitioning of the training data set of drainages was based on the rule labeling each split. If the condition indicated by the rule was met, the drainages were split to the left; otherwise they were split to the right. The value in the box at each terminal node is the estimated probability of the occurrence of Sakhalin taimen. The values labeled n are the total number of drainages categorized to the nodes; their geographical composition is indicated as follows: S = Sakhalin, C = CRFE, J = Japan, and K = the Kuril Islands. The values in parentheses are the numbers of drainages in which taimen are or were present.

used to construct the model) was 0.040 (69 misclassifications out of 1,709). The 69 misclassifications consisted of 26 cases of false negative (species predicted to be absent when in fact they are present) and 43 cases of false positive (species predicted to be present when they are absent). The cross-validation error rate, i.e., cumulative errors committed by 10 submodels when applied to 10 independent data sets, was 0.051.

The most important variable in the historical distribution model was the spatial autocorrelation term (Figure 3). Rivers with an autocorrelation term less than 0.010 had a negligible occurrence probability (zero or 0.042 depending on drainage area). If the spatial autocorrelation exceeded 0.010, taimen occurrence probability depended on the drainage area. When drainages were smaller than 87 km^2, only the drainages with mean elevation less than 131 m and air temperature greater than 0.7°C had a moderate probability of occurrence (0.622). Thirty-seven rivers in the training data set were classified in this category, of which 23 actually had taimen populations. Otherwise, smaller drainages had generally small occurrence probabilities (≤0.155). Although not selected as a predictor variable, presence of lagoons was correlated with the Sakhalin taimen occurrence. Among the 1,709 rivers of presence–absence data, lagoons were observed in 101 rivers (6%), while 43 out of 182 rivers with Sakhalin taimen had lagoons (24%); thus, taimen are disproportionally represented in watersheds that contain lagoons (chi-square test: $P < 0.001$).

Drainages larger than 87 km^2 had higher probabilities of Sakhalin taimen occurrence, especially when monthly mean precipitation fell between 54 and 96 mm (0.821). Most of the observed taimen populations were classified into this category (i.e., 133 out of 182 populations [73%]), but regional contribution to the category was biased toward Sakhalin Island (79%) and CRFE (85%) rather than Japan (63%) or the Kuril Islands (0%). The effect of drainage size was most prominent on Sakhalin Island, where an average drainage area with taimen was three times as great as those without taimen (geometric means = 224 versus 71 km^2, respectively; t-test after log transformation: $P <$ 0.001). Difference between the average drainage sizes with and

