Spatially Explicit Models for Freshwater Fish for Conservation Planning

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Michio Fukushima
National Institute for Environmental Studies

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Introduction

In conservation biology, spatially explicit population models, sometimes known as predictive habitat distribution models (Guisan and Zimmermann 2000), have been widely used to predict distributions of plants (Leathwick 1998), insects (Lobo and Martin-Piera 2002; Gutiérrez et al. 2005), amphibians (Ray et al. 2002), reptiles (Fisher et al. 2002), fishes (Joy and Death 2001; Leathwick et al. 2005), birds (Peterson and Robins 2003), and mammals (Carroll et al. 1999). This modeling technique has been applied to Japan's freshwater ecosystems: for example, to reconstruct historical global distribution of an endangered fish species with an already diminished distribution range (Fukushima et al. 2011) and to predict potential areas susceptible to invasion by exotic fish species (Iguchi et al. 2004). Because spatially explicit modeling is a correlative statistical technique, it basically requires only two sets of data: response and predictor variables. What makes this modeling technique different from classic techniques is that the variables (1) are spatial in nature, (2) are most often observational rather than designed, and (3) are not repetitive in space because the earth is the only unit (Cressie 1993). In a field-based ecological study, it practically means that the data are georeferenced in a given landscape (e.g., by a global positioning system, or GPS).

With the recent advances in technologies related to a geographic information system (GIS), applications of spatially explicit modeling have rapidly expanded. Although spatial data for climate, geography, geomorphology, and human influence have increasingly become available (e.g., MLITT 2010), data for species distributions, especially those in freshwater, are still limited in availability owing to sporadic and sparse sampling and inconsistent sampling schemes in various monitoring programs. For example, two of Japan's largest national censuses for species

M. Fukushima (✉)
National Institute for Environmental Studies, Onogawa 16-2,
Tsukuba, Ibaraki 305-8506, Japan
e-mail: michio@nies.go.jp

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distributions—National Survey on the Natural Environment by the Ministry of the Environment and the National Census on River Environment by the Ministry of Land, Infrastructure, Transport and Tourism (MLITT)—are based on quite different sampling schemes.

Two applications of spatially explicit modeling to freshwater fish are introduced in this chapter. In the first application, a model was developed to determine whether fish species richness had been lost due to damming, to identify the extent of the species' losses, and to quantify the losses throughout Hokkaido, Japan. Dams are a major threat to aquatic biodiversity, especially to migratory species, in many countries (Allan and Flecker 1993; Joy and Death 2001; Marchant and Hehir 2002; Morita and Yamamoto 2002; March et al. 2003). Fish migrate when key habitats essential for their survival (in terms of reproduction and growth) are separated in time and space (Poulsen et al. 2002). At higher latitudes, freshwater productivity becomes too low to support populations of some fish species, so they migrate to the sea to grow large enough to achieve sexual maturity before they return to freshwater to reproduce (McDowall 1988). Located in relatively high latitudes, Hokkaido is dominated by many migratory, especially anadromous and amphidromous, fish species (Goto 1994). Therefore, fish in this island are potentially faced with risks associated with damming more severely than fish in other regions of Japan.

In the second application of spatially explicit modeling, similar models were developed for individual fish species to evaluate the efficacy of the existing network of protected areas in Hokkaido. There are currently 32 river drainages in this island designated as protected water surfaces under the Act on the Protection of Fisheries Resources (hereafter referred to as protected drainages or PDs). Capturing any aquatic organisms within the PDs is strictly prohibited all year round. The PDs were originally designed to protect masu salmon (*Oncorhynchus masou* BREVOORT) populations and their habitats (Kuwata 1963). Masu salmon are a commercially important fisheries resource in Hokkaido, generating an annual income of 0.5–1.0 billion Japanese Yen (Miyakoshi 2006). They are semelparous like other Pacific salmon and spawn in the fall. Although the species is anadromous, they spend at least a year in headwater streams before out-migrating to the sea. Therefore, they rely heavily on freshwater environments to sustain viable populations (Kato 1991).

Since the early 1990s, conservation of another salmonid species, Sakhalin taimen (*Parahucho perryi* BREVOORT), became an added objective of the PDs. Sakhalin taimen are endangered in Japan (Ministry of the Environment, Japan: http://www.biodic.go.jp/rdb/rdb_top.html) and are critically endangered in their global range of Japan and Far Eastern Russia according to IUCN (Rand 2006). Sakhalin taimen are partially anadromous (i.e., there are both anadromous and nonanadromous populations), iteroparous (i.e., multiple spawners during a life cycle), and spring spawners (Yamashiro 1965; Fukushima 1994, 2001; Arai et al. 2004). They live for about 20 years and attain a body size of >1.3 m in length and 24 kg in weight (Zolotukhin et al. 2000). They have been recorded in relatively large rivers with wetland and lagoon habitats (Rand 2006; Fukushima et al. 2008).

