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Article in *Freshwater Biology* · May 2007

DOI: 10.1111/j.1365-2427.2007.01783.x

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# Modelling the effects of dams on freshwater fish distributions in Hokkaido, Japan

MICHIO FUKUSHIMA\*, SATOSHI KAMEYAMA\*, MASAMI KANEKO<sup>†</sup>, KATSUYA NAKAO<sup>‡</sup>  
AND E. ASHLEY STEEL<sup>§</sup>

*\*National Institute for Environmental Studies, Onogawa, Tsukuba, Ibaraki, Japan*

*†Faculty of Environment Systems, Rakuno Gakuen University, Ebetsu, Hokkaido, Japan*

*‡Hokkaido Aquaculture Promotion Corporation, Sapporo, Hokkaido, Japan*

*§National Marine Fisheries Service, Northwest Fisheries Science Center, Montlake Boulevard East, Seattle, WA, U.S.A.*

## SUMMARY

1. We examined the effects of habitat fragmentation caused by dams on freshwater fish species using a database of 7848 fish presence/absence surveys, conducted between 1953–2003 in Hokkaido, Japan.
2. A series of generalised linear models showed that for 11 of 41 taxa examined, the probability of occurrence had been influenced either negatively (eight taxa) or positively (three taxa) by the presence of a dam downstream from their habitat.
3. Maps of modelled predictions revealed that dams had had widespread negative impacts on certain taxa, while for other taxa the impact was limited to specific basins. Two of the three taxa whose probability of occurrence was increased in areas above dams have long been transplanted into reservoirs in Japan.
4. For four of the eight taxa whose probability of occurrence was reduced above dams and all three taxa whose probability of occurrence increased above dams, the temporal length of habitat isolation (i.e. the number of years between dam construction and sampling) was also a significant predictor of the probability of occurrence. This pattern indicates that these taxa experienced a gradual rather than an instantaneous population impact as a result of dam construction.
5. The eight taxa whose probability of occurrence was reduced as a consequence of dams all exhibit migratory life cycles. Although migratory taxa are probably more susceptible to the negative effect of dams, we could not detect significant relationships between migration life histories and the effect of fragmentation by dams.
6. These analyses enable stream and fisheries managers to quantify the impacts of habitat fragmentation because of dams for individual species. The spatially explicit nature of our analyses also enables identification of the areas of the impact at broad geographical scales. Using our results, managers can take effective conservation and restoration measures to predict, mitigate or remove the impact of dams. For example, our results can be used to prioritise dams for removal or to predict losses of biodiversity and ecosystem services in advance of dam construction.

*Keywords:* dams, freshwater fishes, geographical information system, habitat fragmentation, spatial modelling

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Correspondence: Michio Fukushima, National Institute for Environmental Studies, Onogawa 16-2, Tsukuba, Ibaraki 305-8506, Japan.  
E-mail: michio@nies.go.jp

## Introduction

Artificial barriers for water regulation and water resource management are ubiquitous worldwide, fragmenting streams and rivers into habitats isolated

from each other and from marine environments (Dynesius & Nilsson, 1994). Dams currently affect nearly 80% of the total water discharge of the 139 largest river systems in North America, Europe and Russia through flow regulation or habitat isolation (Dynesius & Nilsson, 1994). Exact numbers of dams are not known, but available statistics show that approximately 45 000 large dams (>15-m high) fragment streams and rivers in over 140 countries (World Commission on Dams (WCD), 2000). Impacts of dams may therefore contribute to the decline of aquatic biodiversity throughout the globe (Allan & Flecker, 1993; Marchant & Hehir, 2002; March *et al.*, 2003).

Regardless of their purpose, dams affect fish populations in a number of ways (Bunn & Arthington, 2002). Changes in discharge regime and reduced sediment supply below dams are known to cause elevated base flow; channel incision, constriction, or widening; changes in bed material; and loss of spawning habitat (Leopold, Wolman & Miller, 1964; Stanford & Ward, 1992; Knighton, 1998; Montgomery & Buffington, 1998). These effects can translate to changes in estuarine and coastal ecosystems as a result of decreased riverine inputs of nutrients and organisms and altered fluxes of organic and inorganic matter (Holmquist, Schmidt-Gengenbach & Yoshioka, 1998; March *et al.*, 2003).

The most obvious negative effect, however, is restriction of migration (Joy & Death, 2001; Morita & Yamamoto, 2002; Cumming, 2004). The effects of barriers against migration of Pacific salmon (*Oncorhynchus* spp.) have been relatively well-documented (e.g. Kareiva, Marvier & McClure, 2000; Dauble, Hanrahan & Geist, 2003; Sheer & Steel, 2006). For example, more than half of the Columbia River basin has been inundated or blocked to upstream migrant salmon by an extensive network of hydroelectric dams; the annual return of salmonids to the system has decreased from at least 16 million fish at the end of the 19th century to about 2.5 million at present (Dauble *et al.*, 2003). Construction and operation of hydroelectric dams may delay migration, increase predation from birds and resident fish, and result in substantial mortality of juvenile salmonids passing through turbines (Dauble & Watson, 1997).

However, from the viewpoint of biodiversity conservation, losses of salmonids are not the only consequence of damming freshwaters. Other diadromous fishes, which migrate between the sea and

freshwater during their lives, are equally vulnerable to habitat fragmentation (Holmquist *et al.*, 1998; Angermeier & Winston, 1999; Joy & Death, 2001). Losses of migratory fishes and shrimps upstream from dams can alter the top-down effects of consumers and shift foodweb dynamics (Greathouse *et al.*, 2005). In contrast, non-migratory species may flourish after being introduced into altered habitats like reservoirs, dramatically changing existing fish assemblages (Freidenburg, 1998; Holmquist *et al.*, 1998; Bunn & Arthington, 2002).

Our research objectives were threefold: (i) to identify the suite of fish species being affected by dams across Hokkaido, Japan; (ii) to examine the relationship between migratory life history strategy and the impacts of habitat fragmentation and (iii) to provide spatially-explicit predictions of the distribution and magnitude of the impacts of habitat fragmentation across the entire island of Hokkaido.

## Methods

### *Study area and freshwater fishes*

Hokkaido (41–45°33'N, 139–148°53'E; area = 78 461 km<sup>2</sup>), the second largest and northernmost island of Japan, is surrounded by the Sea of Okhotsk, Japan Sea and Pacific Ocean (Fig. 1a). In the central part of the island, elevation rises to 2287 m.a.s.l. The major land-cover classes include boreal and northern temperate forests (40% broad-leaved and 27% conifer) and agricultural fields (15.6%), including pasture and rice paddy fields. Mean annual precipitation ranges from 800 to 1500 mm and mean annual temperature from 6 to 10 °C (Matsushita *et al.*, 2004).

Hokkaido is inhabited by 60–70 freshwater fish species composed primarily of Gobiidae (20%), Cyprinidae (19%), Salmonidae (12%), Osmeridae (7%), Gasterosteidae (6%) and Cottidae (4%) (Goto, 1994). Strictly freshwater or 'primary freshwater' species (*sensu* Myers, 1938) are limited, and those native to Hokkaido include only several cyprinids (Goto *et al.*, 1978). There are also a number of landlocked species, such as lampreys, salmonids and gasterosteids that were once diadromous when the climate was colder. Diadromous species dominate Hokkaido with roughly half (29 species) of all species performing marine-freshwater migrations during their life cycles. Diadromous species are further classified into either