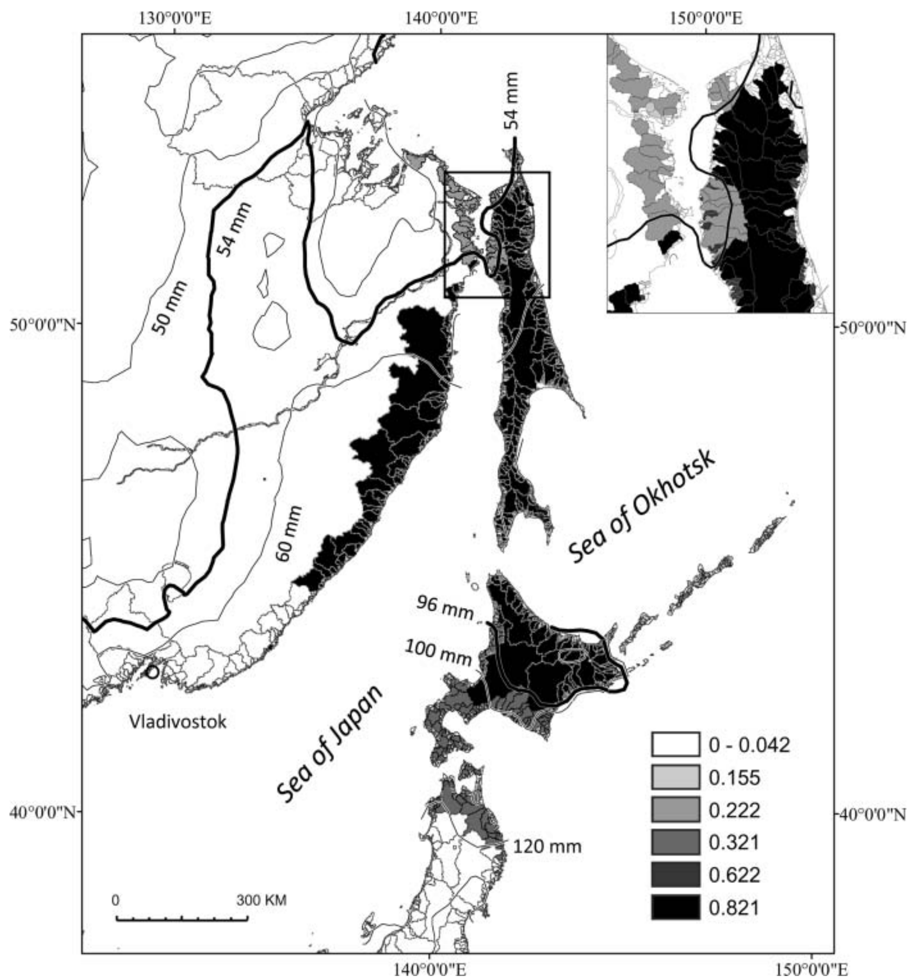

FIGURE 4. Predicted historical distribution of Sakhalin taimen, showing the probability of occurrence in each drainage basin by means of different degrees of shading. Contours of monthly mean precipitation are also shown.

without taimen was smaller in Japan but still significant (280 and 154 km^2 with and without taimen, respectively; $P = 0.04$).

Drainages with precipitation greater than 96 mm (rightmost node in Figure 3) still had a small occurrence probability (0.321), but only drainages in Japan or the Kuril Islands fell into this category.

Predicted Global Distribution

The predicted distribution of Sakhalin taimen was highly contiguous because of a strong effect of spatial autocorrelation (Figure 4). The majority of large rivers in Sakhalin were predicted to have higher probability (0.821) of taimen occurrence. Northern and northwestern parts of Sakhalin Island were predicted to have lower probability (0.222), which agrees with the sporadic occurrence of this species in these areas (Figure 1). The predicted northern limit of the taimen in the CRFE also agrees with the actual northern limit near the Tartar Strait, whereas the predicted southern limit was located higher in latitude than the observed limit. As a result, three rivers with known historical taimen presence near Vladivostok were erroneously predicted not to have taimen populations. Rivers across the northern CRFE to the Tatar Strait and rivers from the central to northern and eastern Hokkaido were predicted to have supported taimen populations (0.821). The rest of Hokkaido and northern Honshu had a moderate occurrence probability (0.321). The Kuril Islands had generally lower probabilities except for several small and flat drainages with a probability of 0.622.

Both the observed and predicted boundaries of the species global range were clearly delineated by monthly precipitation contours of 54 mm to the north and 96 mm to the south (Figures 1, 4).

Causes for Local Extirpations

The extant population model had four predictors and five terminal nodes (Figure 5). The resubstitution error rate was 0.104, or 5 misclassifications out of 48. Sensitivity and specificity were relatively high (0.833 and 0.917, respectively). The most significant variable was annual mean air temperature. Drainages with air temperature above 5.2°C had a probability of zero of having an extant population. The highest probability (0.875) occurred when the temperature was below 5.2°C and mean elevation was less than 82 m. Four stable and three endangered populations were categorized into this class. The second highest probability (0.600) was predicted in cases where the mean elevation was above 82 m but percent farmland was less than 21%; this class contained three stable populations. With the farmland greater than 21%, relatively flat drainages where more than 13% of a drainage area is below 20 m had a small probability (0.400) of having extant taimen populations, although two endangered populations were categorized into this class.

The stable population model had three predictor variables and four terminal nodes (Figure 6). Overall resubstitution error rate was 0.063, or 3 misclassifications out of 48. Sensitivity was not very high (0.71) compared with specificity (0.98). The most significant variable was presence or absence of lagoons in a basin. If there were no lagoons, the chance of there being a currently stable taimen population was nil. None of the 25 rivers without lagoons had stable populations. If there were lagoons and percent farmland was less than 21%, the probability of