Although the two fish species, masu salmon and Sakhalin taimen, belong to the same family, Salmonidae, they have distinct habitat preferences and life histories, as described above. Whether the same set of PDs can protect the both salmonid species simultaneously is an essential question that needs to be addressed by fisheries managers and conservationists alike. Furthermore, from a biodiversity conservation point of view, a question also arises about whether maintaining the existing network of PDs contributes to the conservation of other fish species (e.g., nonsalmonids) or fish species diversity as well.

Methods

Study Area

Hokkaido (41°21'–45°33'N, 139°20'–148°53'E; area 78,461 km^2), the second largest and northernmost island of Japan, is surrounded by the Sea of Okhotsk, the Japan Sea, and the Pacific Ocean (Fig. 1a). The elevation in the central part of the island rises to 2,287 m above sea level. The major land-cover classes include boreal and northern

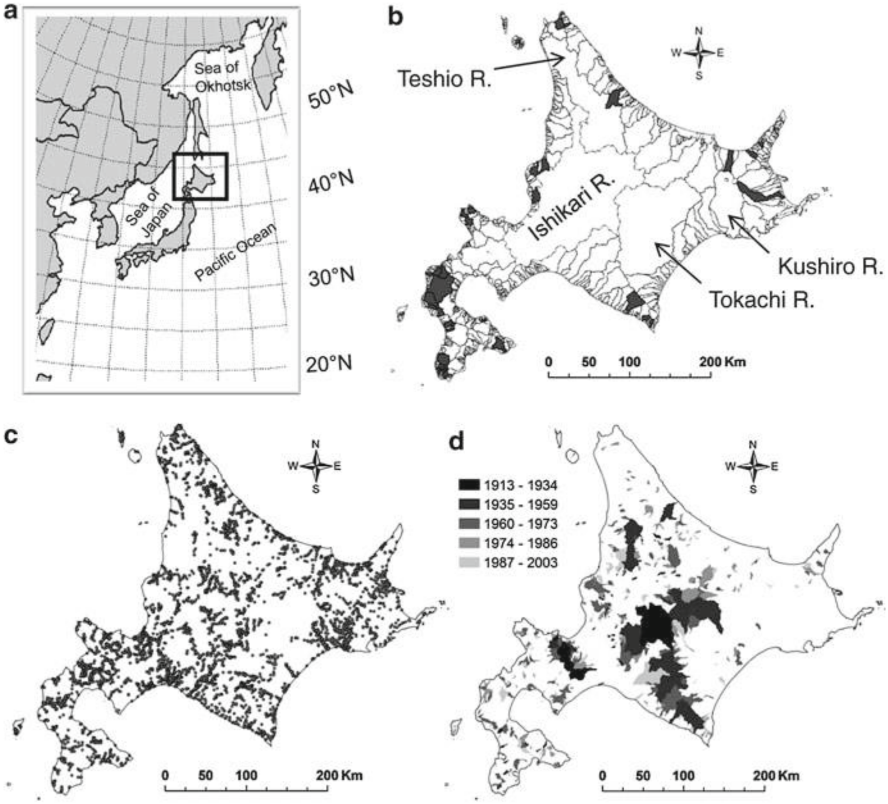


Fig. 1 Study area, Hokkaido (**a**). The 574 river drainages, with the shaded drainages corresponding to the 32 protected drainages (**b**). Fish survey sites conducted during the last half century (**c**). Habitat fragmentation due to damming with different shading representing different years of habitat fragmentation (**d**). (Modified from Fukushima and Kameyama 2006)

temperate forests (40% broad-leaved and 27% conifer) and agricultural fields (15.6%), including pasture and rice paddy fields. The mean annual precipitation ranges from 800 to 1,500 mm, and the mean annual temperature is 6–10°C.

Hokkaido is inhabited by approximately 70 freshwater fish species comprising primarily Gobiidae (20%), Cyprinidae (19%), Salmonidae (12%), Osmeridae (7%), Gasterosteidae (6%), and Cottidae (4%) (Goto 1994). Strictly freshwater species are limited, and those native to Hokkaido include only several cyprinids (Goto et al. 1978).

Based on the 1:25,000 digital topographical maps of Hokkaido, a total of 574 drainages of river basins including the 32 PDs were identified on the island using GIS (Fig. 1b). The largest drainage is the Ishikari River (14,330 km^2), followed by the Tokachi River (9,010 km^2), the Teshio River (5,590 km^2), and the Kushiro River (2,510 km^2).