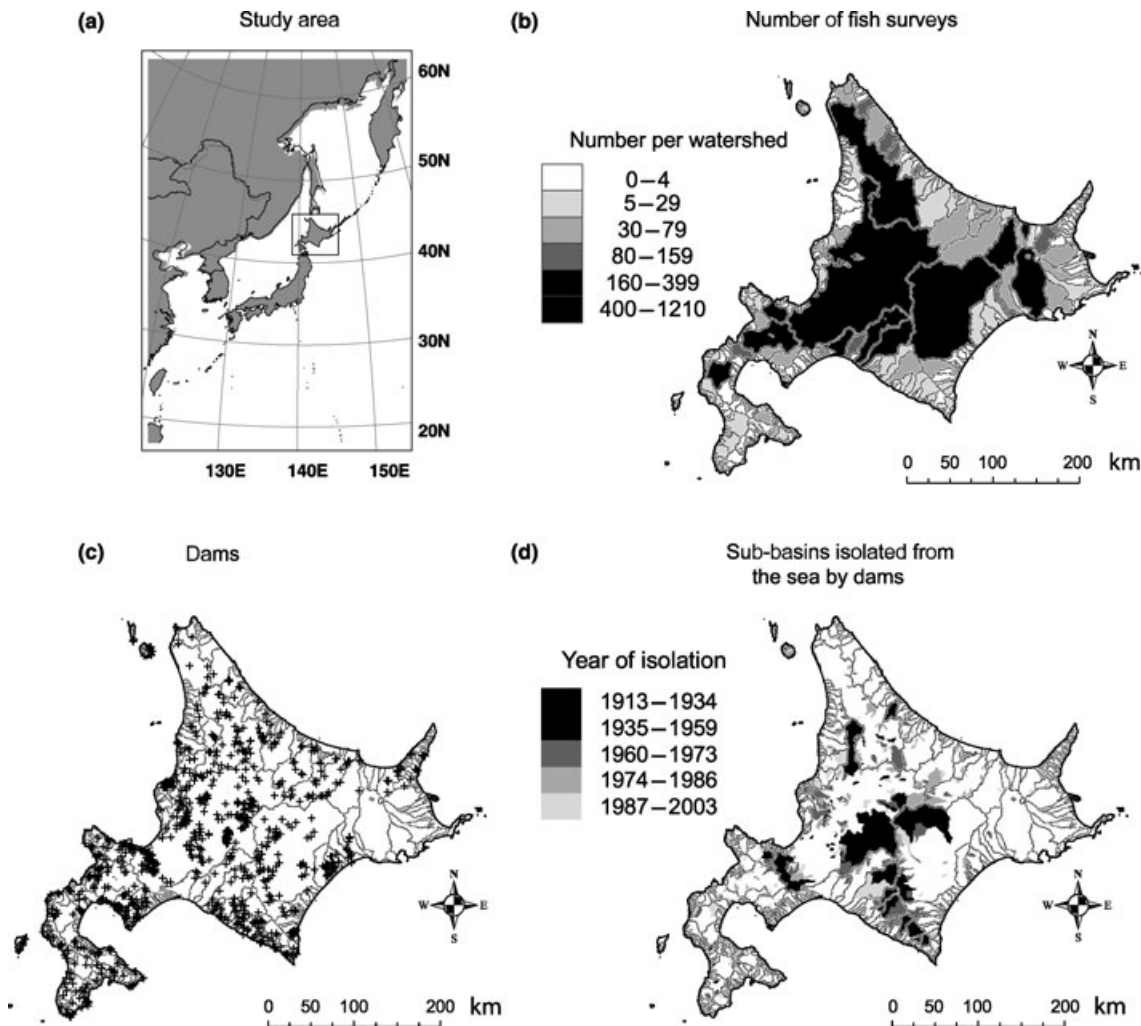


Fig. 1 (a) Map of Hokkaido, Japan, (b) number of fish surveys per catchment, (c) location of dams and (d) sub-basins fragmented by dams, showing years when fragmentation occurred. Catchment boundaries are shown in Hokkaido. Dams (c) which appear to have no corresponding isolated sub-basin (d) have catchment which are too small to be visible on the scale of our map.

anadromous, catadromous or amphidromous. Anadromous species spend most of their lives in the sea and migrate to freshwater to breed, whereas catadromous species migrate from freshwater to the sea for breeding. Amphidromous species migrate between freshwater and the sea not for breeding but as part of the search for food or refuge. Peripheral freshwater species are normally confined to estuarine habitats and enter freshwater only sporadically.

#### Fish database

We compiled a comprehensive database by combining existing fish databases maintained by various agencies (Ministry of the Environment [http://www.](http://www.biodic.go.jp/J-IBIS.html)

[biodic.go.jp/J-IBIS.html](http://www.biodic.go.jp/J-IBIS.html); Hokkaido Fish Hatchery <http://www.fishexp.pref.hokkaido.jp/hatch/honjou/INDEX.htm>; Ministry of Land, Infrastructure and Transport <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 (Fukushima, 2005; Fukushima & Kameyama, 2006). Each record represents presence (indicated as (1) or absence (0) of individual freshwater fish taxa. Surveys were conducted from 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 over 1400 m.a.s.l. Data originating from surveys

targeting specific fish species (often commercially important species) were excluded in this analysis. Where records for multiple years at the same site existed, only the most recent year of data was included. Multiple records for a particular site in the most recent year were aggregated into one observation of presence, if fish were ever detected, and absence, if fish were never detected. By using multiple records where available to determine fish presence and absence, we reduced our risk of false absences.

We excluded fish species that are not native to Japan and species artificially brought from other parts of Japan in recent years. Although the original distribution of common carp may not be precisely known (Kawanabe & Mizuno, 1989), they were included in our analyses because they have probably existed in the island for more than 100 years. The taxonomic resolution in our analyses was generally species, but floating goby (*Gymnogobius* spp.) and common freshwater goby (*Rhinogobius* spp.) were only resolved to genus because, although these genera are now known to consist of multiple species, the majority of the records did not reflect the recent changes in the nomenclature. In summary, we included in our analyses the 7848 presence/absence records of 41 freshwater fish taxa, belonging to six strictly freshwater, 11 landlocked, 11 anadromous, nine amphidromous and four peripheral taxa (Fig. 1b). The scientific names and origins (i.e. native or non-native) of these fish taxa were based on Kawanabe & Mizuno (1989) and Miyadi, Kawanabe & Mizuno (1996), whereas the migration status is based on Goto's (1994) classification.

#### *Dams and habitat fragmentation*

As of 2000, 167 large dams (>15 m in height) and 1040 low-head dams (mean height  $\pm 1$  SD,  $9.1 \pm 6.5$  m) existed in Hokkaido (Fig. 1c). The River Bureau of the Ministry of Land, Infrastructure and Transport (MLIT) constructed the large dams and has managed them since 1913 primarily for the purposes of hydro-electric power generation, water supply for drinking and agriculture and flood control (Japan Dam Foundation <http://www.soc.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, we collectively refer to the large dams and low-head dams as 'dams'. Smaller and

perhaps less impassable types of barriers (e.g. water diversions for paddy fields, structures to prevent erosion on ephemeral headwater streams and culverts) are also numerous on the island. However, we did not consider these barriers in this study because of the incomplete information on their precise location and date of construction. Furthermore, we did not take into account presence or absence of a mitigation device attached to a dam, such as a fishway or fishladder, again because of lack of complete and current information. We estimated, however, that only 6.6% of the small dams in Hokkaido had fishladders as of 2001 (Hokkaido Government <http://www.pref.hokkaido.lg.jp/kn/ssg/>).

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

Using a geographical information system (GIS), we compared the year of each of the 7848 fish surveys to the year of habitat fragmentation at a particular site. We created two potential predictor variables: (i) DAM = whether the survey was conducted above a dam (1) or not (0) and (ii) ISOL = the length of habitat isolation, calculated as the number of years between dam construction of the oldest dam and the fish survey. ISOL equals zero when the fish survey and dam construction coincided.