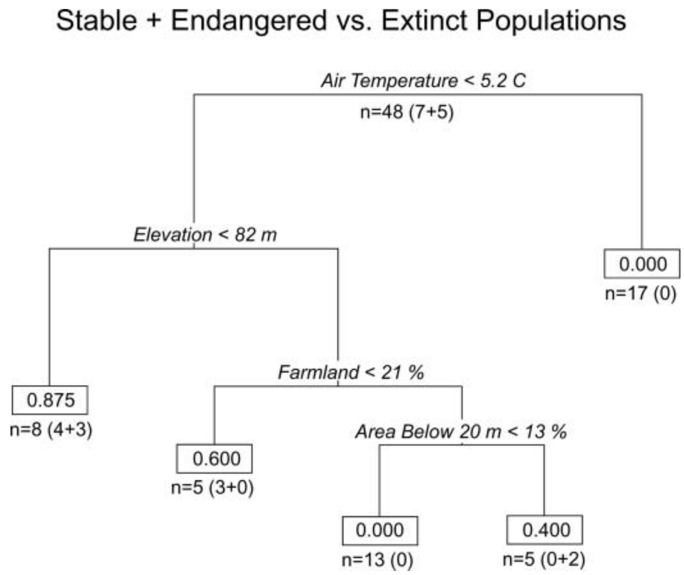

FIGURE 5. Classification tree for the extant population model differentiating extant (i.e., stable plus endangered) from extinct populations of Sakhalin taimen in Japan. The value in the box at each terminal node is the estimated probability of there being an extant taimen population. The values labeled *n* are the numbers of drainages categorized to the different nodes; the values in parentheses are the numbers of drainages with observed stable and endangered populations, respectively.

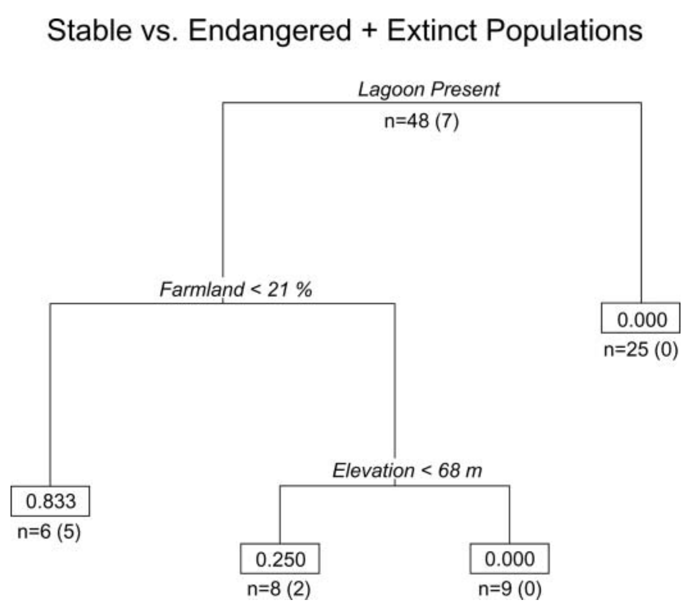

FIGURE 6. Classification tree for the stable population model differentiating stable from endangered plus extinct populations of Sakhalin taimen in Japan. See Figures 3 and 5 for notation.

having a stable population was 0.833. Five out of six drainages in this category had stable taimen populations. If the percent farmland exceeded 21%, chances were again very small with probabilities of either 0.250 or zero, depending on whether mean elevation was less or greater than 68 m, respectively.

DISCUSSION

Global Distribution of Sakhalin Taimen

Sakhalin taimen are distributed in a relatively confined area along the coast of the Russian Far East and northern Japan surrounding the Sea of Japan. Inside this area, we predicted taimen presence in many rivers with no previous observation records but with environmental conditions similar to those in the surrounding rivers with taimen records. However, our model did not enlarge the global range of the species beyond the one previously recognized (Rand 2006).

The relatively confined historical range of Sakhalin taimen contrasts with that of Siberian taimen, which extends over the vast area of Siberia from the Ural Mountains in the west to the Sikhote–Alin Mountain ranges in the east (Holčík et al. 1988; Vander Zanden et al. 2007). Rather, the Sakhalin taimen distribution closely resembles that of masu salmon *O. masou*, the most ancestral form of *Oncorhynchus*, although masu salmon also inhabit the eastern and western shores of the Korean and Kamchatka peninsulas, respectively (Augerot 2005). During the last Ice Age, the Sea of Japan was a single huge brackish lake or lagoon, with most of the present river systems along the shore being tributaries of the lake (Nishimura 1980). This is perhaps the period when Sakhalin taimen established their historical distribution. The Sakhalin taimen range did not extend northward through the narrow (~7 km at the narrowest point) and shallow (~15 m) Tatar Strait (Tyler 2002). It may be due in part to strong salinity northward and in part to a thermal barrier formed by massive warmwater discharge (~20°C) of the Amur River during summer (JAXA 2010).