Fish Database

I compiled a comprehensive database by combining existing fish databases maintained by various agencies (Ministry of the Environment: http://www.biodic.go.jp/J-IBIS.html; Hokkaido Fish Hatchery: http://www.fishexp.pref.hokkaido.jp/hatch/honjou/INDEX.htm; MLITT: http://www.mlit.go.jp/river/IDC/database/databasetop.html; Hokkaido Government: http://rdb.hokkaido-ies.go.jp) and data from published and unpublished reports, which were primarily environmental impact assessments. Each record presents the presence or absence of individual freshwater fish taxa. Surveys were conducted during 1953–2003, mostly (90% of all records) between June and October, using either netting or electrofishing, in both lotic and lentic habitats ranging from sea level to >1,400 m above sea level. Data originating from surveys targeting specific fish species (often commercially important species) were excluded from this analysis.

I excluded fish species that are not native to Japan and species artificially brought from other parts of Japan. Although the original global distribution of common carp (*Cyprinus carpio* LINNAEUS 1758) is not precisely understood (Kawanabe and Mizuno 1989), the species was included because they have probably existed in Hokkaido for more than a century. The taxonomic resolution in this study was generally species, but floating goby (*Gymnogobius* spp.) and common freshwater goby (*Rhinogobius* spp.) were resolved only to the genus level because although it is known that these genera consist of multiple species, most of the records did not reflect the recent changes in the nomenclature. As of 2004, a total of 13,989 fish have been surveyed at 7,903 sites throughout Hokkaido according to the fish database (Fig. 1c).

Dams and Habitat Fragmentation

As of 2,000, there were 167 large dams (>15 m in height) and 1,040 low-head dams (mean height $\pm$ 1 SD, 9.1 $\pm$ 6.5 m) in Hokkaido. The River Bureau of MLITT constructed the large dams and has managed them since 1913 primarily for the purposes of hydroelectric power generation, water supply for drinking and agriculture, and flood control (Japan Dam Foundation: http://wwwsoc.nii.ac.jp/jdf/). Local governments have managed the low-head dams since 1950 to control erosion and sediment transport (Hokkaido Government: http://www.pref.hokkaido.lg.jp/kn/ssg/). Henceforth, both the large and low-head dams are collectively refer to as “dams.” Smaller and perhaps less impassable barriers (e.g., water diversions for paddy fields, structures to prevent erosion on ephemeral headwater streams, culverts) are also numerous on the island. These barriers were not considered in this study because of the incomplete information on their precise location and date of construction. Furthermore, the presence or absence of a mitigation device such as a fishladder was not taken into account, again because of a lack of complete information. It was estimated, however, that as of 2001 only 6.6% of the small dams in Hokkaido had fishladders (Hokkaido Government: http://www.pref.hokkaido.lg.jp/kn/ssg/).

I assigned the year of habitat fragmentation to the subbasins of all 574 rivers in Hokkaido using a database of river networks compiled by Suzuki et al. (2003). The year of fragmentation was assigned as the year of dam construction or the year of the first dam construction in the case of multiple dams. A large proportion of Hokkaido (27% of the total area) is currently inaccessible from the sea because of the dams. These lost habitats are distributed as a number of isolated subbasins (Fig. 1d). In some cases, dams are located at the mouth of rivers, and the entire basin is isolated from the sea.

Using GIS, I superimposed a map of the 13,989 fish surveys onto a map of the habitat fragmentation. By subtracting a fragmentation year from a survey year, I could determine for each survey if there was a dam (or dams) downstream from the survey site and how many years had passed since the stream was dammed. If a fragmentation year was older than a survey year, there was at least one dam; otherwise, there was no dam. This created two candidate predictor variables for the spatially explicit modeling: (1) a “DAM” that was assigned “1” if the survey was conducted above the dam or otherwise “0,” and (2) “DAMMED,” which was a number of years that had passed since it was dammed (i.e., difference between fragmentation and survey years).

Models and Statistical Analysis

I included the 13,989 presence/absence records of 41 native freshwater fish taxa for modeling. Fish species richness was calculated for each fish survey by summing the number of species captured. It was then modeled using a generalized linear model (GLM) assuming a Poisson error structure in the species richness data. There were obvious interactions between predictor variables when explaining the species richness, but GLMs are capable of handling such interaction terms. Occurrence probabilities of dominant fish species were modeled for each species with a series of generalized additive models (GAMs) assuming a binomial error structure in the occurrence data. I used GAMs for occurrence probabilities because nonlinear relations were identified between fish occurrences and some predictor variables, which can be modeled with GAMs. GAMs, however, are currently not capable of fully accommodating interaction terms (Hastie 1992).

A preliminary analysis based on correlograms detected a significant spatial autocorrelation among the Pearson residuals of the GLM of species richness. Because the autocorrelation became insignificant between two survey sites that were distant by more than 6 km, the 13,989 data points were projected onto 6-km grid squares across all of Hokkaido to generate a spatially independent data set of pooled species richness for each grid square. As a result, a sample size for modeling both species richness and occurrence probabilities was reduced to 3,629 (grids). Fish species that occurred at more than 40 grids were considered dominant, for which occurrence probabilities were modeled.