#### *Environmental data*

For each survey site, we also derived a set of environmental descriptors from the grid data of the Digital National Information (MLIT <http://nlftp.mlit.go.jp/ksj/>). These included elevation above sea level (ELEV), annual air temperature (AIRT), annual rainfall (RAIN), maximum snowfall (SNOW), geomorphologic types (GEOM) and average human population for a drainage basin (POPL). We classified GEOM into 10 classes: volcanic landform, mountains, rocky plateau, sandy-gravel plateau, loam plateau,

piedmont lowland, hills, natural levee, alluvial fan and delta plain. The spatial resolution of each grid was 30 s in latitude and 45 s in longitude (approximately 1 km<sup>2</sup>). We derived drainage area (AREA), fish survey year (YEAR) and the Universal Transverse Mercator coordinates of the survey sites (X and Y) by using the GIS. The UTM coordinates as well as their interaction term may explain a large-scale spatial trend, most notably a biogeographical trend (Legendre & Legendre, 1998). There are known biogeographical boundaries in Hokkaido; to the north of the boundaries fish fauna resemble those of the Siberian systems in Russia and, to the south, the fauna resemble those in the southern islands of Japan (Goto, 1994). Pairwise correlation analyses between environmental variables did not reveal any strong correlations (Pearson's  $r < 0.6$ ).

#### Statistical analysis

In the first step, we modelled all 41 fish taxa using generalised linear models (GLM) with DAM and a suite of environmental variables as the potential predictor variables. ELEV, AREA and POPL were log-transformed to normalise their distributions. We applied a stepwise procedure with both backward and forward selection to identify candidate models. Squared terms for the environmental variables except GEOM were also considered in the stepwise procedure. Akaike Information Criterion (AIC) was used to select a set of models with the best overall fit to the data. We then used log-likelihood ratio tests 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. For each of the final models, null and residual deviance and the per cent deviance explained are reported.

Neighbouring areas tend to have not only similar environmental conditions but also similar probability of fish occurrence, leading to invalid statistical test results if such spatial autocorrelation (SPA) is not taken into account (Legendre, 1993). We broke the river network into a series of reaches based on altitudinal intervals of 0–5, 6–20, 21–100, 101–460 and 461–2287 m a.s.l. (roughly, equal intervals on a logarithmic scale). We then defined a SPA term for each datum by examining the presence/absence of a taxon within each reach. For each taxon, SPA took a

positive value (i.e. value of 1) if at least one other datum in that interval included an observation for that taxon. If there were no other records of presence for that taxon in the interval, SPA took a value of 0. We then included this term (SPA) in the stepwise procedure as a potential predictor variable.

As a second step, we examined ISOL as an alternative predictor in the models by replacing DAM with ISOL and updating the models with generalised additive models (GAM). We updated the models to GAM because of evidence of strong non-linearity between occurrence probability and ISOL in some fish taxa (Fukushima & Kameyama, 2006). Generalised additive models are capable of explaining non-linear relationships by transforming individual terms with scatterplot smoothers before adding them together (Chambers & Hastie, 1992). For the GLMs with a significant DAM variable, DAM was replaced with ISOL and corresponding GAMs were fit with the same set of predictors, but without squared terms. These models were constructed based on the subset of data for which a downstream dam is present ( $n = 1839$ ). Only the continuous terms, such as ISOL were transformed using a smoothing spline. The contribution of ISOL to the model fit was decomposed into a linear component and the remaining non-linear component (Hastie, Tibshirani & Friedman, 2001). The linear component was considered significant if the square of the  $t$  value for the coefficient exceeded the critical value for the chi-square distribution with 1 degree of freedom. The non-linear component of the variable was considered significant if the change in deviance from the linear to non-linear term, relative to the change in degrees of freedom, was significant, again using a chi-square test. An ISOL was judged significant if at least one of the tests (linear or non-linear) was significant at the  $P = 0.01$  level.

We employed  $K$ -fold cross-validation (Efron & Tibshirani, 1993) to validate each of the original 41 GLMs. First, we excluded one-tenth of the data from the dataset of a given taxon, then we fitted a model with the remaining nine-tenths of the data, and we used this model to predict the fish occurrence probability of the excluded data. We then repeated this process 10 times until all data were excluded and predicted. To assess overall performance of the models, we integrated the receiver operating characteristic (ROC) curve (Fielding & Bell, 1997). We integrated the ROC by calculating the area under the

curve (AUC) using a non-parametric technique based on the Wilcoxon statistic (Hanley & McNeil, 1982). The AUC of the ROC provides a single measure of overall accuracy that is not dependent upon a particular decision threshold; the metric ranges from 0.5 for models with no discrimination ability to 1 for models with perfect discrimination between presences and absences (Pearce & Ferrier, 2000).

For taxa for which the GLMs detected a significant negative or positive damming effect, we estimated and mapped reductions or gains in the probability of fish occurrence as a result of the presence of dams. First, we predicted fish occurrence probability at every 1-km<sup>2</sup> grid cell of Hokkaido using the observed values for the DAM variable and the environmental variables; secondly, we predicted fish occurrence probability using the same model except with the dam variable being set to null (i.e. DAM = 0) and thirdly, we calculated differences between the two probabilities for each grid cell. Negative differences represent the estimated decrease in the probability of fish occurrence that has resulted from dams, while positive differences represent the estimated increase in probability of occurrence as a result of downstream dams. Finally, we examined the relationship between migration patterns and the modelled impact of dams using Fisher's exact test (Sokal & Rohlf, 1995).

## Results

The presence of a downstream dam was a significant predictor for 11 fish taxa ( $P < 0.01$ ; Table 1). Eight taxa, i.e. arctic lamprey, Far Eastern brook lamprey, whitespotted char, masu salmon, chum salmon, Chinese ninespine stickleback, Sakhalin sculpin and starry flounder, were negatively associated with downstream dams, whereas three taxa, i.e. Japanese smelt, silver crucian carp and rosyface dace were positively associated with downstream dams.

The occurrence of fish taxa was also significantly influenced by geographical, climatic and other environmental variables. In particular, elevation and/or elevation squared were selected in 38/41 models. A significant positive effect ( $P < 0.01$ ) of SPA was detected in the models for all species, except the sporadic peripheral species, striped mullet. Year of survey was positively associated with occurrence in many models, especially after the 1990s. This change over time in occurrence probability is likely because of

increased sampling efficiency with the introduction of electro-fishing or to increased surveyor attention to newly described species, such as Sakhalin sculpin. Deviance explained by the models ranged from 9.3% to 60.1%, and the discrimination performance metric (AUC of ROC) ranged from 0.71 to 0.98 (Table 2). These two indices of predictive ability were highly correlated with each other ( $r = 0.895$ ). We defined fish prevalence as the number of sites at which a species was present divided by the total number of sites surveyed. Both indices of predictive ability were also significantly correlated with fish prevalence ( $r = -0.427$  and  $r = -0.466$ , respectively;  $P < 0.01$ ). Ubiquitous species such as whitespotted char and wrinkle-head sculpin generally were associated with smaller predictive abilities, whereas species with a limited distribution, such as shishamo smelt and Sakhalin sculpin were associated with greater predictive abilities (Table 2).

For 10 of the taxa significantly impacted by dams, we mapped areas for which fish occurrence probability had been altered by the presence of dams. This mapping analysis excluded starry flounder, which have a limited distribution that was not visible in the predictive maps (Fig. 2). Areas affected by dams were distributed as small patches of sub-basins throughout Hokkaido and, as expected, all of the patches were encompassed completely within catchment with downstream dams (Fig. 1d). The magnitude and extent of the impact of downstream dams on occurrence probability varied from taxon to taxon. Reductions in fish occurrence probability were substantial and extensive for ubiquitous taxa, such as Far Eastern brook lamprey, whitespotted char and masu salmon (Fig. 2b,c,d), whereas reductions were limited to specific catchment or regions for taxa with limited distributions, such as Chinese ninespine stickleback and Sakhalin sculpin (Fig. 2f,g). There was a large amount of overlap in the areas of predicted changes in occurrence probability for two of the three taxa positively influenced by downstream dams, Japanese smelt and silver crucian carp (Fig. 2h,i).