The size of a drainage basin was an important determinant for Sakhalin taimen occurrence. Although smaller drainages tend to have received less effort in biological surveys and thus could be underrepresented in the presence data of taimen, a significantly higher probability of taimen occurrence in larger rivers is likely to be a robust conclusion considering the extensive survey efforts in Japan. In small drainages, taimen occur predominantly in flat rivers with lower mean basin elevations (<131 m), which is indicative of the existence of larger floodplains and wetlands. Sakhalin taimen have frequently been associated with the presence of wetland and lagoon habitats, and in fact, some of our taimen records in Japan originated only from inside lagoons and not from upper reaches (Fukushima et al. 2008). The association of taimen occurrence with large rivers, particularly those that contain expansive wetlands and lagoons, may be due in part to their limited anadromy. Taimen require more diverse and productive freshwater habitats than do other anadromous salmonids such as Pacific salmon, which depend on freshwater only for spawning and juvenile rearing. Emerging information on this species indicates that individuals can adopt a variety of life history forms, including fully anadromous, amphidromous, or adfluvial forms. This is suggested through new studies of migration patterns revealed through otolith microchemistry (C. Zimmerman, U.S. Geological Survey, personal communication). The ecological analog to this species in North America may be bull trout *Salvelinus confluentus* or coastal cutthroat trout *O. clarkii clarkii*, and we expect similar relationships may hold for these species as well.

Sakhalin taimen are more likely to persist if they are present in rivers with wetlands and lagoons, a habitat that is becoming increasingly rare in Japan. The strong linkage between taimen survival and wetland–lagoon habitats might relate to the timing of emergence from the gravel. Because spawning takes place in spring (April to May), fry emerge from the gravel relatively late (June to July) compared with other salmonids that normally spawn in autumn and emerge in spring of the following year. Soon after emergence, juvenile Sakhalin taimen with limited swimming ability experience one of the highest river discharges of the year, which normally takes place around September (CRU Climate Data). Although Sakhalin taimen are anadromous, they are not tolerant of higher salinity when they are young of the year (age 0; Kawamula et al. 1983). They do not migrate downstream to an estuary or to the ocean until they spend at least 1 to 2 years in freshwater, according to scale pattern analysis (Yamashiro 1965) and strontium-to-calcium ratios in otoliths (C. Zimmerman, unpublished data). Large rivers with flat topography would benefit juvenile taimen, allowing them to return to their upstream rearing habitats before being completely flushed to the ocean by floods. This is especially true in highly developed watersheds of Japan in which access to the floodplain as a refuge during high flows is very limited. Kondolf et al. (1991) observed that spring-spawning rainbow trout tend to spawn in lower gradient streams than do fall-spawning brown trout *Salmo trutta*. They attributed this pattern of habitat selection to difference in the timing of fry emergence; brown trout fry emerge long before high snowmelt flows, whereas rainbow trout eggs are still in the gravel during the floods, being vulnerable to scour if buried in higher gradient streams. Lagoons are not only a temporal refuge for Sakhalin taimen during catastrophic events but also are rich in nutrients and highly productive, providing taimen with food and, thus, an important nursery area (Kawamula et al. 1983).

Causes for Population Extirpations

Mean air temperature was identified as the most important determinant differentiating drainages with extant and extinct Sakhalin taimen populations in Japan. We document that all taimen populations in drainages with mean air temperature above 5.2°C are now extinct. Mean air temperatures in the Russian Far East and northern Japan have gradually increased by about 0.01°C/year over the past 100 years (CRU Climate Data). Global warming is a serious concern for the survival of extant