For all of the 6-km grids with fish data, I prepared a set of environmental predictor variables based on the Digital National Information (MLITT 2010). These variables included elevation above sea level (ELEV), annual air temperature (AIRT), annual rainfall (RAIN), maximum snowfall (SNOW), geomorphological types (GEOM) and average human population for a drainage basin (POPL). The original spatial resolution of these environmental data was 30″ latitude and 45″ longitude (~1 km^2), which were then averaged over the 6-km grids (36 km^2). I also derived drainage area (AREA), the fish survey year (YEAR), the number of fish survey(s) (VISIT), and the UTM coordinates of the survey sites (X and Y) for the 6-km grids using GIS. Pairwise correlation analyses between environmental variables did not reveal any strong correlations (Pearson's r <0.6) except between ELEV and AIRT, which were not used simultaneously in a single model.

I applied a stepwise procedure with both backward and forward selection to identify candidate models. Akaike Information Criterion (AIC) was used to select a set of models with the best overall fit to the data. Log-likelihood ratio tests were then used to determine the significance of potential predictors within this set of candidate models; only models in which all terms were significant ($P < 0.01$) were retained.

Predicted species richness and occurrence probabilities of individual fish species were mapped throughout Hokkaido using GIS. I also mapped predicted loss of species richness due to damming by the following procedure. First, species richness distribution was predicted using the best species richness model with the DAM variable forced to take 0 for all the grids of the island (i.e., hypothetical species richness distribution under a no-dam scenario). Second, species richness distribution was predicted using the same model with the observed DAM data (i.e., more realistic distribution under an actual dam scenario). Third, two distributions were superimposed in the GIS software, and differences in the predicted species richness between the two scenarios were calculated for all the grids, producing a map of the predicted loss of species richness due to damming.

I averaged the predicted occurrence probabilities of each of the dominant fish species for the 574 drainages of Hokkaido. Then I ranked the drainages according to the average occurrence probability separately for each fish species (i.e., highly ranked drainages for one species do not necessarily rank high for another species).

If 32 drainages were sampled randomly from a total of 574 drainages that were serially numbered from 1 through 574 and the average of the 32 numbers was calculated, the expected mean becomes

$$\bar{X} = \sum_{i=1}^{574} \overline{X_i} = \frac{(1+574)}{2} = 287.5$$

The standard error of the mean with the finite population correction is

$$\sigma_{\bar{X}} = \sqrt{\frac{\sigma^2}{n}\left(1 - \frac{n}{N}\right)}$$

where

$$\sigma^2 = \sum \left(X_i - \bar{X}\right) / N$$

Therefore, the 95% confidence interval of the mean becomes

$$\bar{X} \pm t_{0.05(2),32}\sigma_{\bar{X}}$$

which equaled 230 and 345 for lower and upper confidence limits, respectively. If the average ranking of the 32 drainages is higher than 230 for a fish species, that species has significantly higher occurrence probability in the PDs than expected from random sampling. If the average is lower than 345, the species has significantly lower occurrence probability in these drainages.

The efficacy of the PDs in protecting the two salmonids (i.e., masu salmon and Sakhalin taimen) is examined first. Similar analyses are then performed on other dominant fish species to examine collectively the efficacy of the drainages in protecting fish species diversity. Further details of the modeling such as occurrence models selected for individual fishes and model validation can be found in Fukushima et al. (2007).

Results

Effects of Dams on Fish Species Richness

Of the 13,989 fish surveys, 10,860 were conducted with no dams downstream, whereas 3,129 surveys were conducted with at least one dam between the survey site and a river mouth. The fish surveys were grouped into six combinations of the two damming status (i.e., no dam versus dammed) and three survey periods

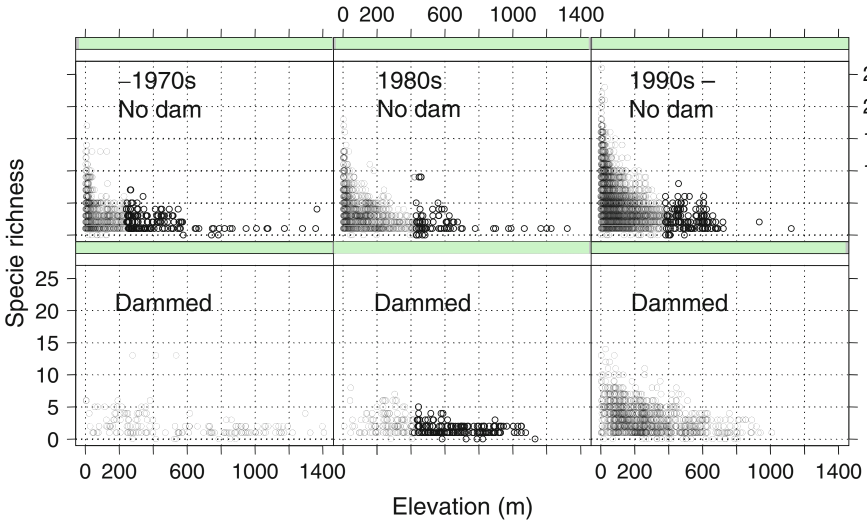


Fig. 2 Fish species richness plotted against elevation of survey sites for no-dam and dammed status and for three survey periods (Modified from Fukushima 2010)

