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Elucidating the distribution of potential spawning habitat and determinants of productivity for anadromous salmonids

(遡河性サケ科魚類の産卵適地推定および再生産効率規定要因の解明)

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農学専攻 環境フロンティアコース

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1. General Introduction

Importance and current population status of anadromous salmonids

The relationship between anadromous salmonids and humans has a long-standing history. Early humans in North America considered anadromous salmonids an important source of food for at least 11,500 years (Butler and O'Connor 2004, Halffman et al. 2015). Similarly, in Japan, anadromous salmonids have been a significant food source for at least 6,000 years (Ishida et al. 2001). Today, anadromous salmonids are still used by humans and are one of the most valuable commercial fishery resources, with landed values of 45 billion yen in 2021 in Hokkaido, northern Japan.

In addition to their commercial value, anadromous salmonids contribute to the transport of marine-derived nutrients to freshwater and terrestrial systems as a spatial subsidy (Gende et al. 2002, Schindler et al. 2003). After spawning, salmon carcasses increase nutrient levels, biofilm, and the abundance of aquatic invertebrates in the river (Richey et al. 1975, Schuldt and Hershey 1995, Wipfli et al. 1998, 1999). Furthermore, their effect reaches not only river ecosystems but also multiple surrounding ecosystems. Anadromous salmonids affect the abundance and distribution of terrestrial top predators and scavengers (Boulanger et al. 2004, Christie and Reimchen 2005, Levi et al. 2012, Field and Reynolds 2013, Walters et al. 2021) and the growth and fruit production of riparian vegetation (Helfield and Naiman 2001, Siemens et al. 2020). In addition to live salmon and carcasses, salmon eggs also play an important role; they are consumed by freshwater fish and riparian birds during the salmon spawning season (Goodge 1959, Obermeyer et al. 1999, 2006, Scheuerell et al. 2007, Moore et al. 2008, Whitehorne 2010, Armstrong and Bond 2013, Reimchen 2017), increasing their abundance (Denton et al.

2009, Yamada et al. 2022a). In this way, salmon have wide-ranging impacts across multiple ecosystems.

Despite their significant commercial and ecological importance, declines in the abundance of anadromous salmonids have been reported in various regions of the world (Ruckelshaus et al. 2002, Mills et al. 2013, Ward et al. 2015, Nicola et al. 2018). The interannual variance in the mortality of anadromous salmonids is greater in freshwater than in marine habitats (Bradford 1995), and the number of returning adults is mainly determined by the number of fry migrating downstream (Morita et al. 2015); therefore, attention should be given to factors affecting reproduction. Several factors discussed below can negatively affect reproduction and may lead to population declines.

Notably, anadromous salmonid populations at the freshwater life stage are affected by river alterations: hydropower production and damming (Thorstad et al. 2021). In particular, the habitat fragmentation caused by dams blocks spawning migration of anadromous salmonids (Limburg and Waldman 2009, Nakamura and Komiyama 2010, Hilborn 2013, Watz et al. 2022), resulting in declining abundance and recruitment and extremely local population extinction. Thus, habitat fragmentation is a critical factor for anadromous salmonid population viability.

Also, anadromous salmonids are vulnerable to increasing water temperature because they are cold-adapted species. If the water temperature exceeds critical values for the survival of salmon eggs and fry (Elliott and Elliott 2010), the population of salmonids at that location will decline significantly or disappear. Forestry practices are one of the factors that cause changes in water temperature. Forest harvesting can contribute to the increase in stream temperature by allowing more sunlight to reach the stream (Brown and Krygier 1970, Holtby 1988, Johnson and Jones 2000, Pollock et al.

2009); therefore, severe clearcutting can lead to a reduction in suitable thermal habitat for salmon. Moreover, climate change has an especially significant impact on water temperature. Beyond the increase in stream temperatures due to climate change that has already been observed (Kaushal et al. 2010, Isaak et al. 2012), future climate change is expected to result in even higher water temperatures (Selbig 2015, Du et al. 2019). Several studies have predicted a significant reduction in anadromous salmonid habitat due to the increasing water temperatures caused by climate change (Ruesch et al. 2012, van Vliet et al. 2013, Isaak et al. 2018).

Climate change-induced frequent flooding also affects the recruitment of anadromous salmonids. Flood disturbance leads to high mortality in the egg to alvine stage by scouring redds (Seegrist and Gard 1972, Holtby and Healey 1986, Thorne and Ames 1987, Montgomery et al. 1996, Greene et al. 2005, Waples et al. 2008, 2009, Milner et al. 2013). Future climate change has also been predicted to lead to more frequent flooding and increased flood risk (Milly et al. 2002, Arnell and Gosling 2016). Thus, flooding disturbances in future climates may result in high mortality of anadromous salmonids in freshwater systems.

Additionally, anadromous salmonid populations are adversely affected by nonnative species through biological interactions within freshwater ecosystems (Houde et al. 2015, 2016). A meta-analysis study showed that the presence of nonnative species imposes negative effects on the performance (behaviour, habitat use, growth, and survival) of Atlantic salmon *Salmo salar* (Grant and Weir 2022). In Japan, a significant number of wild and hatchery-reared chum salmon *Oncorhynchus keta* fry were observed to fall prey to the nonnative brown trout *Salmo trutta* (Honda et al. 2023).

Also, hatchery stocking programs negatively influence anadromous salmonid populations. This program has been conducted to conserve and enhance salmonids around the world (Morita et al. 2006b, 2006a, Naish et al. 2007, Laikre et al. 2010, Kitada 2018, 2020). Continuous hatchery release decreases reproductive success (Araki et al. 2007, Christie et al. 2012, Willoughby and Christie 2019, O'Sullivan et al. 2020). Moreover, it increases competition between fish of wild and hatchery origin, undermining population stability and decreasing abundance (Terui et al. 2023).

Research gaps

Given the degradation of habitat for natural reproduction and the adverse effects of hatchery release, it is critical to conserve and restore essential habitats for wild populations to sustain the benefits from anadromous salmonids. Therefore, there is a pressing need to conduct quantitative assessments of their habitat.

To clarify the essential habitat for wild populations, an assessment should focus on two key points. First, an evaluation of the distribution of spawning habitat is critical for anadromous salmonids because they cannot spawn anywhere; environmental conditions determine their spawning habitat. Substrate particle size should be examined since it is the major determinant of their suitable spawning habitat (Kondolf and Wolman 1993). Additionally, since habitat fragmentation by artificial structures leads to a reduction in spawning habitat, it is necessary to quantify the reduction of spawning habitat due to fragmentation. However, few studies have implemented a quantitative assessment of spawning habitats on a broad scale based on substrate particle size or determined the impact of fragmentation.

Furthermore, since freshwater productivity (i.e., the number of juveniles entering the ocean per reproducing parent) influences the lifetime productivity (adult offspring per parent) of salmon (Bradford 1995, Morita et al. 2015) and is affected by environmental conditions, such as water discharge and temperature (Jensen and Johnsen 1999, Anderson and Topping 2018, Honkanen et al. 2019, Warkentin et al. 2022), it is important to understand the factors that determine the freshwater productivity of anadromous salmonids to evaluate their habitat. For example, high thermal conditions and high water discharge reduce freshwater productivity (Anderson and Topping 2018, Honkanen et al. 2019). Because these environmental factors are typically spatially heterogeneous, freshwater productivity may vary among rivers and watersheds. Nevertheless, spatial comparisons of freshwater productivity are scant, and the spatial pattern of freshwater productivity and its determinants have not been adequately elucidated.

Thus, the following studies are required to guide the conservation and restoration of spawning habitats for wild anadromous salmonid populations.

1. A study that elucidates the distribution of potential spawning habitat for anadromous salmonids on a broad scale and assesses the impact of fragmentation.

2. A study that clarifies the determinant factors of spatial patterns in freshwater productivity of anadromous salmonids.

Study aims and study design

This study comprises a sequence of investigations conducted to appraise the spawning habitat of anadromous salmonids in Hokkaido, northern Japan. Anadromous salmonids have been an essential fishery resource in Japan for a considerable time, necessitating population recovery efforts. Hokkaido is the main distribution area for anadromous salmonids in Japan (Figure 1-1).

In Chapter 2, I evaluated the amount of suitable spawning habitat for anadromous salmonids in Hokkaido, northern Japan, based on riverbed particle size prediction and then assessed the impact of fragmentation on their spawning habitats. Dams are ubiquitous across the globe (Grill et al. 2019, Belletti et al. 2020), and Japan has the third largest number of dams according to a database that presents information on dams around the world (Lehner et al. 2011), as well as many small dams. Therefore, the available suitable spawning habitat for anadromous salmonids is expected to have been greatly reduced.

In Chapter 3, I examined the diel pattern of downstream migration of pink salmon *O. gorbuscha* fry in the Shiretoko Peninsula, northern Japan. To evaluate the freshwater productivity of anadromous salmonids in the next chapter, it was necessary to understand the diel migration pattern of salmon fry and to quantitatively evaluate salmon fry migration. While previous studies have examined the diel migration of pink salmon (Neave 1955, Pavlov et al. 2015, Kirillov et al. 2018), these studies have reported inconsistent results across rivers or surveys, and a comprehensive understanding of the diel pattern has not been achieved.

In Chapter 4, I examined the relationship between the freshwater productivity of pink salmon and environmental factors on a watershed scale that conceivably influences freshwater productivity in the Shiretoko Peninsula, Hokkaido, northern Japan. While several environmental factors were addressed in this study, I particularly focused on watershed hydrogeomorphology, which regulates stormflow water yields, sediment yield and transport, and channel stability (Moore and Burch 1986, Moore et al. 1991, Aalto et al. 2006, Koskelo et al. 2018), due to the significant impact of flood disturbance on freshwater productivity and the possibility of its exacerbation by climate change.