Of the 11 taxa significantly impacted by downstream dams, the occurrence probabilities of seven taxa were also significantly related to the length of time since dam construction (ISOL) (Fig. 3). For these taxa, the effect of dams is related to the length of time that the upstream habitat has been isolated from the sea. For instance, whitespotted char were negatively affected

**Table 1** GLMs for the 41 fish taxa, showing their migratory status and model formulae. All the variables are significant ( $P < 0.01$ )

Common name	Scientific name	Model formula
Strictly freshwater taxa		
Common carp	<i>Cyprinus carpio</i> Linnaeus	$-\text{ELEV} + \text{AREA}^2 - \text{AREA} \pm \text{GEOM} + \text{SPA}$
Hokkaido eight-barbel loach	<i>Lefua costata nikkonis</i> Jordan et Fowler	$-\text{ELEV}^2 \pm \text{GEOM} + \text{YEAR} + \text{POPL} + \text{SPA}$
Oriental weatherfish	<i>Misgurnus anguillicaudatus</i> Cantor	$-\text{ELEV}^2 + \text{ELEV} + \text{AREA}^2 - \text{AREA} \pm \text{GEOM} + \text{YEAR} + \text{SNOW}^2 - \text{SNOW} - \text{X}^2 + \text{X} - \text{Y}^2 + \text{SPA}$
Sakhalin lake minnow	<i>Phoxinus phoxinus sachalinensis</i> Berg	$-\text{ELEV}^2 + \text{ELEV} \pm \text{GEOM} - \text{YEAR}^2 + \text{YEAR} - \text{AIRT}^2 - \text{SNOW} - \text{X} - \text{Y}^2 + \text{Y} + \text{SPA}$
Siberian stone loach	<i>Noemacheilus barbatulus toni</i> Dybowski	$-\text{ELEV}^2 + \text{ELEV} - \text{AREA}^2 + \text{AREA} \pm \text{GEOM} + \text{YEAR}^2 - \text{YEAR} + \text{POPL} - \text{AIRT}^2 + \text{AIRT} + \text{SNOW}^2 - \text{SNOW} - \text{X}^2 + \text{X} - \text{Y}^2 + \text{Y} + \text{SPA}$
Silver crucian carp	<i>Carassius gibelio langsdorffi</i> Valenciennes	$-\text{ELEV}^2 + \text{ELEV} + \text{AREA}^2 - \text{AREA} \pm \text{GEOM} - \text{AIRT}^2 + \text{DAM} - \text{X}^2 + \text{X} - \text{Y}^2 + \text{Y} + \text{SPA}$
Landlocked taxa		
Chinese ninespine stickleback	<i>Pungitius sinensis</i> Guichenot	$-\text{ELEV} + \text{AREA}^2 - \text{AREA} \pm \text{GEOM} - \text{POPL}^2 + \text{POPL} - \text{RAIN}^2 + \text{RAIN-SNOW}^2 - \text{DAM} + \text{Y} + \text{SPA}$
Dolly varden	<i>Salvelinus malma</i> Walbaum	$+\text{ELEV}^2 - \text{ELEV} - \text{AREA} \pm \text{GEOM} + \text{AIRT}^2 - \text{RAIN}^2 + \text{SNOW} + \text{X}^2 - \text{X} + \text{Y}^2 - \text{Y} + \text{SPA}$
Far eastern brook lamprey	<i>Lethenteron reissneri</i> Dybowski	$-\text{ELEV}^2 + \text{ELEV} + \text{AREA}^2 - \text{AREA} \pm \text{GEOM} - \text{AIRT}^2 + \text{AIRT} - \text{DAM} + \text{SPA}$
Juzukake-haze	<i>Gymnogobius castaneus</i> O'Shaughnessy	$-\text{ELEV} - \text{YEAR}^2 + \text{YEAR} - \text{AIRT}^2 - \text{X}^2 - \text{Y}^2 + \text{SPA}$
Landlocked Siberian lamprey	<i>Lethenteron kessleri</i> Anikin	$-\text{AREA} - \text{YEAR}^2 + \text{YEAR} - \text{SNOW} + \text{SPA}$
Ninespine stickleback	<i>Pungitius pungitius</i> Linnaeus	$-\text{ELEV}^2 + \text{ELEV} \pm \text{GEOM} + \text{POPL}^2 - \text{AIRT} - \text{RAIN}^2 + \text{RAIN-SNOW} - \text{X}^2 - \text{Y}^2 + \text{SPA}$
Pond smelt	<i>Hypomesus olidus</i> Pallas	$-\text{ELEV} + \text{POPL} + \text{RAIN-SNOW}^2 + \text{SNOW} + \text{SPA}$
Rosyface dace	<i>Leuciscus ezoe</i> Okada et Ikeda	$-\text{ELEV}^2 + \text{ELEV} \pm \text{GEOM} - \text{YEAR}^2 + \text{YEAR} - \text{POPL}^2 + \text{POPL} - \text{AIRT}^2 + \text{AIRT} + \text{RAIN}^2 + \text{DAM} - \text{X}^2 + \text{X} + \text{SPA}$
Sakhalin stickleback	<i>Pungitius tymensis</i> Nikolsky	$-\text{ELEV}^2 + \text{ELEV} \pm \text{GEOM} + \text{YEAR}^2 - \text{YEAR} - \text{AIRT}^2 - \text{SNOW}^2 + \text{X}^2 + \text{X} + \text{Y} - \text{X} : \text{Y} + \text{SPA}$
Sakhalin taimen	<i>Hucho perryi</i> Brevoort	$+\text{AREA}^2 - \text{AREA} \pm \text{GEOM} - \text{POPL}^2 + \text{SPA}$
Wrinklehead sculpin	<i>Cottus nozanue</i> Günther	$+\text{ELEV}^2 + \text{AREA}^2 - \text{AREA} \pm \text{GEOM} + \text{YEAR}^2 - \text{YEAR} - \text{AIRT}^2 + \text{AIRT} + \text{SNOW}^2 - \text{SNOW} + \text{SPA}$
Anadromous taxa		
Arctic lamprey	<i>Lethenteron japonica</i> von Martens	$-\text{ELEV}^2 + \text{ELEV} - \text{AREA}^2 + \text{AREA} + \text{YEAR}^2 - \text{YEAR} + \text{RAIN}^2 - \text{RAIN} - \text{DAM} + \text{SPA}$
Big-scaled redfin	<i>Leuciscus hakonensis</i> Günther	$-\text{ELEV}^2 + \text{ELEV} \pm \text{GEOM} - \text{POPL}^2 - \text{AIRT}^2 + \text{AIRT} + \text{RAIN}^2 + \text{SPA}$
Chum salmon	<i>Oncorhynchus keta</i> Walbaum	$-\text{ELEV}^2 + \text{YEAR} - \text{POPL}^2 + \text{AIRT}^2 - \text{DAM} + \text{X} + \text{SPA}$
Japanese smelt	<i>Hypomesus transpacificus</i> McAllister	$+\text{ELEV}^2 - \text{ELEV} + \text{AREA}^2 - \text{AREA} + \text{AIRT} - \text{RAIN}^2 + \text{RAIN-SNOW}^2 + \text{SNOW} + \text{DAM} - \text{X}^2 + \text{X} + \text{Y}^2 + \text{SPA}$
Masu salmon	<i>Oncorhynchus masou</i> Brevoort	$-\text{ELEV}^2 + \text{ELEV} - \text{AREA}^2 + \text{AREA} \pm \text{GEOM} + \text{YEAR} - \text{POPL}^2 + \text{AIRT} + \text{RAIN}^2 - \text{SNOW}^2 - \text{DAM} - \text{X} - \text{Y} + \text{X} : \text{Y} + \text{SPA}$
Olive rainbow smelt	<i>Osmerus eperlanus mordax</i> Mitchell	$-\text{ELEV}^2 + \text{ELEV} - \text{POPL}^2 - \text{SNOW} + \text{X}^2 + \text{SPA}$
Pacific redfin	<i>Leuciscus brandtii</i> Dybowski	$-\text{ELEV} + \text{SPA}$
Pink salmon	<i>Oncorhynchus gorbuscha</i> Walbaum	$-\text{ELEV}^2 + \text{ELEV} - \text{AREA} - \text{X}^2 + \text{X} + \text{Y} + \text{SPA}$
Shishamo smelt	<i>Spirinchus lanceolatus</i> Hikita	$-\text{ELEV}^2 + \text{AIRT} + \text{X} - \text{Y}^2 + \text{Y} + \text{SPA}$
Threespine stickleback	<i>Gasterosteus aculeatus</i> Linnaeus	$-\text{ELEV} + \text{AREA}^2 - \text{AREA} \pm \text{GEOM} + \text{AIRT} + \text{RAIN-SNOW}^2 - \text{X}^2 + \text{X} - \text{Y}^2 + \text{Y} + \text{SPA}$
Whitespotted char	<i>Salvelinus leucomaenis</i> Pallas	$+\text{ELEV}^2 - \text{ELEV} - \text{AREA}^2 \pm \text{GEOM} + \text{YEAR}^2 - \text{YEAR} + \text{POPL}^2 - \text{AIRT}^2 + \text{AIRT} + \text{RAIN}^2 - \text{RAIN} - \text{DAM} + \text{X}^2 + \text{X} + \text{Y}^2 - \text{Y} - \text{X} : \text{Y} + \text{SPA}$
Amphidromous taxa		
Ayu	<i>Plecoglossus altivelis</i> Temminck et Schlegel	$-\text{ELEV}^2 + \text{ELEV} - \text{AREA} - \text{YEAR}^2 + \text{YEAR} + \text{POPL} + \text{SNOW}^2 - \text{X}^2 + \text{SPA}$
Chestnut goby	<i>Gymnogobius breunigii</i> Steindachner	$-\text{ELEV}^2 - \text{AREA} + \text{YEAR}^2 - \text{YEAR} + \text{SPA}$
Flathead goby	<i>Luciogobius guttatus</i> Gill	$+\text{YEAR} - \text{POPL} + \text{AIRT} + \text{SPA}$