(i.e., 1970s and earlier, 1980s, 1990s and after). For each dam–period combination, fish species richness was plotted against elevation above sea level of the survey site (Fig. 2). Species richness decreased exponentially with increasing elevation from about 20 species at a river mouth to 1 species at about 1,000 m above sea level. The species richness of the 1990s appeared to be larger than that of previous two periods across an entire elevation range for both no dam and dammed status. In fact, the average species richness of the 1990s (5.12) was significantly larger than those of 1970s (3.25, $P<0.001$, *t*-test) and 1980s (3.13, $P<0.001$), whereas the averages of the 1970s and 1980s were not statistically different ($P>0.05$).

Regardless of the survey periods, the species richness of dammed status was smaller than that of no-dam status, with the increasing discrepancy of richness observed toward lower elevations. The average species richness of dammed status across all survey periods (3.08) was significantly smaller than that of no-dam status (4.89, $P<0.001$, *t*-test). The species richness had positive associations with drainage area, survey year, the number of visits, and slope; it had negative associations with elevation and dam. The dam variable had a significantly negative effect on fish species richness ($t=3.932$). Among several interaction terms selected in the model, the dam variable had a significantly positive interaction with elevation ($t=3.592$) and a negative interaction with survey year ($t=1.439$), indicating that the loss of species richness due to damming was greater for the surveys conducted at lower elevations and in more recent years, respectively (Fig. 3). On average, nine species were predicted to have had disappeared from an estuarine habitat where a dam was constructed at a river mouth (Fig. 3a). Species richness was more or less constant until the 1990s, after which it increased rapidly by more than two species both under no-dam and dammed status (Fig. 3b).

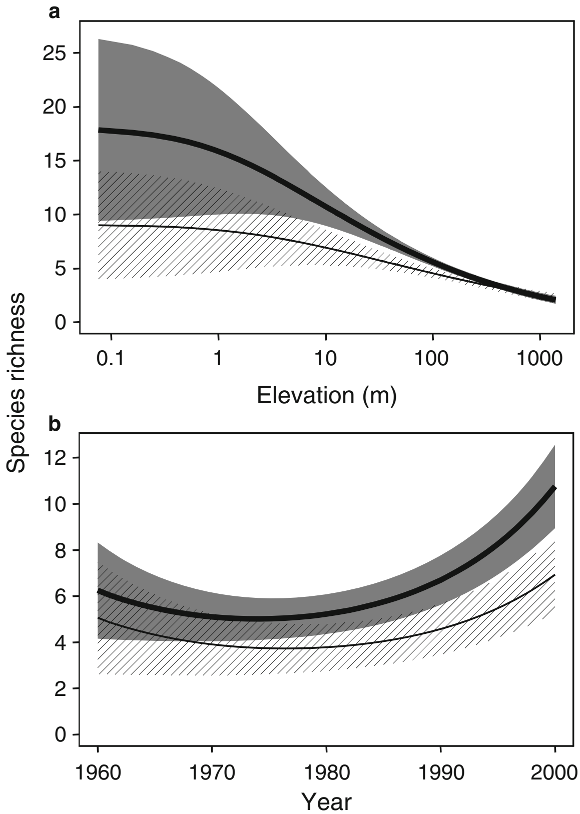


Fig. 3 Predicted species richness plotted against elevation of survey sites (**a**) and survey year (**b**). Prediction under no-dam scenario (*thick line*) and dammed scenario (*thin line*) are shown with the corresponding 95% confidence intervals

The distribution of predicted fish species richness revealed that lower basins of larger rivers such as the Ishikari, Tokachi, and Kushiro Rivers were rich in freshwater fish species, whereas upper basins in mountainous areas such as Daisetsu and Hidaka or areas with steeper topography such as Shiretoko Peninsula were species-poor (Fig. 4).

Because of the construction of dams, fish species richness has decreased in a number of small patches throughout Hokkaido (Fig. 5). In each patch, loss of species richness was greater at lower elevations, which agreed well with the observed pattern (Fig. 2) and model prediction (Fig. 3a). Extensive patches of species loss were found particularly in the central region of Hokkaido (i.e., Daisetsu and Hidaka Mountains). Relatively fewer patches were found in the eastern and northern regions where fewer dams block the rivers.