Finally, in Chapter 5, I evaluated the restoration value of each watershed for salmon spawning on the Shiretoko Peninsula, Hokkaido, northern Japan, based on the results of Chapters 2 and 4. In addition, I discuss the implications of the results for the future conservation and restoration of salmonids.

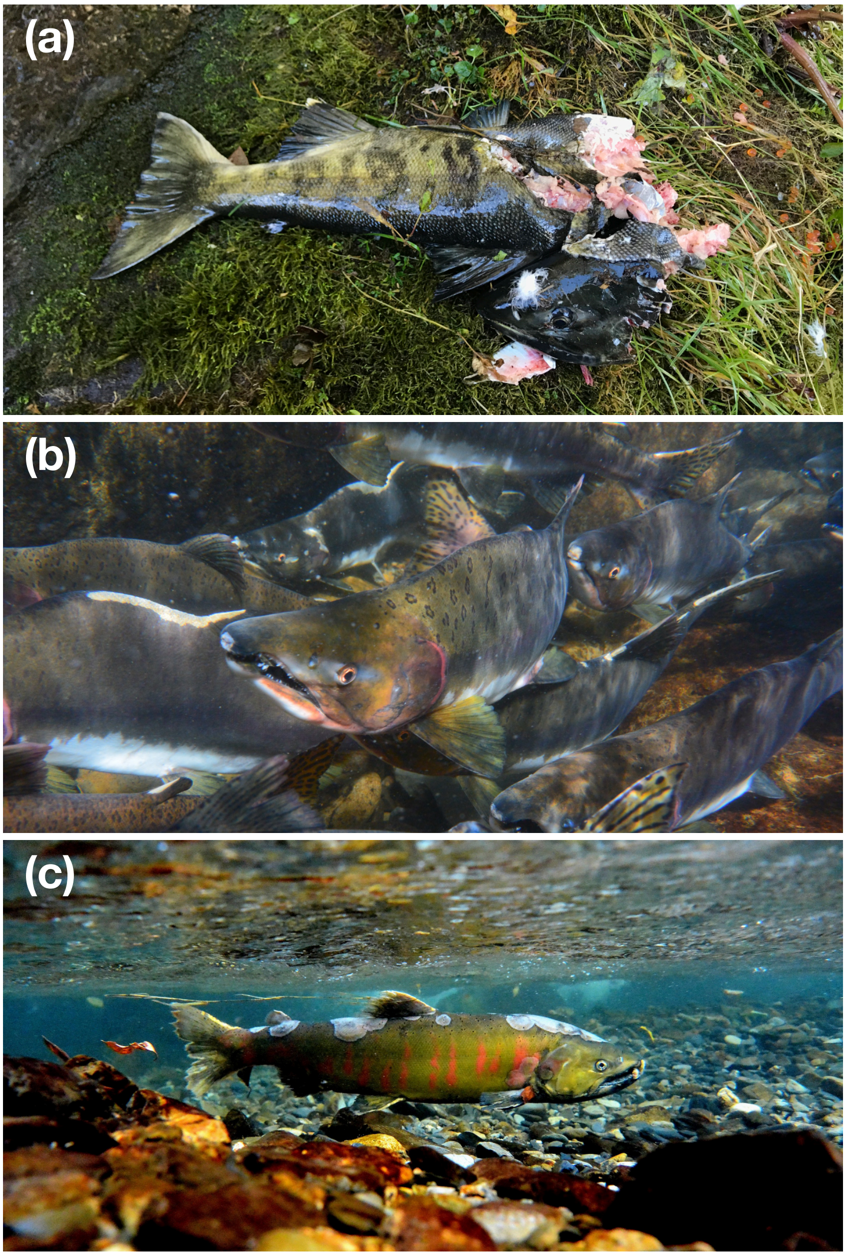

Figure 1-1 Photos of three major species of anadromous salmonids migrating upstream in Japan: (a) chum salmon predated by a brown bear (*Ursus arctos*), (b) pink salmon running upstream, and (c) masu salmon (*O. masou*) after spawning.

2. Fragmentation status in spawning habitat of anadromous salmonids in Hokkaido, northern Japan

2-1. Introduction

Freshwater ecosystems have suffered from habitat fragmentation caused by dams (Strayer and Dudgeon 2010, Wu et al. 2019, Reid et al. 2019). The consequences of habitat fragmentation are numerous and include impeding the migration of organisms (Puijenbroek et al. 2019), restricting their distribution (Fukushima et al. 2007), and undermining biodiversity (Liermann et al. 2012, Liu et al. 2019). Dams have been constructed worldwide (Grill et al. 2019, Belletti et al. 2020), and 48% of the world's rivers have been affected by fragmentation, flow regulation, or both (Grill et al. 2015). Furthermore, since innumerable dams and hydropower plants are under construction or are planned for construction (Zarfl et al. 2015, Winemiller et al. 2016, Couto and Olden 2018), the negative effects of fragmentation on freshwater ecosystems are likely to intensify in the future.

Habitat restoration, such as the installation of fishways and partial and complete removal of dams, has been conducted to mitigate the adverse effects of fragmentation on freshwater ecosystems (Garcia de Leaniz 2008, Kiffney et al. 2009, Nakamura and Komiyama 2010, Fjeldstad et al. 2012, Birnie-Gauvin et al. 2018). However, due to numerous barriers, resources and time for restoration are scarce. Thus, restoration efforts should be prioritized based on some criteria to maximize benefits. Given that many stream fishes migrate through rivers to spawn (Fredrich et al. 2003, Kume et al. 2005, Jackson and Moser 2012, Quinn 2018, Kazyak et al. 2020, Watanabe 2022), factors determining the suitability of spawning habitats can be useful for prioritization; thus, mapping spawning habitat suitability for target species based on those factors and assessing the impact of dams on them is necessary for prioritization. For several freshwater fish species, such as salmonids and sculpins, substrate particle size is a critical factor that determines suitable spawning habitat (Kondolf and Wolman 1993, Watanabe 2022). While some studies have predicted riverbed particle size based on geospatial information on a broad scale (Snelder et al. 2011, Haddadchi et al. 2018), these predictions have not been used to assess the effects of fragmentation on the spawning habitat of organisms.

In this study, I investigated the distribution of spawning habitats for anadromous salmonids and the impact of fragmentation on spawning habitats in Hokkaido, northern Japan, by developing a particle size prediction model. Although anadromous salmonids are commercially and ecologically important fish species, declines in the abundance of anadromous salmonids have been observed in many regions (Ruckelshaus et al. 2002, Mills et al. 2013, Ward et al. 2015, Nicola et al. 2018). Fragmentation has hindered their spawning migration, i.e., reproduction (Limburg and Waldman 2009, Nakamura and Komiyama 2010, Hilborn 2013, Watz et al. 2022). Restoring connectivity is an important consideration for improving their populations.

2-2. Methods

Particle size data

I obtained riverbed particle size data (median particle size, d_{50}) from the Hokkaido Regional Development Bureau. These data were derived from particle size distribution surveys conducted in 33 rivers in Hokkaido, northern Japan, encompassing a total of 1584 sampling points (Table 2-1). Most of these rivers are currently or were formerly used for spawning by salmon. The mean ± SD distance between sampling points within each river was 0.99 ± 1.15 km. At each sampling point, 1 to 3 samples of riverbed material were collected and subsequently conveyed to the laboratory for further analysis, wherein the d_{50} was calculated by sieve analysis. In cases where two or three samples were collected from a single sampling point, an average value was calculated. The collection of riverbed materials was conducted between 1996 and 2019.

Table 2-1 Summary statistics for the riverbed particle size (d_{50} [mm]) for each river.

River	n	Mean ± SD	Range
Teshio River	281	18.50 ± 14.52	0.09–87.10
Onobunai River	3	5.60 ± 1.59	3.97–7.15
Toikanbetsu River	20	7.01 ± 3.47	2.97–15.63
Nayoro River	35	25.30 ± 10.32	9.24–50.76
Furenbetsu River	3	15.83 ± 3.38	12.19–18.87
Rumoi River	24	8.19 ± 7.83	0.19–37.84
Ishikari River	214	19.55 ± 20.30	0.10–96.51
Toyohira River	23	31.27 ± 31.42	0.34–90.72
Chitose River	46	1.63 ± 2.86	0.20–15.62
Izari River	15	8.77 ± 6.07	0.42–17.92
Yubari River	45	23.77 ± 27.22	0.53–140.80
Ikushunbetsu River	36	25.57 ± 19.02	0.23–65.74
Sorachi River	50	37.00 ± 12.24	0.98–56.83
Uryu River	71	37.73 ± 36.53	0.69–238.33
Osarappe River	13	23.29 ± 9.58	7.77–39.42
Chubetsu River	34	90.01 ± 83.91	17.90–336.26
Biei River	67	28.88 ± 13.02	3.31–73.62
Ushubetsu River	15	27.50 ± 7.52	17.82–42.40
Nagayamashin River	6	25.51 ± 10.45	13.61–40.40
Shiribeshitoshibetsu River	50	26.21 ± 17.93	1.24–71.36
Mu River	43	8.02 ± 9.65	0.69–44.00
Saru River	27	18.83 ± 7.98	3.01–41.61
Tokachi River	98	15.02 ± 13.38	0.11–57.84
Toshibetsu River	43	20.67 ± 13.85	2.48–50.36
Satsunai River	46	69.17 ± 45.35	15.50–165.05
Otofuke River	30	32.22 ± 12.28	10.54–59.18
Kushiro River	66	10.34 ± 11.88	0.61–56.45
Abashiri River	34	29.13 ± 13.39	3.88–48.75
Bihoro River	4	7.49 ± 2.51	4.86–10.27
Tokoro River	75	13.06 ± 8.93	0.32–27.70
Muka River	12	23.18 ± 8.17	12.14–39.77
Yubetsu River	31	51.30 ± 23.54	2.50–104.86
Shokotsu River	24	34.11 ± 20.85	3.20–77.00

Predictors

For statistical analyses, I derived 12 predictors (Table 2-2). These predictors were selected based on previous studies (Snelder et al. 2011, See, Haddadchi et al. 2018). The description and derivation of these characteristics are provided below.