Table 1 (Continued)

Common name	Scientific name	Model formula
Floating goby	<i>Gymnogobius</i> spp.	$-\text{ELEV}^2 + \text{ELEV} + \text{AREA}^2 - \text{AREA} \pm \text{GEOM} + \text{YEAR} + \text{SPA}$
Japanese trident goby	<i>Tridentiger brevispinis</i> Katsuyama, Arai et Nakamura	$-\text{ELEV}^2 - \text{AREA}^2 + \text{AREA} \pm \text{GEOM} - \text{YEAR}^2 + \text{YEAR} + \text{AIRT} - \text{X}^2 + \text{X} + \text{Y}^2 + \text{SPA}$
Common freshwater goby	<i>Rhinogobius</i> spp.	$-\text{ELEV}^2 + \text{ELEV} \pm \text{GEOM} - \text{YEAR}^2 + \text{YEAR} - \text{X} + \text{SPA}$
Sakhalin sculpin	<i>Cottus amblystomopsis</i> Schmidt	$-\text{ELEV}^2 + \text{YEAR}^2 - \text{YEAR} - \text{DAM} - \text{X}^2 + \text{X} + \text{Y}^2 - \text{Y} + \text{SPA}$
Tyuman-river sculpin	<i>Cottus hangiangensis</i> Mori	$-\text{ELEV}^2 + \text{ELEV} - \text{AREA}^2 + \text{AREA} + \text{YEAR} + \text{AIRT}^2 - \text{X} + \text{SPA}$
White-ventral goby	<i>Acanthogobius laticipes</i> Hilgendorf	$-\text{ELEV} - \text{AREA} - \text{YEAR}^2 + \text{YEAR} - \text{POPL} + \text{AIRT}^2 - \text{RAIN}^2 + \text{RAIN} - \text{X}^2 + \text{X} + \text{Y}^2 + \text{SPA}$
Peripheral taxa		
Japanese icefish	<i>Salangichthys microdon</i> Bleeker	$-\text{ELEV} + \text{SPA}$
Japanese surfmelt	<i>Hypomesus pretiosus</i> Girard	$-\text{ELEV}^2 - \text{AREA} - \text{YEAR} + \text{SPA}$
Starry flounder	<i>Platichthys stellatus</i> Pallas	$-\text{ELEV}^2 - \text{AREA}^2 - \text{YEAR}^2 + \text{YEAR} - \text{POPL} + \text{AIRT} - \text{RAIN}^2 + \text{RAIN} - \text{SNOW}$
Striped mullet	<i>Mugil cephalus</i> Linnaeus	$-\text{DAM} - \text{X}^2 + \text{X} + \text{SPA}$ $-\text{ELEV} - \text{YEAR}^2 + \text{YEAR} + \text{POPL} + \text{AIRT} - \text{RAIN}^2 + \text{Y}^2$

GLM, generalised linear models; GEOM, geomorphologic types; AREA, drainage area; YEAR, fish survey year; SPA, spatial autocorrelation; DAM, dams; ELEV, elevation above sea level; SNOW, maximum snowfall; AIRT, annual air temperature; RAIN, annual rainfall; POPL, average human population for a drainage basin; X and Y, coordinates of the survey sites. Although a categorical variable, GEOM, consists of 10 levels with different coefficients (with different signs), these 10 levels were omitted for brevity. DAM variable is highlighted with bold.

by dams, but the negative effect was more significant in recently isolated habitats than in habitats isolated for a long time (>40 years; Fig. 3b). Masu salmon showed an opposite response to length of isolation (Fig. 3c). Japanese smelt and silver crucian carp, two of the taxa whose probabilities of occurrence were positively impacted by the presence of downstream dams, also showed similar patterns with respect to length of time as isolation (Fig. 3e,f). Their probabilities of occurrence increased with increasing isolation periods.

Of the 41 taxa studied, 20 taxa can be classified as 'diadromous' (11 anadromous and nine amphidromous), while 35 taxa studied were tentatively classified as 'migratory' (20 diadromous, 11 landlocked and 4 peripheral). We identified no significant negative relationship between diadromy and the presence of downstream dams. In other words, the probability of occurrence for diadromous taxa was not particularly reduced by the presence of downstream dams ( $P = 0.454$ , Fisher's exact test; Table 3). Neither did we find that the probability of occurrence of migratory taxa was significantly impacted by the presence of downstream dams ( $P = 0.323$ ).

## Discussion

Dams have extensively deprived many migratory fish taxa of their habitats in Hokkaido. Although not all migratory species studied were negatively impacted by the presence of a downstream dam, we were able to detect significant reductions in the probability of occurrence for eight species, all of which were migratory. Dams also increased the probability of occurrence of three species which may be positively affected by lentic habitats or declines in migratory predators above dams. By comparing maps of current occurrence probabilities to maps of occurrence probabilities predicted without downstream dams, we have demonstrated the large spatial extent of dam impacts for multiple species. These maps illuminate subtle differences in habitat use by similar species. For example, three salmonid species negatively impacted by the presence of downstream dams, whitespotted char, masu salmon and chum salmon, generally inhabit streams at different but overlapping altitudes, and are listed above in decreasing order of altitude. Mapped predictions of changes in occurrence probabilities as a result of dams reflect this altitudinal gradient (Fig. 2c,d,e). Management efforts to reduce the im-

**Table 2** Summary statistics of the 41 generalised linear models, showing deviances, residual degrees of freedom and area under the receiver operating characteristic curves (AUC of ROC)