Efficacy of PDs in Protecting Fish Species

The average occurrence probabilities of masu salmon and Sakhalin taimen were plotted for the 574 drainages in the decreasing order of occurrence probability or

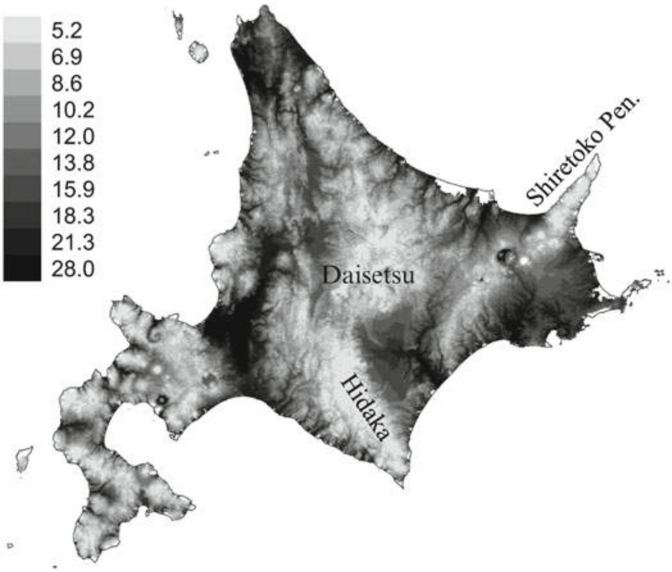


Fig. 4 Geographic Information System (GIS) output of predicted fish species based on the species richness model. (Modified from Fukushima 2010)

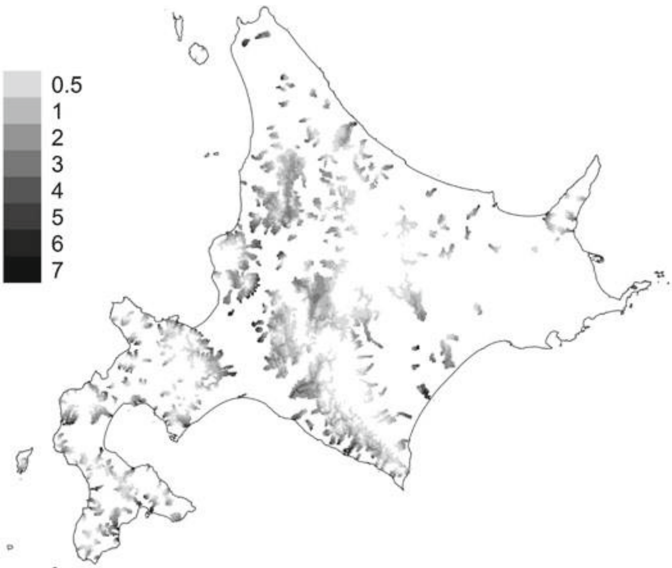
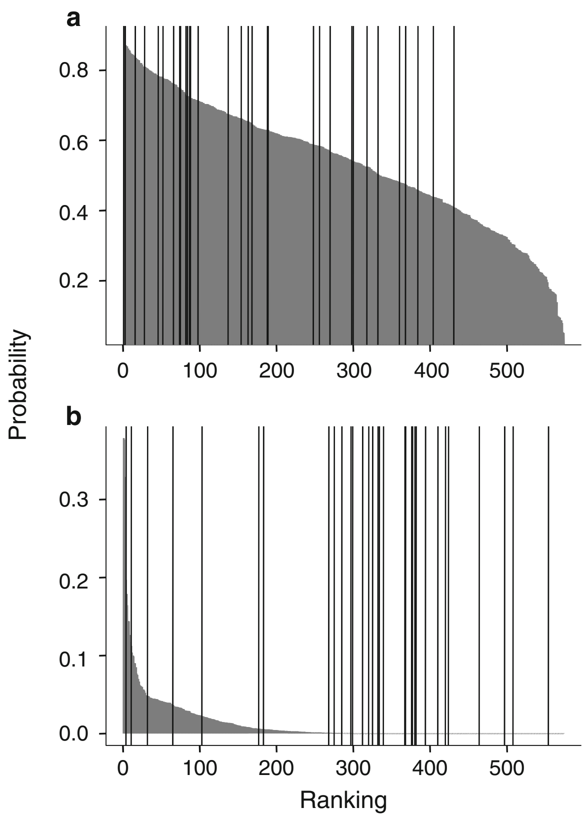


Fig. 5 GIS output of the loss of species richness due to damming (Modified from Fukushima 2010)

Fig. 6 Predicted average occurrence probabilities of masu salmon (**a**) and Sakhalin taimen (**b**) for the 574 drainages of Hokkaido. *Vertical lines* correspond to the ranking of the protected drainages



equivalently increasing order of drainage ranking (Fig. 6). The masu salmon occurrence probabilities were generally high in most river drainages in Hokkaido. The PDs supported masu salmon populations with relatively higher probabilities of occurrence, so the mean ranking of the PDs for this species (179.4) was higher than the upper confidence limit ($P<0.01$). The occurrence probabilities of Sakhalin taimen, on the other hand, were generally low in most drainages and particularly so in the PDs with the mean ranking of 353.6, which was lower than the lower confidence limit ($P<0.05$).