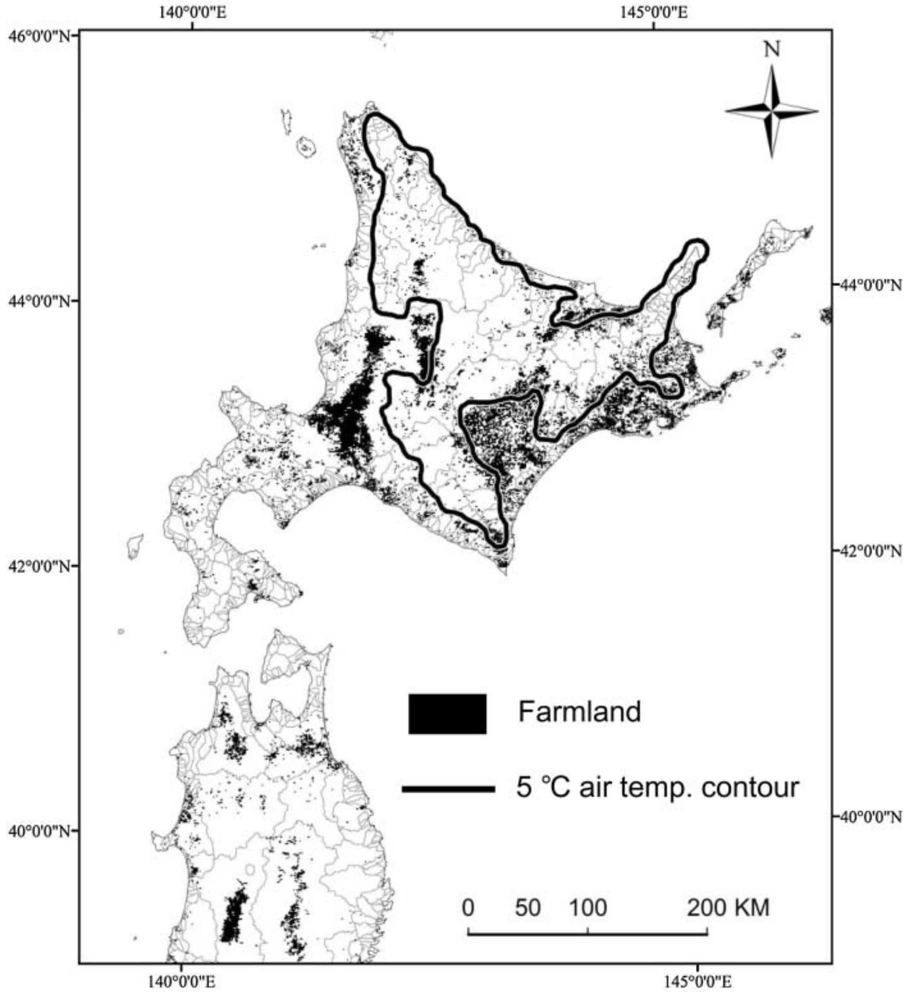

FIGURE 7. Distribution of farmland and the 5°C contour of annual mean air temperature in northern Japan. Watershed boundaries are also shown.

taimen populations, especially those located near the southern limits of their global distribution. In fact, taimen populations in Honshu, Japan, went extinct during the 1960s (Fukushima et al. 2008), long before some of the northern populations in Hokkaido did. Furthermore, taimen populations near Vladivostok, Russia, a southern limit along the coast of the CRFE, were considered extinct by the 1990s, while populations in the northern CRFE are relatively healthy (Zolotukhin et al. 2000). It has long been known that salmonid populations generally have an increased risk of extinction at lower latitudes across their geographic ranges (Augerot 2005; Gustafson et al. 2007; Williams et al. 2007).

While temperature per se can be an important determinant of the geographical range of fishes through physiological constraints, temperature also determines geographical distribution of arable lands, which in turn could affect fish distributions. In fact, the extent of farmland distribution throughout Hokkaido closely matches an air temperature pattern, such that major farmlands are distributed almost exclusively outside a 5°C temperature contour (i.e., areas higher than 5°C; Figure 7). Thus, the proximate cause of the observed relationship between air temperature and Sakhalin taimen persistence may in fact be agricultural development.

We also found a significant effect of the proportion of farmland by drainage basin (i.e., watershed-scale agricultural development) in both the extant and stable population models. Sakhalin taimen population presence, especially those that are stable, decreases considerably when more than one-fifth (21%) of a drainage basin is converted to farmland. The proportion of farmland by drainage was the only variable selected by the model among anthropogenic factors that included human population, nonnative species richness, rainbow trout invasion, and dams. Development of rice fields and cropland in the lower Ishikari River basin dates to about 100 years ago, and the last observations of healthy taimen populations from this area were made during the 1950s and 1960s. In eastern Hokkaido, grassland development for livestock grazing expanded rapidly in the 1970s (Nakamura and Yamada 2005), and the last taimen observations there were documented mostly from the 1980s (Fukushima et al. 2008).