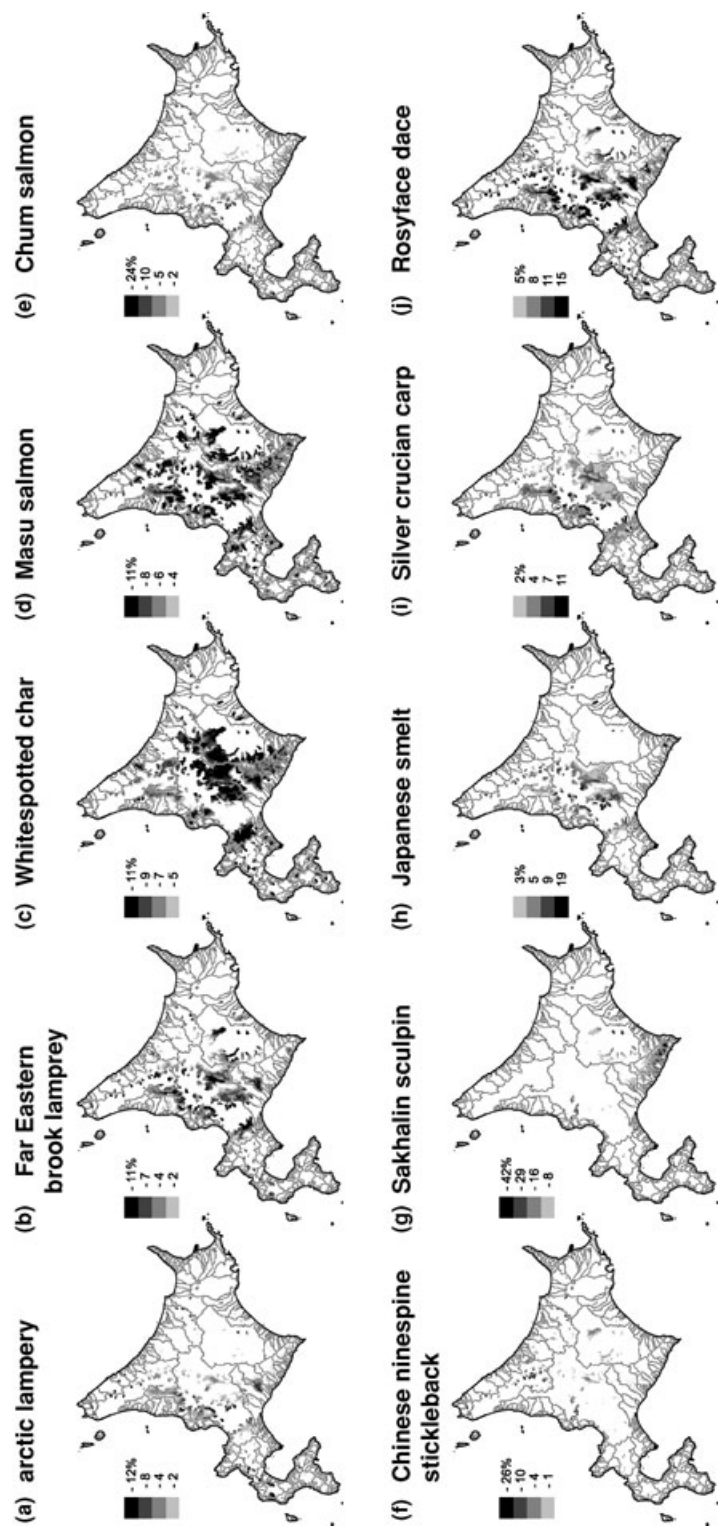
Taxa	Null deviance	Residual deviance	Deviance explained	d.f.	AUC of ROC
Strictly freshwater taxa					
Common carp	2188	1707	0.22	7834	0.854
Hokkaido eight-barbel loach	1208	912	0.245	7834	0.886
Oriental weatherfish	4502	3535	0.215	7827	0.829
Sakhalin lake minnow	2188	1698	0.224	7828	0.857
Siberian stone loach	10820	8017	0.259	7822	0.822
Silver crucian carp	5332	3982	0.253	7827	0.846
Landlocked taxa					
Chinese ninespine stickleback	3591	2443	0.32	7827	0.892
Dolly varden	5086	2030	0.601	7827	0.967
Far eastern brook lamprey	5820	5275	0.093	7830	0.709
Juzukake-haze	3838	2419	0.37	7840	0.913
Landlocked Siberian lamprey	1132	769	0.321	7842	0.927
Ninespine stickleback	5345	3548	0.336	7828	0.887
Pond smelt	947	556	0.413	7841	0.956
Rosyface dace	8426	6548	0.223	7825	0.817
Sakhalin stickleback	2430	1507	0.38	7827	0.923
Sakhalin taimen	1413	682	0.517	7834	0.97
Wrinklehead sculpin	9062	7644	0.156	7828	0.76
Anadromous taxa					
Arctic lamprey	4630	3477	0.249	7837	0.852
Big-scaled redbfin	9280	7760	0.164	7831	0.764
Chum salmon	4483	3600	0.197	7840	0.822
Japanese smelt	4626	2988	0.354	7833	0.903
Masu salmon	10805	7964	0.263	7824	0.825
Olive rainbow smelt	554	335	0.397	7841	0.944
Pacific redbfin	2077	1470	0.292	7845	0.903
Pink salmon	1429	1098	0.232	7840	0.88
Shishamo smelt	565	280	0.503	7841	0.982
Threespine stickleback	5508	3749	0.32	7827	0.882
Whitespotted char	7916	6385	0.193	7821	0.793
Amphidromous taxa					
Ayu	3090	1635	0.471	7838	0.954
Chestnut goby	1484	956	0.356	7842	0.938
Flathead goby	303	140	0.538	7843	0.945
Floating goby	6948	4621	0.335	7832	0.88
Japanese trident goby	3547	2202	0.379	7828	0.919
Common freshwater goby	4440	3243	0.269	7832	0.864
Sakhalin sculpin	1539	838	0.455	7838	0.954
Tyuman-river sculpin	2215	1171	0.472	7839	0.944
White-ventral goby	2256	1221	0.459	7835	0.952
Peripheral taxa					
Japanese icefish	819	585	0.286	7845	0.918
Japanese surfsmelt	534	353	0.339	7843	0.931
Starry flounder	3435	1920	0.441	7833	0.94
Striped mullet	492	318	0.352	7840	0.95

pacts of dams for particular species must consider these large-scale environmental gradients in habitat.

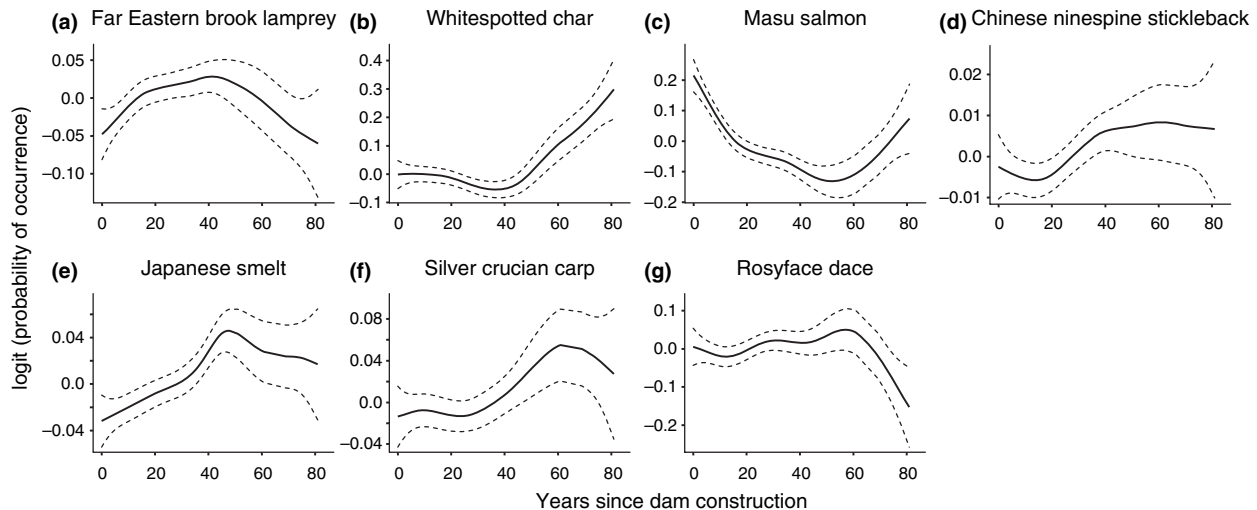
#### *Influence of life-history strategy on the species-specific impacts of downstream dams*

An initial estimation of the mechanisms by which downstream dams impact species occurrence proba-

bilities must include detailed life-history information. For example, of the three salmonids showing a negative influence of dams, only two (whitespotted char and masu salmon) were also influenced by the length of time as isolation by a downstream dam (Fig. 3b,c). Although these two salmonids are normally classified as anadromous, this is not true of all of their populations in Hokkaido. In addition, the



**Fig. 2** Predicted changes in the probabilities of occurrence for fish taxa significantly negatively impacted by the presence of downstream dams (a–g) or positively impacted by the presence of downstream dams (h–j). Starry flounder were negatively affected by the presence of downstream dams (Tables 1 & 2) but were omitted because of their limited distribution and the extremely small areas of reduced occurrence probability. Catchment boundaries are shown in each panel.