Elev, *segElev*, *Area, Slope*, *segSlope*, and *DrainDen* were calculated based on a 10 m digital elevation model provided by the Geospatial Information Authority of Japan (https://fgd.gsi.go.jp/download/menu.php). The delineation criterion for a segment was stream confluence. I also used existing streamline data from the National Land Numerical Information download service provided by the Ministry of Land, Infrastructure and Transport of Japan (https://nlftp.mlit.go.jp/ksj/index.html). *AnnRain* and *AnnTemp* were calculated based on average precipitation and temperature data for the past thirty years with a 1-km grid resolution provided by the Ministry of Land, Infrastructure and Transport of Japan (Climatological Normals 2010 data, https://nlftp.mlit.go.jp/ksj/index.html). *Urban*, *Agric*, and *Forest* were calculated based on nation-wide land use census data provided by the Ministry of Land, Infrastructure and Transport of Japan (https://nlftp.mlit.go.jp/ksj/index.html). *Alluv* was calculated based on the 1:200,000 Seamless Digital Geological Map of Japan provided by the Geological Survey of Japan (https://gbank.gsj.jp/seamless/2d3d/). These geospatial analyses were performed using ArcGIS Pro (Esri, version 2.4.0).

Table 2-2 Summary of the predictor variables.

Parameter	Unit	Description
Climate		
AnnRain	mm	Watershed average annual rainfall
AnnTemp	°C	Watershed average annual air temperature
Geomorphology		
Slope	%	Watershed average hill slope
segSlope	%	Average slope of the segment
Area	km^2	Watershed area
Elev	m	Average elevation of the watershed
segElev	m	Average elevation of the segment
DrainDen	km/km^2	Mean drainage density of the watershed
Land cover		
Urban	%	Proportion of watershed covered by urban land cover
Agric	%	Proportion of watershed covered by agricultural land cover
Forest	%	Proportion of watershed covered by forest land cover
Geology		
Alluv	%	Percentage of watershed occupied by alluvium

Statistical modelling

Before the analysis, I evaluated the correlation among predictor variables and found a strong negative correlation (|r| >0.7, Dormann et al. 2013) between *Slope* and *Forest*; *segElev* and *Elev*. I excluded *Forest* and *Elev*, which had low correlations with the response variable (d_{50}), from the analysis.

The following analyses were conducted with R v. 4.2.0 (R Core Team 2022) using "caret" v. 6.0.92 (Kuhn 2022) and "pdp" v. 0.8.1 (Greenwell 2017). The dataset was randomly partitioned into two datasets: training (75% of observations) and testing (25% of observations) datasets. All predictor variables were scaled and centred in a preprocessing stage. I then trained three regression algorithms using the training dataset: the model-averaged neural network (*avNNet* function) (Ripley 1996), support vector machine (*svmRadial* function), and k-nearest neighbours (*kknn* function). These models were trained with 10-fold cross validation to optimize the hyperparameters of the models. I evaluated the goodness-of-fit of the regression based on the coefficient of determination (R^2), the root-mean square error (RMSE) and mean squared error (MSE) using the testing dataset. The best performing model, across all measures, was selected. The importance of predictor variables was calculated with the *varImp* function of the caret package. In addition, the relationships between each predictor and response variable were visualized by a partial dependence plot (Friedman 2001) with the *partial* function of the pdp package.

Mapping

Anadromous salmonids can generally spawn in gravels with a median diameter from 5.4 mm up to approximately 10% of their body length (Kondolf and Wolman 1993). Masu salmon, chum salmon, and pink salmon are the major anadromous salmonids that migrate upstream to Hokkaido, northern Japan. The body lengths are similar between species, but chum salmon are slightly larger, and the average length of chum salmon returning to Hokkaido from 2017 to 2019 was 66.6 cm (Salmon Database, http://salmon.fra.affrc.go.jp/zousyoku/fri_salmon_dept/sdb.html). Following the average length of chum salmon and the criteria of a previous study (Kondolf and Wolman 1993), I defined the range of median gravel diameters suitable for salmon spawning in this study as 5.4 to 66.6 mm. I created a map of average particle size based on the constructed model and determined whether the particle size on the map was suitable or unsuitable for spawning according to the criterion. In addition, to assess the impact of fragmentation, the dam location data (GSI Vector Tile Experiment, https://maps.gsi.go.jp/vector/), which have geographic information about weirs, dams, and sluice gates, were overlaid on the created spawning habitat map. Then, reaches located upstream of the dam were considered unavailable.

2-3. Results

The R^2, RMSE and MAE of the median particle size estimates were 0.68, 14.85 and 9.70 for the neural network, 0.59, 16.85 and 10.07 for the support vector machine, and 0.67, 15.02 and 10.03 for k-nearest neighbours, respectively. The prediction model using the neural network had the highest prediction accuracy. Importance measures based on the neural network indicated that *segElev* made the greatest contribution to model accuracy, followed by *segSlope* (Figure 2-1). The median particle size increased with increasing *segElev* and *segSlope* (Figure 2-2).

The estimated length of the suitable spawning reach throughout Hokkaido was 40738.62 km, and 49.84% of the suitable spawning habitat (20302.49 km) was unavailable due to fragmentation (Figure 2-3). The Tokachi River basin had the longest fragmented suitable spawning reach (3963.44 km), followed by the Ishikari River basin (3119.18 km). These two basins had notably longer fragmented reaches than the third (Teshio River basin, 1571.16 km), accounting for 34.89% of the total fragmented reach in Hokkaido.

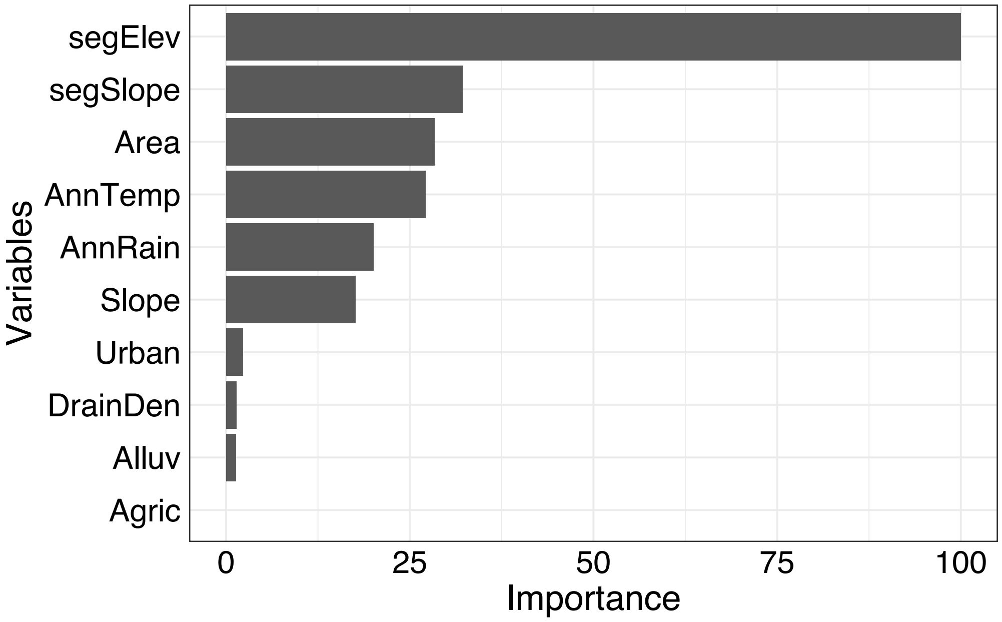

Figure 2-1 The relative importance of predictor variables for the neural network regression model.

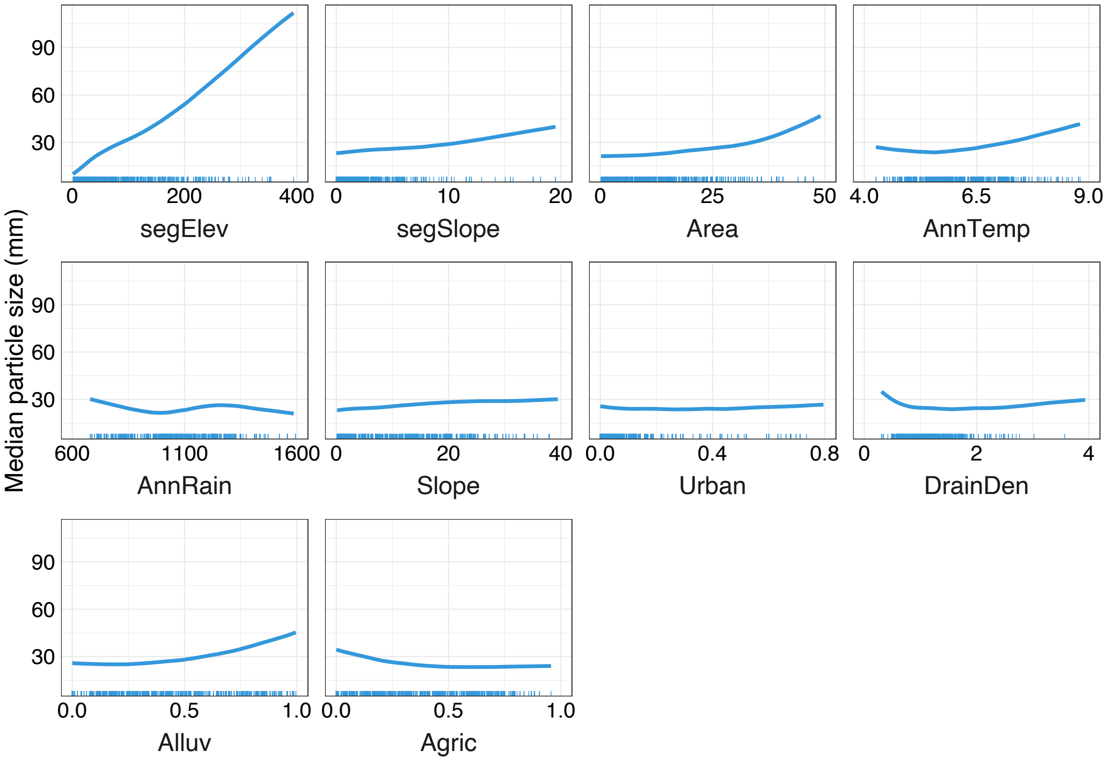

Figure 2-2 Partial dependence plots for each predictor variable against d_{50} in the neural network regression model.