The occurrence probabilities of other dominant fish species were similarly predicted by the GAMs. Of the total 37 fish species, masu salmon ranked highest in the PDs, followed by white-spotted charr (*Salvelinus leucomaenis* PALLAS 1814), wrinklehead sculpin (*Cottus nozawae* SNYDER 1911) and ayu (*Plecoglossus altivelis* Temminck and Schlegel 1846), all of which were above the upper confidence limit (Fig. 7). These are the species that are most likely to occur in the PDs. Six species ranked within the confidence interval of 230–345. The other 27 species ranked lower than the lower confidence limit and included Sakhalin taimen and another endangered species, Hokkaido eight barbel loach (*Lefua costata nikkonis* Jordan and Fowler 1903). Three least likely species that occur in the PDs were common

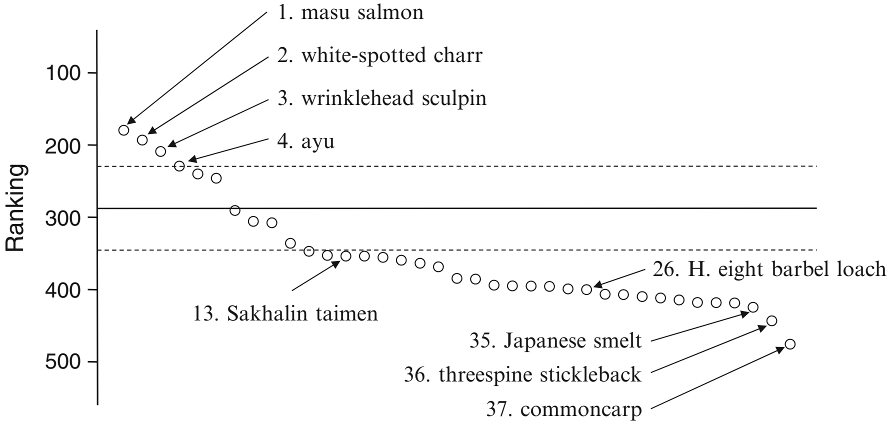


Fig. 7 Average rankings of the protected drainages for the 37 dominant fish species plotted in the increasing order of the ranking. Three horizontal lines indicate the mean (*solid line*) and the upper and lower 95% confidence limits of the mean (*broken lines*)

carp, followed by threespine stickleback (*Gasterosteus aculeatus* Linnaeus 1758) and Japanese smelt (*Hypomesus transpacificus* Mcallister 1963).

Discussion

Estimating the Loss of Fish Biodiversity

Fish species richness has decreased because of dam construction in Hokkaido over approximately the last half century. The loss of species richness was greater when dams were constructed at lower elevations. In addition, areas that are upstream from and closer to a dam site lost a greater number of fish species than areas further upstream because fish species richness decreases exponentially with increasing elevation. If a river is blocked by a dam at a mouth, an average of nine fish species was predicted to disappear just from around that area. Several more species were likely to disappear from upper parts of the river. Those fish that disappeared above dams are most likely to have gone extinct locally from those rivers and streams. Morita and Yamamoto (2002) surveyed white-spotted charr populations in headwater streams with and without dams and identified three factors responsible for their local extinction: isolation period, watershed area above the dam, and channel gradient. The reason for the increased species richness during the 1990s is likely the more efficient sampling technique of electrofishing used during that period than the classic techniques of netting (e.g., cast nets, gill nets) used in the previous periods.

These findings based on the modeling were to some extent evident in the observed species richness data (Fig. 2) because of the extraordinarily large data size.

The spatially explicit models simply extrapolated the fish species richness and richness loss to every grid of Hokkaido. Using the same modeling and GIS techniques, Fukushima et al. (2007) identified eight fish species that had been negatively affected by downstream dams in Hokkaido. They also identified areas and the magnitude of the impact on each fish species.

Coupled with the GIS analysis, the spatially explicit models could identify dams that may contribute to significant recovery of locally extinct fish species if those dams were removed. Dam removal has been a viable management option in the United Sates over the last two to three decades because of growing concerns over environmental quality, endangered species, aesthetics of landscapes, and dam safety and security (Heinz Center 2002; Stanley and Doyle 2003). Aided by a spatially explicit modeling approach to dam removal, a process of decision-making as to whether a dam should be removed and which dams have a priority for removal can become scientifically based and proceed efficiently, which would otherwise be a contentious issue among conflicting stakeholders (Stanley and Doyle 2003).