**Fig. 3** Effect of the length of isolation period (ISOL) on probability of occurrence by taxa. The average contribution of ISOL in the logit scale (solid line) with  $\pm 2$  SE (dashed line) is plotted against year since dam construction. Changes in probability of occurrence are modelled for those taxa whose probability of occurrence was significantly altered by the length of time since habitat isolation, using generalised additive models. Higher values of ISOL indicate a less negative or a more positive effect on negatively or positively impacted fish taxa, respectively.

**Table 3** Cross-classification of the 41 fish taxa according to their life history patterns and damming effect. See text for the definition of diadromous and migratory taxa

Damming effect	Diadromous		Migratory	
	Yes	No	Yes	No
Negative effect	5	3	8	0
Positive or no effect	15	18	27	6
Total	20	21	35	6

strength of anadromy differs between the sexes; about half of the male masu salmon remain in freshwater for their entire life cycle and mature precociously (Kawanabe & Mizuno, 1989). Furthermore, there are artificially landlocked populations of both species in large catchments above large reservoirs (Morita, Yamamoto & Hoshino, 2000; Morita & Yamamoto, 2002; Tamate & Maekawa, 2002). All these specifics about their life-histories blurred the impacts of dams, making the impacts appear gradual and strongly non-linear with respect to the length of time as isolation. In contrast, all chum salmon populations are strictly anadromous, and the impact of dams on their populations was instantaneous. Occurrence probabilities for chum salmon were not significantly explained by the period of isolation since dam construction. In fact, for all three taxa with obligatory diadromy which

were significantly negatively impacted by the presence of a downstream dam (arctic lamprey, chum salmon and Sakhalin sculpin), none were significantly impacted by the length of time since dam construction.

The three taxa whose probability of occurrence was significantly higher in areas above dams, i.e. Japanese smelt, silver crucian carp and rosyface dace, are anadromous but easily landlocked (Miyadi *et al.*, 1996), strictly freshwater and landlocked, respectively. Although they are considered to be native to Hokkaido, Japanese smelt and species of the genus *Carassius*, including silver crucian carp, have a long history of translocation into Japanese reservoirs for commercial and recreational fishing (Kawanabe & Mizuno, 1989; Miyadi *et al.*, 1996). Similarities both in the spatial patterns of increased occurrence probabilities (Fig. 2h,i) and in their responses to the length of time since dam construction (Fig. 3e,f) suggest these species may have been introduced into the same set of reservoirs at similar times. The positive effect of downstream dams on rosyface dace, a non-commercial species, may be explained by changes in food webs because of exclusion of migratory predators or competitors (c.f., Oberdorff *et al.*, 2001; Novinger & Rahel, 2003; Greathouse *et al.*, 2005). Elimination of the top-down predator effects of migratory shrimp and fishes upstream from reservoirs was shown to

dramatically alter a variety of species interactions in tropical streams (Greathouse *et al.*, 2005).

The lack of a significant relationship between migratory status and changes in probability of occurrence is at first surprising. One might expect that migratory fishes would be at greater risk from habitat fragmentation. Our results may simply be due to the relatively stringent significance level ( $P = 0.01$ ) used for variable selection and to the small sample size (number of taxa). Our preliminary modelling results using a significance level of 0.05 indicated that diadromous and landlocked taxa were more susceptible to the negative impacts of habitat fragmentation than were non-migratory taxa. Another reason for failing to detect a negative impact of downstream dams in all migratory taxa may be the non-random distribution of dams. Most dams and habitats fragmented by the dams are located at higher elevations (Fig. 1d). Peripheral and amphidromous taxa and even some anadromous taxa, such as pink salmon and smelt inhabit exclusively lower reaches of river systems. Although they are potentially threatened by the impacts of upstream dams, they are unlikely to be impacted by dams downstream of their prime habitat. Despite diadromous life cycles, gobies were unaffected by dams probably because they can climb dams of several meters with the aid of their pelvic fins (Holmquist *et al.*, 1998; Yuma, Maruyama & Rusuwa, 2000).

#### Management implications

In the United States, an increasing number of dams have been removed to reconnect once fragmented upstream habitats, to enhance local fisheries, or to restore endangered salmon populations (Graf, 2003; Stanley & Doyle, 2003). None of the dams in Japan have been removed or breached specifically for conservation purposes. If such a radical option is to be seriously considered for Japanese rivers, our approach can provide key predictions for prioritising barrier removals and predicting the potential multi-species response to such restoration efforts. By quantifying fragmented habitats with a GIS, identifying affected fish species and creating predictive models of the impacts of habitat fragmentation, and providing spatially-explicit predictions of the areas of greatest impact, our analyses can inform a wide range of potential management actions. Catchment and fisher-

ies managers can remove dams or test other restoration techniques, such as the installation of fishladders, using our virtual GIS analyses. They would be able to identify catchment that become reconnected and accessible for migratory fishes, obtain important habitat characteristics, and predict fish response in advance of applying the techniques on the ground. Furthermore, because managers can identify the suite of fish species that would most benefit from dam removals or habitat reconnections and can estimate quantitatively the resource gains and associated increased ecosystem services, cost-benefit analyses for large-scale restoration actions will become more feasible and realistic.

Although dam construction in developed countries has considerably slowed down in the last decade, an increasing number of large dams are now being built in large river systems in developing countries in Asia (World Commission on Dams (WCD), 2000). Large rivers such as the Mekong River support the world's largest inland fishery (Jensen, 2001) which is now threatened by the construction of a series of large dams (Lu & Siew, 2006). Assessing and quantifying the potential impacts of dams in large river systems is a formidable challenge. However, if aquatic data were available, our approach would enable initial predictions of the biodiversity losses or gains that could result from the construction or removal of dams even in large river systems.

#### Acknowledgments

We thank M. Takada and R. Kitagawa for providing us with various environmental data for Hokkaido and assisting in compiling the fish database. The manuscript was improved by invaluable comments from H. Mitsunashi, P. Rand, K. Koski and anonymous reviewers.

#### References

- Allan J.D. & Flecker A.S. (1993) Biodiversity conservation in running waters. *BioScience*, **43**, 32–43.
- Angermeier P.L. & Winston M.R. (1999) Characterizing fish community diversity across Virginia landscapes: prerequisite for conservation. *Ecological Applications*, **9**, 335–349.
- Bunn S.E. & Arthington A.H. (2002) Basic principles and ecological consequences of altered flow regimes for