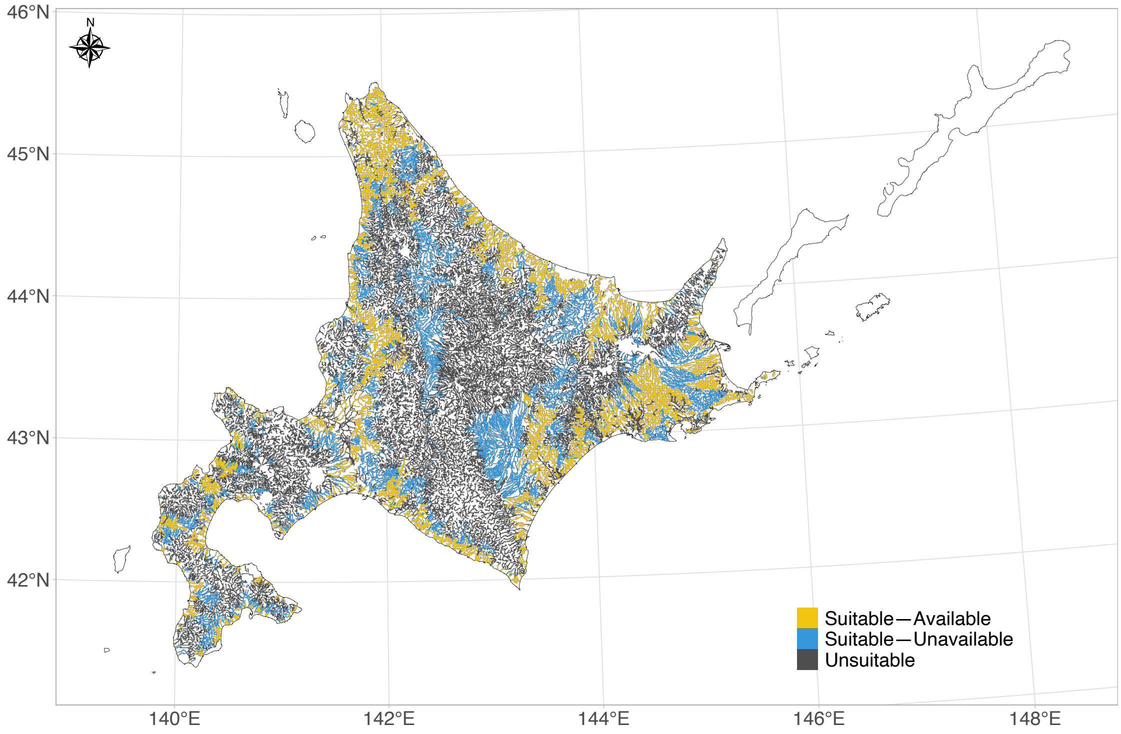

Figure 2-3 Map of estimated habitat fragmentation status on the spawning habitat for anadromous salmonids for the entire Hokkaido mainland, northern Japan.

2-4. Discussion

Predicting substrate particle size helps determine the area of suitable spawning habitats of salmonids, which ultimately aids in selecting the rivers best suited to the implementation of restoration projects for spawning habitat of anadromous salmonids. The particle size prediction model developed in this study demonstrated high prediction accuracy, and the predictions derived from this model revealed the presence of numerous suitable spawning habitats for anadromous salmonids in Hokkaido, northern Japan. These results suggest that the particle size prediction model based on the machine-learning algorithm helps estimate the suitable spawning habitat and evaluating the impact of fragmentation on such habitats. The analysis revealed that approximately half of these habitats have been lost due to fragmentation resulting from the construction of dams.

The finding that *segElev* was an important predictor variable was similar to that of a previous study (Haddadchi et al. 2018). Particle size distributions are determined by complex sediment production or transport processes, and elevation does not directly explain them. Furthermore, *segElev* was not significantly correlated with any variables other than *Elev*. Thus, elevation may mask other factors explaining sediment production and transport that were not included as predictor variables in this study. Although additional predictors that could potentially explain sediment production or transport processes should be included to comprehensively interpret the mechanisms that determine particle size distribution, the range of available predictors is limited, requiring further data collection. The second most important predictor was *segSlope*. In general, steep rivers are those with high flow velocities, and the flow velocities affect riverbed particle size. Therefore, *segSlope* was probably selected as the second most important predictor.

Since the Tokachi River and Ishikari River basins were the most fragmented watersheds, these basins should be considered when prioritizing areas for habitat restoration. Within these basins, river alterations have been extensively executed to exploit the downstream regions for agricultural and residential purposes. In Kamishihoro Town, located in the upper reaches of the Tokachi River, abundant salmon runs were previously found (Kamishihoro Town History Compilation Committee 1992). Today, however, most of the rivers in Kamishihoro Town are fragmented, and only a few masu salmon with higher swimming ability have been observed (T. Yamada, personal observations). Past runs may have imparted numerous benefits to the organisms and ecosystems in the region by transporting marine-derived nutrients (Gende et al. 2002, Schindler et al. 2003). Improving connectivity can revive anadromous salmonid functions that have been lost over a vast region.

While the present study focused on habitat fragmentation caused by dams, weirs to collect broodstock for hatchery programs are installed only during the salmon run season in enhanced rivers in Japan (Kitada 2014). In 2009, hatchery brood stocks were caught in 84 rivers in Hokkaido, northern Japan (Miyakoshi et al. 2012). Natural reproduction of anadromous salmonids in these rivers is largely hindered. In addition to interference with natural spawning, hatchery programs decrease reproductive success and increase competition between fish of wild and hatchery origin (Araki et al. 2007, Christie et al. 2012, Willoughby and Christie 2019, O’Sullivan et al. 2020, Ohlberger et al. 2022, Terui et al. 2023). To sustainably receive ecosystem services from salmon, it may be a good practice to stop or reduce hatchery releases in rivers with abundant spawning habitats by resolving fragmentation.

Dams exist across the world (Grill et al. 2019, Belletti et al. 2020), and Japan has the highest number of dams after the United States and China, according to a database that includes dams from around the world (Lehner et al. 2011). Furthermore, innumerable small dams exist. There are several ways to resolve fragmentation: installation of fishways and partial and complete removal of dams (Garcia de Leaniz 2008, Kiffney et al. 2009, Nakamura and Komiyama 2010, Fjeldstad et al. 2012, Birnie-Gauvin et al. 2018, Ishiyama et al. 2018). However, these are costly to implement and must be simulated to ensure that removing the dam will not cause safety problems in a disaster. Thus, these measures cannot be implemented indiscriminately. The present study can guide decisions regarding where best to focus and invest in restoration efforts for anadromous salmonids.

The present study focused only on the distribution of available suitable spawning habitat based on the substrate particle size; however, several environmental conditions, such as depth, water velocity, and spring water can affect spawning site selection of anadromous salmonids (Geist et al. 2002, Louhi et al. 2008, Aruga et al. 2023). I do not consider these factors to have a significant influence on my results because they are microscale factors. Indeed, a recent study revealed that even in an urban river where spawning habitat is severely limited, salmon selectively use spring water for their purposes within a river (Aruga et al. 2023). However, additional studies are needed to support the assumptions of this study. In addition to spawning site selection, several factors, including water discharge and temperature, can significantly affect the freshwater productivity of anadromous salmonids (Jensen and Johnsen 1999, Anderson and Topping 2018, Honkanen et al. 2019, Warkentin et al. 2022). Further studies considering the effect of these factors on freshwater productivity are required to select rivers with high contributions to population sustainability.

3. Diel migration pattern of pink salmon fry in small streams

3-1. Introduction

Many animals exhibit “migration” as a behaviour to acquire more favourable feeding grounds, habitats, and spawning sites (Dingle and Drake 2007, Dingle 2014). Anadromous salmonids migrate according to the stages of their life cycles (Quinn 2018): “downstream migration” to rapidly grow using marine environments with better growing conditions than those of most freshwater habitats and “homing migration” to return to natal rivers to spawn. Downstream migration is a critical stage of the anadromous salmonid life cycle because the high mortality of salmon during downstream migration affects adult populations and overall population persistence (Williams et al. 2001, Thorstad et al. 2012).