Mechanisms of the damming impact on aquatic organisms, especially freshwater fishes, are mainly twofold: migration barrier and habitat degradation in downstream reaches (Allan and Flecker 1993). This study focused only on the former (i.e., effects of a dam as a migration barrier). No downstream effects—changes in flow, temperature, sediment transport (Bunn and Arthington 2002)—were examined in this study. Although modeling these effects would be technically more complex than modeling barrier effects, it is not impossible if topological relations between thousands of fish survey sites and upstream dams (in contrast to downstream dams) can be systematically understood for statistical and GIS analyses.

Assessing Efficacy of Protecting Fish Biodiversity

The existing network of the PDs was highly effective in protecting masu salmon populations in Hokkaido, and in this context the original objective of the PDs was successfully achieved. Masu salmon were highly likely to reside in these drainages because the biogeographic distribution of this species closely matched the distributions of the PDs or because various measures taken to protect this species resulted in enhanced viability of the species. Two of three other fish species of above-average ranking in the PDs (i.e., white-spotted charr, wrinklehead sculpin) have habitat and dietary preferences similar to those of masu salmon (Goto 1980; Kishi et al. 2003), inhabiting streams with cascade, step-pool, and plane-bed reaches (Montgomery and Buffington 1998) with abundant benthic macroinvertebrates on which they feed. The fourth species, ayu, in the high-ranking fish group prefer rather downstream areas with plane-bed reaches for feeding on periphyton algae (Kawanabe and Mizuno 1989). All these reach types preferred by the four species are predominant in the PDs.

Apart from the four species above, most of the other fish species received below-average benefits in the PDs. These species in the lower ranking fish group are more likely to occur in streams with lower gradients or lacustrine habitats, which are quite distinct from habitats available in the PDs. In particular, the two endangered species in this fish group, Sakhalin taimen (Fukushima et al. 2008) and Hokkaido eight barbel loach (Nagatsu et al. 2007), are typical of wetland habitats. Sakhalin taimen occur in meandering river systems frequently with a lagoon habitat, which has been developed for agriculture and is becoming increasingly rare in Japan (Fukushima et al. 2008, 2011).

Maintaining the existing network of the PDs is obviously not sufficient to protect the endangered fish species or to protect fish biodiversity in Hokkaido, although these were not the original goals set by the government of Hokkaido. If the goal was to protect the endangered species, conservation efforts should have focused on drainages with higher occurrence probabilities of such species. Instead, if the goal was to protect as many fish species, often with as few drainages (or small cost) as possible, species-rich drainages would have had higher priorities to be selected. Subsequent selection of drainages may rely on a concept of irreplaceability (Pressey et al. 1994). Irreplaceability is a continuum measure that ranges from 0 (containing no additional species to the existing set of reserves) to 1 (containing one or more new species and therefore irreplaceable). Between these two extremes, values reflect varying degrees of potential to replace an area with other areas in the region. Therefore, areas with rarer species would have higher irreplaceability than areas with more common species, for which there would be multiple options for selecting areas to be protected.

The second application of the spatially explicit modeling allowed us to assess the efficacy of the existing network of the PDs by detecting gaps between areas that ought to be protected and the actual configuration of the PDs. Gap analysis is a technique to identify gaps in the existing reserve network systematically, frequently by utilizing remote sensing data and GIS technology (e.g., Scott et al. 1993). It was developed and widely tested in the United States and regarded as a most practical guide for reserve selection (Prendergast et al. 1999). Once goals are prioritized, spatially explicit modeling coupled with gap analysis and other reserve selection algorithms such as irreplaceability could help researchers and managers identify the best "theoretical" solution to an ideal reserve network to meet the goals.

Conclusions

Two applications of spatially explicit population models were discussed. The first related to Japan's extensive network of dams. Spatially explicit statistical models were developed to assess the effects of dams and habitat fragmentation on fish species richness in Hokkaido. A total of 13,989 fish surveys conducted in Hokkaido over the last half century were used to develop the model. The predictor variables of the model included geomorphological and climatological attributes as well as the damming status of each fish survey. The model predicted species richness under two scenarios: a hypothetical status of no dams and the actual dam status. The fish species richness with the two scenarios were superimposed, and the differences between the scenarios were calculated for each grid square of Hokkaido using GIS, generating a map showing the spatial pattern of loss of species richness due to damming.

In the second application, similar models for occurrence probabilities of individual fish species were developed to assess the efficacy of the 32 protected drainages (PDs) for fish conservation in Hokkaido. The objective was to determine whether the same set of PDs could effectively protect multiple fish species with potentially different habitat preferences, and whether the choice of PDs was consistent with science. The relative performance of the PDs was compared to that of randomly selected drainages. The PDs performed better for the commercially important masu salmon and slightly worse for the endangered Sakhalin taimen than expected from a set of 32 randomly chosen drainages. Similar modeling for other freshwater fish revealed that the PDs provided above-average benefits for four fish species, average benefits for six species, and below-average benefits for the remaining 27 species. Although some species were effectively protected by the existing network of PDs, most of the freshwater fish, and therefore fish species diversity, were not protected.

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