It is important to determine what aspect of farmland development has driven taimen populations to go locally extinct. Pess et al. (2002) found that coho salmon *O. kisutch* spawner abundance is negatively correlated with the percentage of the drainage area that is in agricultural use at both reach and watershed scales in the Columbia River basin. They attributed this relationship to channelization and associated loss of tributary, floodplain, and riparian habitats for adult spawning and juvenile rearing. Farmland development has typically been accompanied by extensive channelization or channel straightening for flood control and land drainage (Brookes 1988). However, meandering channels are crucial for spawning Sakhalin taimen because they spawn strictly in pool–riffle habitats created by sinuous reaches (Fukushima 2001). Since channelization increases channel gradient, juvenile taimen are more likely to be flushed out during floods. Increased channel gradient, otherwise, has led to construction of numerous instream structures, like weirs, to lessen the elevated gradient and prevent bank erosion and channel incision (Brookes 1988). Therefore, the significant relationship we found between farmland development and taimen extinction is probably due to extensive channelization and associated instream modifications that deprive taimen of critical habitats and impede spawning migration.

Conservation Implications

In conservation biology, predictive habitat modeling has often been applied to identify areas that are susceptible to invasion by exotic or nonindigenous species (e.g., Mercado-Silva et al. 2006; Herborg et al. 2007). Rarely has it been used to reconstruct historical ranges of imperiled species or to identify areas where restoration efforts should be directed more intensively. Although we could not provide a statistically significant model for predicting areas at risk of further extirpation, special attention needs to be paid to farmland development and associated losses of coastal wetlands and lagoons within the natural range of Sakhalin taimen. In fact, there are several drainages in Sakhalin and more than a dozen in the Kuril Islands where taimen were predicted to occur and percent farmland per drainage exceed 21%. With increasing air temperatures due to global warming, farmland development is expected to expand northward, threatening even the currently stable taimen populations. However, it is not farmland itself but the way humans have developed lands for agriculture that is detrimental to taimen populations. Best practices for agricultural development that meet salmonid conservation goals are urgently needed, and we suggest they be implemented within the natural range of Sakhalin taimen to provide an important measure of protection in the future. These land-use best practices are likely to benefit other salmonids in these systems, including Pacific salmon (particularly masu salmon) and char species.

In the meantime, it is important to realize that there are a suite of other threats to Sakhalin taimen populations, including unsustainable, unregulated sportfishing in Japan (Fukushima et al. 2008), oil and gas development, poaching, bycatch, and rapidly expanding logging practices in the Russian Far East (Newell 2004). Pipelines of oil and gas constructed in Sakhalin crossed more than 1,000 rivers supporting salmon populations and many taimen populations (Augerot 2005). It may be argued that the life history traits of Sakhalin taimen by nature make them susceptible to extinction (Olden et al. 2006). Specifically, traits that include late age at maturity, lower fecundity, and iteroparity that necessitates multiple journeys between saltwater and headwater habitat place them at a disadvantage given this suite of future threats (Groot and Margolis 1991; Rand 2006).

Although living in artificial and perhaps disturbed systems, the landlocked Sakhalin taimen populations above reservoirs in the Ishikari River basin have been relatively abundant and stable at least since the construction of the dams (Edo 2007). These populations apparently have benefited from the large water bodies contained in the reservoirs as feeding habitats. It is still uncertain how these populations will fare in the long term, considering how these dams have disrupted their anadromous behavior. Dams in general are highly detrimental to migratory freshwater fishes including salmonids and have led to extirpations of local fish populations in Hokkaido (Fukushima et al. 2007).

CONCLUSIONS

The historical global distribution of Sakhalin taimen was restricted mostly to rivers around the northern half of the Sea of Japan. While their occurrence by drainage basin was explained by the topographic and climatic characteristics of drainages, their global range was shaped by a biogeographical boundary established when the Sea of Japan was isolated from the Pacific Ocean.

Sakhalin taimen in Japan have a higher risk of extinction than other populations across their global range. If one-fifth of a drainage basin is converted to farmland, the probability of extirpation increases significantly. Wetland and lagoon habitats were also found to be of prime importance for the persistence of taimen in Japan. We hypothesized that this relationship between taimen occurrence and survival and basin topography stems from the species' peculiar life history trait, by which they spawn in spring and emerge from the gravel in summer, not long before the annual peak in river discharge occurs. Rivers with steep channels or extensively channelized rivers can displace juvenile Sakhalin taimen into downstream saltwater habitats during floods, which would be detrimental because of their dependence on freshwater during early life stages.

Given less agricultural development, the causes for the drastic decline of Sakhalin taimen populations in Russian rivers are probably different from those in Japan. The causes for the taimen decline in Russia must also be determined to reduce the global risk of extinction. Further, our study suggested that recovery efforts applied to depressed populations should be targeted toward those river basins with the highest probabilities of historical occurrence, which represent the best habitat left for the species.

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