Several salmonids perform downstream migration at night (Johnston 1997, Hintz and Lonzarich 2012, Pavlov and Mikheev 2017). In general, except for some large rivers, high turbidity conditions, and polar-day conditions, the fry of the pink salmon perform downstream migration at night (Ali and Hoar 1959) and finish their migration overnight (Heard 1991); however, since the previous studies about diel migration of pink salmon have been conducted in rivers of various sizes (Neave 1955, Pavlov et al. 2015, Kirillov et al. 2018), these studies have shown different results between rivers or surveys. Thus, a comprehensive understanding of the diel migration pattern of pink salmon fry has not been achieved. Here, I examined the diel migration pattern of pink salmon fry in three small streams on the Shiretoko Peninsula, Japan. Since small streams have less variation in environmental factors along their course, they are the most suitable model system for examining the diel migration pattern of pink salmon fry. Many surveys have been conducted to evaluate the migration of salmon fry from an ecological and fisheries perspective. Elucidating the diel migration pattern can contribute to optimize the field survey effort to evaluation the migration of pink salmon fry.

3-2. Methods

I selected three small streams on the Shiretoko Peninsula as the study streams (44.07°N, 145.12°E; Table 3-1): Chienbetsu stream, Funbe stream, and Shoji stream. Hatchery programs have never been implemented in these streams, and natural spawning sustains the pink salmon populations (T. Yamada, unpublished data). In each stream, I established a sampling point for salmon fry that was located near the mouth of the stream and was not affected by sea waves.

In May 2021, to determine the diel migration pattern of pink salmon, I conducted fish collection over a 24-h period in each stream (Table 3-1). In Japan, the peak of downstream migration of pink salmon fry occurs in May. I placed two drift nets (Matsui Corp., Tokyo, Japan; 50 cm squared opening, 100 cm long, 3 mm mesh) at a sampling point for 15 minutes at hourly intervals. Since long-term sampling with drift nets would result in the death of many fry, I limited the sampling effort. I used stakes to fix the nets to the streambed so that the net openings ranged from the stream surface to the streambed. Drift nets have often been used to capture the fry of salmonids (Johnston 1997, Hintz and Lonzarich 2012). I recorded the number of individuals without using anaesthesia and then immediately released all individuals. All surveys started at 10:00 and finished at 09:15 the following day. To evaluate stream discharge at each sampling point, I constructed a transect and measured the wetted width. Then, I measured the depth and current velocity at 0.2 × depth and 0.8 × depth at ten points along the transect. I calculated the sectional areas between the measurement points or between the measurement point and the streambank, multiplied each sectional area by the average velocity, and summed them to calculate stream discharge. To evaluate the water filtered by drift nets, I measured the wetted sectional area of the net and current velocity at 0.2 × depth and 0.8 × depth at three points (left, right, and centre) on each net. I multiplied the wetted sectional area of each net by the average velocity and summed them to calculate filtered water by drift nets. All measurements were taken between 15:00 and 17:00. Finally, I used the ratio of the water filtered by drift nets to stream discharge to estimate the total migrants in each stream at each time point.

Then, I analysed the data using a generalized additive mixed model (GAMM) with a binomial distribution and logit link function. I used the migration activity of pink salmon fry as a response variable and the cumulative time from survey start time as a smooth term and stream ID as a random effect. Migration activity represents the proportion of the estimated number of migrants at each time to the estimated total number of migrants obtained through each 24-hour survey. All data analysis was conducted with R v. 4.2.0 (R Core Team 2022) using “mgcv” v. 1.8.38 (Wood 2004)for GAMM.

From April to June 2021, I conducted a “peak survey” to confirm whether the downstream migration pattern obtained from the 24-hour survey described above is universal. This peak survey was conducted six, six, and three times in the Chienbetsu stream, Funbe stream, and Shoji stream, respectively. The survey was conducted between 18:00 and 22:15 based on a previous study conducted in a stream with a runnable reach length close to those in my study streams (Neave 1955). I used the same method to catch pink salmon fry as that used in the 24-hour survey. Additionally, I estimated the total number of migrants using the same method as that used in the 24-hour survey. I conducted all surveys, including 24-hour surveys, when the water in the streams was transparent and flooding conditions were not observed. In addition to pink salmon, the fry of chum salmon and juveniles of southern Asian Dolly Varden *Salvelinu curilus* were also collected in these surveys.

Table 3-1 Physical characteristics and environmental conditions on the dates of the 24-hour survey of the three studied streams. RunnableL represents the reach length from the sampling point to the unpassable dam or fall; DistFromSG represents the distance between the upstream edge of the main spawning grounds and the sampling points.

Metric	**Chienbetsu stream**	**Funbe stream**	**Shoji stream**
RunnableL (m)	409.1	348.2	211.3
DistFromSG (m)	326.5	348.2	169.2
Start date	2021-05-15	2021-05-05	2021-05-21
Sunset time	18:38:17	18:27:43	18:44:42
Sunrise time	3:51:50	4:04:24	3:46:06
Sunshine duration (min / 24 h)	334	411	0
Weather condition at night	Cloudy	Cloudy then clear	Cloudy
Precipitation (mm / 24 h)	0.0	0.0	0.0
Lunar age	3.3	23.0	9.3
Average water tempereture (C°)	8.1	6.3	7.8
Stream discharge (m^3)	65.1	91.6	166.8
Filtered water by drift nets (m^3)	20.5	21.2	19.7

3-3. Results

The 24-hour survey showed that pink salmon fry mainly migrated downstream within a few hours after sunset (Figure 3-1a). The model indicated that time was significant ($P < 0.0001$, adjusted R2 = 0.564), with 89.9% of the migrations occurring between 18:00 and 23:00 (Figure 3-1a). Additionally, all peak surveys indicated that the peak for downstream migration of pink salmon fry was between 19:00 and 22:00 (Figure 3-1b).

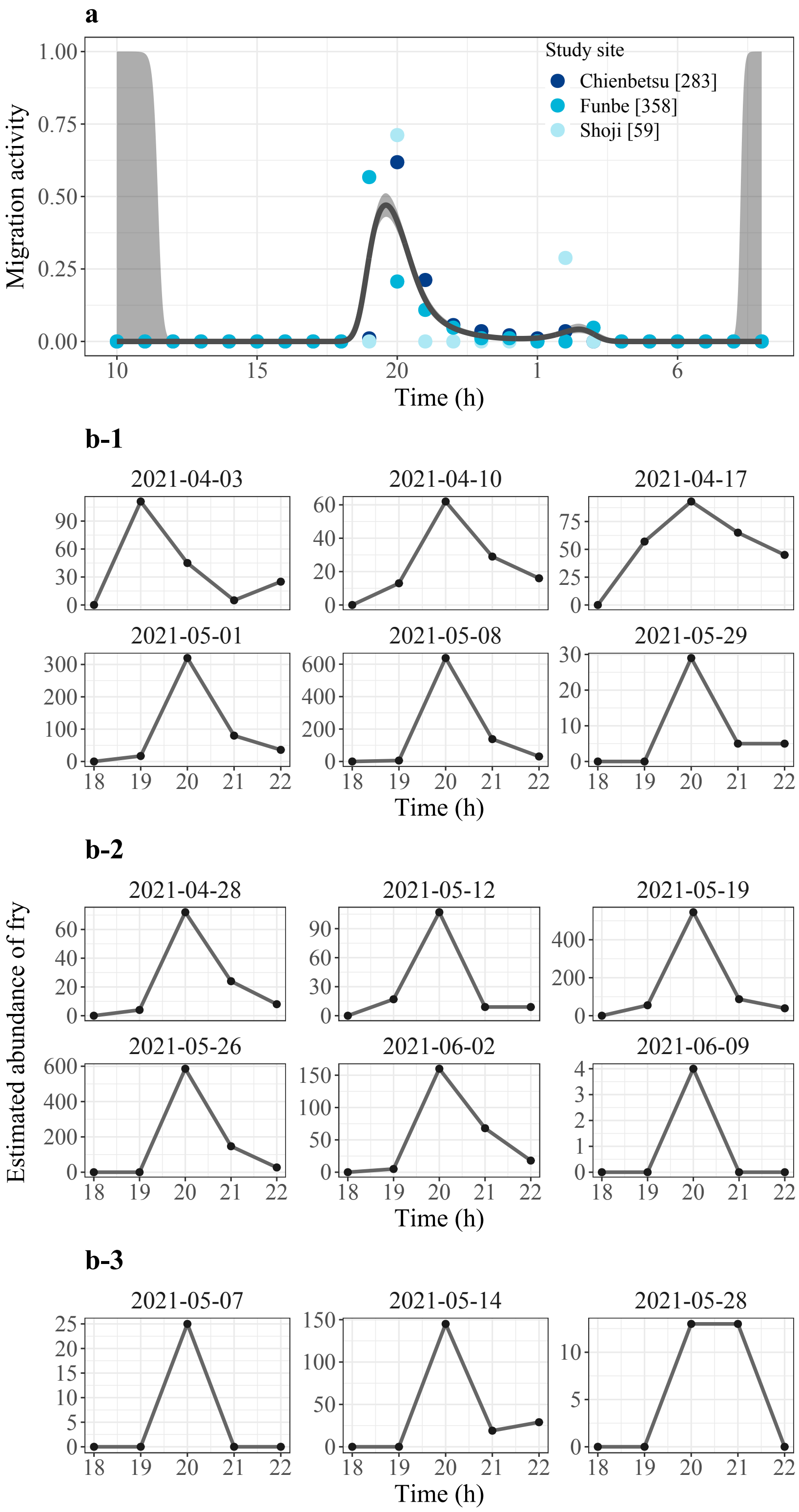

Figure 3-1 (a) Estimate of migration activity in relation to time in three streams. Confidence interval (95%) is shown as the shaded area. The numbers in the brackets

indicate the estimated total number of pink salmon fry. (b) Results of the peak survey in the Chienbetsu stream (1), Funbe stream (2), and Shoji stream (3).