- aquatic biodiversity. *Environmental Management*, **30**, 492–507.
- Chambers J.M. & Hastie T.J. (1992) *Statistical Models in S*. Wadsworth & Brooks/Cole Advanced Books & Software, Pacific Grove CA.
- Cumming G.S. (2004) The impact of low-head dams on fish species richness in Wisconsin, U.S.A. *Ecological Applications*, **14**, 1495–1506.
- Dauble D.D. & Watson D.G. (1997) Status of fall chinook salmon populations in the mid-Columbia River, 1948–1992. *North American Journal of Fisheries Management*, **17**, 283–300.
- Dauble D.D., Hanrahan T.P. & Geist D.R. (2003) Impacts of the Columbia River hydroelectric system on mainstem habitats of fall chinook salmon. *North American Journal of Fisheries Management*, **23**, 641–659.
- Dynesius M. & Nilsson C. (1994) Fragmentation and flow regulation of river systems in the northern third of the world. *Science*, **266**, 753–762.
- Efron B. & Tibshirani R.J. (1993) *An Introduction to the Bootstrap*. Chapman & Hall, New York, NY.
- Fielding A.H. & Bell J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.
- Freidenburg L.K. (1998) Physical effects of habitat fragmentation. In: *Conservation Biology for the Coming Decade* (Eds P.L. Fiedler & P.M. Kareiva), pp. 66–79. Chapman & Hall, New York, NY.
- Fukushima M. (2005) The dam-related decline of freshwater fish diversity – analyses of the data collected from Hokkaido during the last half century. *Japanese Journal of Ecology*, **55**, 349–357.
- Fukushima M. & Kameyama S. (2006) The effects of damming on masu salmon and the Sakhalin taimen and the assessment of their conservation areas based on predictive habitat models. *Ecology and Civil Engineering*, **8**, 233–244.
- Goto A. (1994) Fishes in rivers and lakes – its origins and adaptive strategies. In: *The Nature of Hokkaido* (Eds K. Ishigaki & M. Fukuda), pp. 150–166. Hokkaido University Publishing, Sapporo, Japan.
- Goto A., Nakanishi T., Utoh H. & Hamada K. (1978) A preliminary study of the freshwater fish fauna of rivers in southern Hokkaido. *Bulletin of the Faculty of Fisheries, Hokkaido University*, **29**, 118–130.
- Graf W.L. (2003) *Dam Removal Research – Status and Prospects. Proceedings of the Heinz Center's Dam Removal Research Workshop, October 23–24, 2002*. The H. John Heinz III Center for Science, Economics and the Environment, Pennsylvania Avenue, Washington D.C.
- Greathouse E.A., Pringle C.M., McDowell W.H. & Holmquist J.G. (2005) Indirect upstream effects of dams: consequences of migratory consumer extirpation in Puerto Rico. *Ecological Applications*, **16**, 339–352.
- Hanley J.A. & McNeil B.J. (1982) The meaning and use of the area under the receiver operating characteristic (ROC) curve. *Radiology*, **143**, 29–36.
- Hastie T., Tibshirani R. & Friedman J. (2001) *The Elements of Statistical Learning – Data Mining, Inference, and Prediction*. Springer Series in Statistics. Springer, New York, NY.
- Holmquist J.G., Schmidt-Gengenbach J.M. & Yoshioka B.B. (1998) High dams and marine-freshwater linkages: effects on native and introduced fauna in the Caribbean. *Conservation Biology*, **12**, 621–630.
- Jensen J.G. (2001) Managing fish, flood plains and food security in the Lower Mekong Basin. *Water Science and Technology*, **43**, 157–164.
- Joy M.K. & Death R.G. (2001) Control of freshwater fish and crayfish community structure in Taranaki, New Zealand: dams, diadromy or habitat structure? *Freshwater Biology*, **46**, 417–429.
- Kareiva P., Marvier M. & McClure M. (2000) Recovery and management options for spring/summer chinook salmon in the Columbia River basin. *Science*, **290**, 977–979.
- Kawanabe H. & Mizuno N. (1989) *Freshwater Fishes of Japan*. Yama-Kei Publishers Co. Ltd, Tokyo, Japan.
- Knighton D. (1998) *Fluvial Forms and Processes – a New Perspective*. Arnold, London.
- Legendre P. (1993) Spatial autocorrelation – trouble or new paradigm? *Ecology*, **74**, 1659–1673.
- Legendre P. & Legendre L. (1998) *Numerical Ecology*, 2nd English edn. Elsevier, Amsterdam.
- Leopold L.B., Wolman M.G. & Miller J.P. (1964) *Fluvial Processes in Geomorphology*. Dover Publications, Inc., Mineola, NY.
- Lu X.X. & Siew R.Y. (2006) Water discharge and sediment flux changes over the past decades in the Lower Mekong River: possible impacts of the Chinese dams. *Hydrology and Earth System Sciences*, **10**, 181–195.
- March J.G., Benstead J.P., Pringle C.M. & Scatena F.N. (2003) Damming tropical island streams: problems, solutions, and alternatives. *BioScience*, **53**, 1069–1078.
- Marchant R. & Hehir G. (2002) The use of AUSRIVAS predictive models to assess the response of lotic macroinvertebrates to dams in south-east Australia. *Freshwater Biology*, **47**, 1033–1050.
- Matsushita B., Xu M., Chen J., Kameyama S. & Tamura M. (2004) Estimation of regional net primary productivity (NPP) using a process-based ecosystem model: how important is the accuracy of climate data? *Ecological Modelling*, **178**, 371–388.

- Miyadi D., Kawanabe H. & Mizuno N. (1996) *Colored Illustration of the Freshwater Fishes of Japan*. Hoikusha Publishing Co., Ltd., Osaka, Japan.
- Montgomery D.R. & Buffington J.M. (1998) Channel process, classification, and response. In: *River Ecology and Management Lessons from the Pacific Coastal Ecoregion* (Eds R.J. Naiman & R.E. Bilby), pp. 13–42. Springer-Verlag, New York, NY.
- Morita K. & Yamamoto S. (2002) Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. *Conservation Biology*, **16**, 1318–1323.
- Morita K., Yamamoto S. & Hoshino N. (2000) Extreme life history change of white-spotted char (*Salvelinus leucomaenis*) after damming. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 1300–1306.
- Myers G.S. (1938) Fresh-water fishes and West Indian zoogeography. *Annual Report of the Board of Regents of the Smithsonian Institution*, **92**, 339–364.
- Novinger D.C. & Rahel F.J. (2003) Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. *Conservation Biology*, **17**, 772–781.
- Oberdorff T., Pont D., Hugueny B. & Chessel D. (2001) A probabilistic model characterizing fish assemblages of French rivers: a framework for environmental assessment. *Freshwater Biology*, **46**, 399–415.
- Pearce J. & Ferrier S. (2000) An evaluation of alternative algorithms for fitting species distribution models using logistic regression. *Ecological Modelling*, **128**, 127–147.
- Sheer M.B. & Steel E.A. (2006) Lost watersheds: barriers, aquatic habitat connectivity, and salmon persistence in the Willamette and Lower Columbia River basins. *Transactions of the American Fisheries Society*, **135**, 1654–1669.
- Sokal R.R. & Rohlf F.J. (1995) *Biometry: the Principles and Practice of Statistics in Biological Research*, 3rd edn. W.H. Freeman and Company, New York, NY.
- Stanford J.A. & Ward J.V. (1992) Management of aquatic resources in large catchments: recognizing interactions between ecosystem connectivity and environmental disturbance. In: *Watershed Management: Balancing Sustainability and Environmental Change* (Ed. R.J. Naiman), pp. 91–124. Springer-Verlag, New York, NY.
- Stanley E.H. & Doyle M.W. (2003) Trading off: the ecological effects of dam removal. *Frontiers in Ecology and the Environment*, **1**, 15–22.
- Suzuki N., Murasawa K., Nansai K., Sakurai T., Moriguchi Y., Tanabe K., Nakasugi O. & Morita M. (2003) *River Networking Database for Geo-referenced Fate Modeling of Japanese Rivers*, Research Report 179. The National Institute for Environmental Studies, Tsukuba, Japan.
- Tamate T. & Maekawa K. (2002) Individual growth and phase differentiation of lacustrine masu salmon, *Oncorhynchus masou*, under artificial rearing conditions. *Ichthyological Research*, **49**, 397–400.
- World Commission on Dams (WCD) (2000) *Dams and Development: a New Framework for Decision-Making*. The Report of the World Commission on Dams, Earthscan Publications Ltd., London.
- Yuma M., Maruyama A. & Rusuwa B. (2000) Behavior and distribution of upstream-migrating juvenile *Rhinogobius* sp (the orange form). *Ichthyological Research*, **47**, 379–384.

(Manuscript accepted 28 March 2007)