3-4. Discussion

My results indicated that sunset time influences the diel migration pattern of pink salmon fry in small streams. Pink salmon fry emerged from the riverbed and moved actively to the current for downstream migration in the first two (maximum three) hours after nightfall (Pavlov et al. 2019). Therefore, my study shows that individuals emerging in small streams quickly migrated to the sea. Other salmonids show nocturnal downstream migration: the brown trout, coho salmon *O. kisutch*, Atlantic salmon, and rainbow trout *O. mykiss* (Johnston 1997, Hintz and Lonzarich 2012, Pavlov and Mikheev 2017). Nocturnal migration may be a strategy to avoid predation (Johnston 1997, Ibbotson et al. 2011, Kennedy et al. 2018). Selection may have favoured the nocturnal migration strategy in pink salmon fry, as observed in other salmonids.

There are several reasons why the peak of downstream migration for pink salmon fry occurs within a few hours after sunset. First, early night may be the best time to avoid predation. The Dolly Varden, which occasionally preys on fish (Denton et al. 2009), is dominant in the studied streams (T. Yamada, unpublished data). The foraging activity of the Arctic charr *S. alpinus*, which is closely related to Dolly Varden, declines just after sunset (Björnsson 2001). If Dolly Varden have the same feeding pattern as that of Arctic charr, then the best time for pink salmon fry to avoid predation is just after sunset. An alternative explanation for the timing of peak migration is the strategy of completing downstream migration during the night in rivers with various channel lengths. If pink salmon spawned far from the mouth of the river, then fry would need a longer time to reach the mouth of the river. Therefore, by starting downstream migration immediately after sunset, pink salmon fry can reach the river mouth at night in small streams when predation pressure is low. Pavlov et al. (2019) suggested that pink salmon in a longer river would repeat this behaviour for several nights. Pink salmon, with their higher straying rate among Pacific salmon (Hendry et al. 2004), may have adapted to complete their downstream migration at night even if they were born in rivers different from their natal rivers.

This study revealed the diel migration pattern of pink salmon fry; however, previous studies have shown different results between the studied rivers or between surveyed dates (Neave 1955, Pavlov et al. 2015, Kirillov et al. 2018). Genetic drift between neighbouring river populations of pink salmon often occurs (Hendry et al. 2004) due to their higher straying rate. Therefore, genetic differences between neighbouring river populations in the same year class are small (Aspinwall 1974, Gharrett et al. 1988, Shaklee et al. 1991, Hendry et al. 2004); thus, the differences in diel patterns between neighbouring rivers should be determined by factors other than genetic factors. By selecting rivers as study sites with different lengths of spawnable reaches between the studied rivers (range 1.6–16.1 km) or longer spawnable reach lengths (maximum distance 21 km), these studies may not have identified the diel migration patterns of pink salmon fry. In the case of differing spawnable reach lengths between rivers, even if pink salmon fry start their downstream migration at the same time, the time for the fry to reach the mouth of the river would vary among rivers. Additionally, when rivers have longer spawnable reach lengths, the location of the spawning redds makes a difference in terms of the time it takes to reach the mouth of the river. In this study, by selecting streams that have the same spawnable reach lengths between streams and short spawnable reach lengths, I was able to elucidate the diel migration pattern.

The migration of salmon fry has been often evaluated with several reasons: emergence timing, survival, and freshwater productivity evaluation (Hintz and Lonzarich

2012, Morita et al. 2015, Manhard et al. 2017). Since long-time sampling with drift nets and other traps would result in the death of many fry, the sampling effort should be optimized and reduced. My results showed that 89.9% of migration occurred between 18:00 and 23:00. The sampling effort for pink salmon fry can be reduced in small streams by concentrating on this time window based on my results, thus possibly helping to avoid unnecessary mortality as well as representing approximate fry abundance.

This study indicated that pink salmon fry exhibit a diel downstream migration pattern that depends on the time of sunset in the small streams. The diel pattern of organisms is affected by light pollution (Longcore and Rich 2004). Pink salmon fry avoid light (Hoar et al. 1957); therefore, the diel pattern of pink salmon fry may change dramatically with light pollution, and the survival rate of salmon fry may decline as optimal downstream strategies cannot be selected. Future studies should examine the effect of light pollution on the diel pattern and survival of pink salmon fry.

4. Watershed hydrogeomorphology drives freshwater productivity of anadromous salmonids

4-1. Introduction

Biodiversity is threatened by anthropogenic activities across our planet (Barnosky et al. 2011, Cardinale et al. 2012, Johnson et al. 2017, Reid et al. 2019, Dudgeon 2019). Although habitat conservation and restoration are needed to maintain and improve biodiversity, given the spatial omnipresence of the threat and limited resources and time, it is crucial to identify targets and prioritize these activities based on critical criteria (Brooks et al. 2006). While several reproductive statuses, such as productivity and recruitment, are often included in the index for prioritization (Waples and Hendry 2008, Cruz et al. 2015), related studies are scarce. A recent study attempted to predict habitat quality using geospatial information to prioritize conservation areas in a district (Atlas et al. 2020). If geospatial information could explain the reproductive status of target species, the estimation could be extrapolated over a broader region, and moreover, this could help prioritize conservation areas and create restoration plans.

Anadromous salmonids contribute significantly to biodiversity maintenance in freshwater and surrounding ecosystems and are an important natural resource for human beings; however, declines in anadromous salmonid abundance have been observed in various regions worldwide (Ruckelshaus et al. 2002, Mills et al. 2013, Ward et al. 2015, Nicola et al. 2018). Given that declines in anadromous salmonid abundance may be influenced by anthropogenic activities, conservation of wild populations and restoration of their habitats for reproduction are needed. The lifetime productivity of anadromous salmonids is influenced mainly by population regulation during the freshwater life stage

(Bradford 1995, Morita et al. 2015). Therefore, freshwater productivity is a key parameter that should be examined and predicted when evaluating population persistence. The freshwater productivity of salmonids is driven by several factors, such as water discharge, temperature, and competition for suitable spawning habitat (Fukushima et al. 1998, Jensen and Johnsen 1999, Essington et al. 2000, Manhard et al. 2017, Anderson and Topping 2018, Honkanen et al. 2019, Warkentin et al. 2022). In particular, flood disturbance causes high mortality in the egg to alvine stage by scouring redds (Seegrist and Gard 1972, Holtby and Healey 1986, Thorne and Ames 1987, Montgomery et al. 1996, Carline and McCullough 2003, Greene et al. 2005, Waples et al. 2008, 2009, Milner et al. 2013). Since flood disturbance is controlled by water and sediment discharge, which are determined by watershed hydrogeomorphology (e.g., Moore et al. 1991, Aalto et al. 2006, Koskelo et al. 2018), hydrogeomorphic characteristics at the watershed scale may reflect the intensity of flood disturbance in a watershed and therefore may regulate the freshwater productivity of salmonids. However, few studies have examined the relationship between watershed hydrogeomorphic characteristics and salmonid freshwater productivity. If I can elucidate this relationship, I may be able to predict watershed productivity over a broader region without detailed information obtained from field surveys, thereby contributing to the effective conservation and restoration of anadromous salmonids.

In this study, I examined the relationship between the number of total escapes and emergent fry of the pink salmon and environmental factors at a watershed scale that potentially affect the freshwater productivity in the Shiretoko Peninsula of Hokkaido, northern Japan, based on the hypothesis that watershed hydrogeomorphic characteristics drive the freshwater productivity of anadromous salmonids. Specifically, I predicted that watershed slope and stream power would negatively affect the freshwater productivity of pink salmon. Pink salmon are the most abundant and widely distributed salmonid species in the Northern Pacific region (Heard 1991, Quinn 2018) and function ecologically as a spatial subsidy transporting marine-derived nutrients (Koshino et al. 2013, Yamada et al. 2022a). My research findings can contribute to selecting streams and rivers where conservation and restoration efforts for pink salmon should be prioritized.

4-2. Methods

Study site

I selected ten streams on the Shiretoko Peninsula as the study streams (Figure 4-1; Table 4-1). These streams have never been targeted for hatchery programs for pink salmon. However, in only one stream (Mosekarubetsu Stream), fry of chum salmon were released. The central part of the Shiretoko Peninsula has been designated as a World Natural Heritage site since 2005 because of the close linkages between the marine and terrestrial ecosystems via pink salmon and chum salmon (IUCN 2005). The whole or upper reaches of the study streams are included in the Shiretoko World Natural Heritage site (excluding Kanayama Stream). Study sections were set in each stream from the mouth of the stream to the migration barriers (i.e., check dam or waterfall) (study section length mean ± SD and range: 210.99 ± 115.36 [range 62.6–409.1] m).

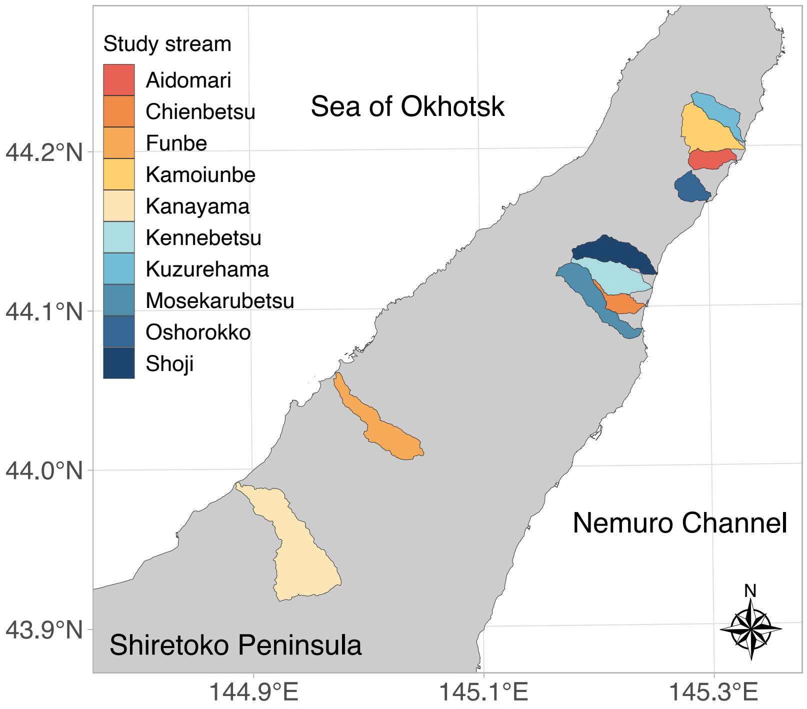

Figure 4-1 Map of the study area. Colour-coded areas indicate each watershed.

Estimation of total escapement

To estimate total spawners, I counted the number of pink salmon in the study sections every 7–11 days from mid-August until early November in 2020 and 2021 (Figure A4-1), the spawning period of pink salmon. I walked upstream and counted all live pink salmon. The survey was conducted only when water visibility was good enough to see to the bottom. I determined the total number of spawners per stream using the area under the curve (AUC) estimation method (English et al. 1992, Bue et al. 1998). This method requires "stream life" and "observer efficiency". The former was defined as 7.85 days based on previous research conducted in the same region as this study (Yokoyama et al. 2010). To evaluate observer efficiency, I established a 10–20 m additional survey section where all fish could be observed from the riverbank or bridge and recorded the number of individuals (true fish number). Thereafter, I counted the fish while walking through the section (observed fish number). I defined the observed fish number/true fish number as observer efficiency. This survey was conducted 1–7 times in 6 streams (Aidomari Stream, Osyorokko Stream, Shoji Stream, Kennnebetsu Stream, Funbe Stream, and Kanayama Stream) when there were 10 or more pink salmon in the section. I calculated the average observer efficiency for each stream, and then the overall average was calculated. The calculated observer efficiency was 0.92 ± 0.07 (range 0.79–1.00).

Estimation of the total number of fry migrants

In each stream, I established a sampling point for collecting salmon fry, which migrate to the ocean near the mouth of the stream. From April to June in 2021 and 2022, I collected pink salmon fry in each stream every week except for one survey, which was conducted at a four-day interval (Figure A4-2). I placed one or two drift nets (Matsui Corp., Tokyo, Japan; 50 cm squared opening, 100 cm long, 3 mm mesh), which are often used to capture salmon fry (Johnston 1997, Hintz and Lonzarich 2012, Yamada et al. 2022b), at a sampling point for 15 minutes at hourly intervals (Yamada et al. 2022b). Since long-term sampling with drift nets would result in higher fry mortality, I set the sampling duration to be as short as possible. I used stakes to fix the nets to the streambed so that the net openings spanned from the stream surface to the streambed. All surveys started between 18:00 and 18:30 and finished between 22:15 and 22:45 because downstream migration of pink salmon fry is almost always observed at night (Neave 1955, Kirillov et al. 2018), and its peak was found at approximately 20:00 in this study area (Yamada et al. 2022b). However, if pink salmon fry were not collected throughout the first to fourth trials, the survey was finished between 21:15 and 21:45. I recorded the number of individuals and then immediately released all individuals. Stream discharge at each sampling point was estimated as follows: based on the depth and current velocity at 0.2 × depth and 0.8 × depth at ten measurement points along the cross-sectional transect and the wetted width, the water volume passing through the sectional area was calculated by multiplying each sectional area by the average velocity and summing them. To evaluate the water filtered by drift nets, I measured the wetted sectional area of the net and current velocity at 0.2 × depth and 0.8 × depth at three points (left, right, and centre) on each net. I multiplied the wetted sectional area of each net by the average velocity and summed them to calculate the water filtered by the drift nets. The total number of migrants (T) was estimated for each stream each day, D, as follows:

Eq. 4-1. $\boldsymbol{T_D = (C_D \times (S_D/F_D) \times 4)/0.899}$

where C_D, F_D, and S_D are captured fry, water filtered by drift nets, and stream discharge on day D, respectively. In the equation, "4" is the value used to convert the number of migrants per 15 minutes to that per hour, and "0.899" is the proportion of fry that migrated during the survey time relative to the whole sampling day, as indicated by Yamada et al. (2022b). I also determined the total number of pink salmon fry during the sampling period per stream using the AUC estimation method (English et al. 1992, Bue et al. 1998). I assumed that "stream life" and "observer efficiency (i.e., collection efficiency)" were 1 day and 100%, respectively.

Environmental variables

For statistical analyses, I derived eight environmental characteristics: average watershed slope, stream power index, maximum daily precipitation averaged over the watershed, predator density, average autumn temperature, average winter temperature, average spring temperature, and area available for spawning per individual (Table 4-1). The description and derivation of these characteristics are provided below.

The average watershed slope and stream power index (average stream slope [%] times watershed area [km^2]) affect stormflow water yields, sediment yield and transport, and channel stability (Moore and Burch 1986, Moore et al. 1991, e.g., Aalto et al. 2006, Koskelo et al. 2018). These characteristics were calculated based on a 10 m digital elevation model provided by the Geospatial Information Authority of Japan (https://fgd.gsi.go.jp/download/menu.php). I also used existing streamline data from the National Land Numerical Information download service provided by the Ministry of Land, Infrastructure and Transport of Japan (https://nlftp.mlit.go.jp/ksj/index.html). In addition, maximum daily precipitation averaged over the watershed (hereafter maximum daily precipitation) was used as an indicator of flood disturbance intensity during the incubation period. For the estimation, I calculated the daily precipitation averaged over the watershed based on precipitation data with a 1-km grid resolution and then extracted the maximum precipitation from September to November. The precipitation data were obtained from the Agro-Meteorological Grid Square Data, NARO (https://amu.rd.naro.go.jp), which is often used in the ecological studies (e.g., Kobayashi et al. 2023, Mori et al. 2023). These geospatial analyses were performed using ArcGIS Pro (Esri, version 2.4.0).

The presence of predators may negatively affect salmonid survival (Hawkins et al. 2020). In this study, I considered only instream organisms (i.e., piscivorous fish) as predators because pink salmon fry migrate only at night, and nocturnal terrestrial predators were not observed during the survey. To estimate predator density, I established an additional study section extending approximately 10 times the wetted width in length within each study section and caught the stream fish by 2-pass electrofishing using a backpack electrofishing unit (LR-20B Electrofisher; Smith-Root, Inc., Vancouver, WA, USA). This survey was conducted after the downstream migration of fry had finished (i.e., summer). I anaesthetized the captured fish with eugenol (FA100; DS Pharma Animal Health Co., Ltd., Osaka, Japan), recorded the number of fish captured for each species, and measured the fork length of each fish to the nearest 1 mm. After that, all fish were released near the capture sites. In each stream, the southern Asian Dolly Varden, which occasionally preys on fish (Denton et al. 2009), was dominant. Thus, I regarded large southern Asian Dolly Varden individuals (≥ 100 mm) as potential predators and estimated their abundance in each stream using the Carle–Strub method (Carle and Strub 1978), which is widely used to estimate population abundances from two-pass electrofishing data (Bergerot et al. 2019, Kanno et al. 2020). Predator density was calculated by dividing the estimated population abundance by the study section area. The population estimates were obtained with R v. 4.2.0 (R Core Team 2022) using "FSA" v. 0.9.3 (Ogle et al. 2022).

Stream temperature, which influences the freshwater productivity (Honkanen et al. 2019), was measured at the midpoint of each section at hourly intervals using data loggers (HOBO 64K Pendant Temperature/Alarm Data Logger; Onset Computer Corp., Bourne, MA, USA). However, water temperature data for a certain period of time in several streams (Kamoiunbe, Kanayama, Mosekarubetsu, Oshorokko, and Shoji streams) were missing due to machine failure or loss by flood. Therefore, these missing values were estimated by generalized additive models with a gamma distribution and log link function (Figure A4-3; Table A4-1). I constructed five models (i.e., a model was constructed for each river) with stream temperature as a response variable and air temperature as a smoothing term. Finally, I calculated the average autumn temperature (September - October), average winter temperature (December - February), and average spring temperature (April - May). The temperature estimates were performed in R v. 4.2.0 (R Core Team 2022) using "mgcv" v. 1.8.40 (Wood 2004).

In addition, the area available for spawning per individual was evaluated because redd superimposition leads to a decline in the freshwater productivity (Fukushima et al. 1998, Essington et al. 2000). Since salmonids can spawn in gravels with a median diameter up to approximately 10% of their body length (Kondolf and Wolman 1993) and the length of returning pink salmon is generally 40–60 cm (LeBrasseur and Parker 1964), I considered gravel (2–32 mm) and pebbles (32–64 mm) as suitable spawning grounds for pink salmon within the grain size categories usually used: bedrock, sand (<2 mm), gravel (2–32 mm), pebble (32–64 mm), cobble (64–128 mm), or boulder (>128 mm) (e.g., Ishiyama et al. 2020). I identified substrate categories by visual observation and measured the area of the streambed dominated by gravel or pebbles in the fall or winter. Finally, the area available for spawning per individual was calculated by dividing the total measured area by the total spawner abundance.

Table 4-1 Abiotic and biotic characteristics of the study streams.

Variable	**Mean ± SD**	**Range**
Watershed area (km^2)	7.29 ± 5.20	3.08–24.14
Stream slope (%)	29.81 ± 5.65	22.35–38.35
Watershed slope (%)	42.73 ± 6.44	30.82–51.03
Stream power index	216.06 ± 144.05	78.80–650.54
Maximum daily precipitation (mm/day)	84.83 ± 32.97	53.82–179.61
Predator density ($/m^2$)	0.35 ± 0.24	0.02–0.77
Autumn temperature (°C)	10.30 ± 0.85	9.18–11.92
Winter temperature (°C)	1.95 ± 0.87	0.54–3.69
Spring temperature (°C)	5.80 ± 0.34	5.33–6.47
Available area (m^2)	0.24 ± 0.43	0.01–1.74

Data analysis

Before the analysis, I evaluated the correlation among explanatory variables and found that average winter temperature had a strong negative correlation ($|r| > 0.7$, Dormann et al. 2013) with average watershed slope. Since the present study focused on the effect of hydrogeomorphic characteristics, average winter temperature was excluded from the analysis. The effects of watershed hydrogeomorphology and some explanatory variables on the freshwater productivity of pink salmon were evaluated by fitting generalized linear mixed models (GLMMs). The GLMMs were fitted with a negative binomial error distribution and a log-link function to address any overdispersion in the data (Zuur et al. 2009). Total fry abundance was the response variable, the study stream ID and brood year ID were treated as random intercepts, and log-transformed total spawner abundance was included as an offset term. I built six GLMMs with the following explanatory variables: average watershed slope, stream power index, average autumn temperature, average spring temperature, area available for spawning per individual, and predator density. Only two models (average watershed slope and stream power index) had a covariate (maximum daily precipitation) because disturbance intensity probably relates to precipitation intensity. All explanatory variables and the covariate were standardized (mean = 0, SD = 1) before the analysis. Variance inflation factors (VIFs) were calculated before the analysis for models with covariates to avoid multicollinearity; all variables had values less than 2.5, the threshold indicative of troubling collinearity for regressions (Johnston et al. 2018). For each GLMM, the significance of the explanatory variables was evaluated using type II Wald chi-square tests ($P < 0.05$). I used leave-one-out cross validation to evaluate the prediction accuracy of the models with significant explanatory variables based on the root-mean squared error (RMSE) and mean absolute error (MAE).

These analyses were conducted with R v. 4.2.0 (R Core Team 2022) using “glmmTMB” v. 1.1.3 (Brooks et al. 2017) for GLMM fitting and “MuMIn” v. 1.47.1 (Bartoń 2022) for marginal and conditional R^2 calculations.

4-3. Results

The average ± SD (range) was 1504.25 ± 1918.32 (43–7933) for the estimated total escapement number, 12316.12 ± 23181.35 (200–72374) for the estimated total number of fry, and 18.65 ± 27.68 (0.20–84.09) for freshwater productivity. Average watershed slope, stream power index, and maximum daily precipitation had significant negative effects on freshwater productivity (Table 4-2; Figure 4-2). However, maximum daily precipitation in the stream power index model was nonsignificant (Table 4-3). The other variables had no significant effects (Table 4-2; Table 4-3). The RMSE and MAE of the productivity estimates were 27.26 and 19.58 for the average watershed slope model and 149.62 and 55.16 for the stream power index model, respectively.

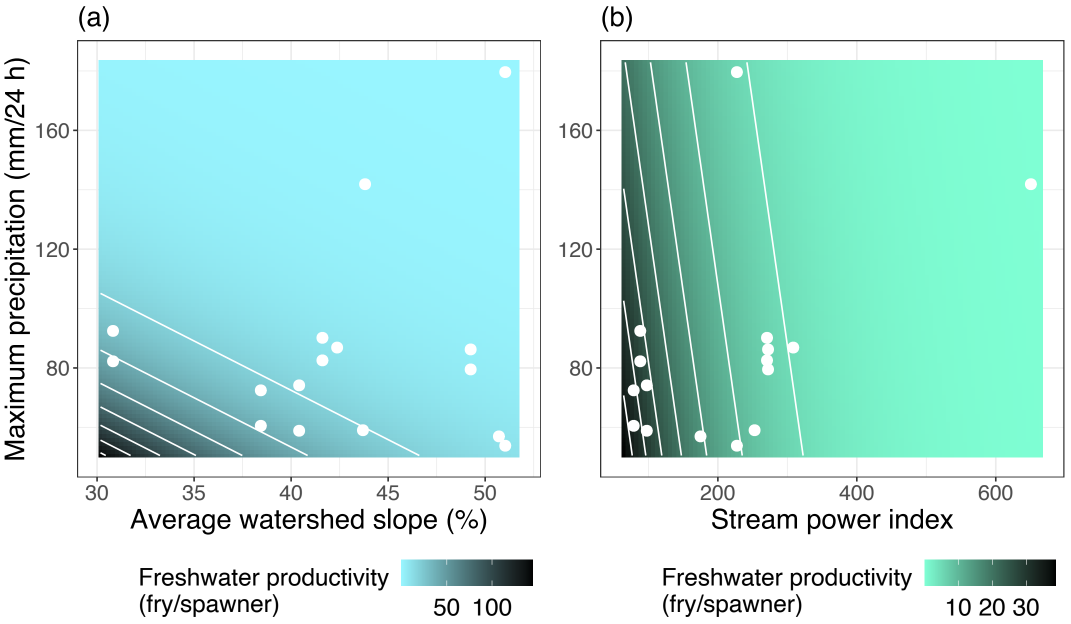

Figure 4-2 Contour plots of the effects of (a) average watershed slope and (b) the stream power index on freshwater productivity by different levels of maximum daily precipitation (covariate). Coloured bars indicate the range of values for estimated freshwater productivity.

Table 4-2 Parameters of GLMMs, a test of the effect of six explanatory variables and a covariate (maximum daily precipitation) on freshwater productivity. AIC, Akaike information criterion; R2m, Marginal R2; R2c, Conditional R2.

Model	**Estimate**	**se**	***p***	**AIC**	**R2m**	**R2c**
Intercept	2.22	0.60	0.0002	325.7	0.478	0.597
Watershed slope	-0.78	0.24	0.0011			
Maximum daily precipitation	-1.20	0.36	0.0009			
Intercept	2.29	0.52	0.0000	327.3	0.357	0.447
Stream power index	-1.14	0.39	0.0035			
Maximum daily precipitation	-0.16	0.78	0.8388			
Intercept	2.65	0.51	0.0000	332.5	0.068	0.126
Predator density	0.57	0.34	0.0923			
Intercept	2.77	0.51	0.0000	334.3	0.026	0.076
Autumn temperature	-0.37	0.39	0.3519			
Intercept	2.69	0.65	0.0000	333.5	0.032	0.154
Spring temperature	0.40	0.31	0.1990			
Intercept	2.77	0.54	0.0000	333.8	0.215	0.216
Available area	1.18	0.86	0.1698			

Table 4-3 Results of the type II Wald chi-square tests for each model.

Variable	**$\chi 2$**	***p***
Watershed slope	10.58	0.0011
Maximum daily precipitation	11.06	0.0009
Stream power index	8.55	0.0035
Maximum daily precipitation	0.04	0.8388
Predator density	2.83	0.0923
Autumn temperature	0.87	0.3519
Spring temperature	1.65	0.1990
Available area	1.88	0.1698

4-4. Discussion

In the present study, I found that the freshwater productivity of pink salmon can be explained by watershed hydrogeomorphic characteristics (average watershed slope and stream power) and maximum daily precipitation and that these variables have negative effects on freshwater productivity. The results support my hypothesis that watershed hydrogeomorphology drives the productivity of pink salmon and indicate that the intensity of flood disturbance negatively affects the freshwater productivity of pink salmon. In a similar way, the freshwater productivity of other anadromous salmonids may be influenced by watershed hydrogeomorphology because all of them have the same spawning behaviour, i.e., burying eggs in gravel (Quinn 2018). In particular, salmonid species that temporarily reside in streams after emerging from the streambed, for example, chinook salmon, may be strongly affected by flood disturbance because floods have a greater impact on fish when they are residing in the stream as juveniles than when they are eggs (Neuswanger et al. 2015).

Why watershed hydrogeomorphic characteristics drive the freshwater productivity of pink salmon can be explained by the relationship between hydrogeomorphology and streambed disturbance intensity. Watershed slope and the stream power index have been used as indices of flood disturbance intensity (Nislow et al. 2002, Waite et al. 2010). Watershed slope is positively correlated with stormflow water yields and sediment yield (Aalto et al. 2006, Koskelo et al. 2018). The stream power index is also related to sediment transport and channel stability (Moore and Burch 1986, Moore et al. 1991). Therefore, streams with high watershed slopes and stream power undergo severe bed scouring during storm events, which may wash salmon eggs and/or juveniles away cause low productivity in pink salmon. However, in addition to scouring eggs from redds, floods can also suffocate developing embryos by sediment and low oxygen levels (Waples et al. 2009); however, present study could not address these effects. To comprehensively understand the effects of hydrogeomorphology on salmonid productivity, an additional study incorporating sediment deposition is needed.

Although several studies have indicated that competition for suitable spawning habitat and temperature affect the freshwater productivity of anadromous salmonids (Fukushima et al. 1998, Essington et al. 2000, Manhard et al. 2017, Honkanen et al. 2019), no significant effects of these parameters on the freshwater productivity were found in this study. While water temperature within the redds was unfortunately not measured, since the average water temperatures for each season in this study were not greatly below or above the typical critical water temperatures for survival of salmon eggs (Elliott and Elliott 2010), it is assumed that the effect was not significant. Additionally, Manhard et al. (2017) showed that the carrying capacity for spawning in pink salmon in a small stream with a size similar to those of the investigated streams in this study was 16581 spawners. The carrying capacity converted to spawner density (spawner/stream length [m]) was 51.33. In contrast, the present study estimated that only a maximum of 7933 individuals run upstream, and moreover, the maximum spawner density was 22.78. Thus, the present study may have been conducted below the carrying capacity, resulting in the density effect not being significant. In addition, these previous studies were conducted in a single watershed, and the effects of disturbance may have been similar among the study streams, lead to apparent effects of temperature and spawner density. In contrast, since the present study was conducted in multiple watersheds with differing disturbance intensities, it is possible that the effect of disturbance was more distinct than others. However, the watersheds investigated in the present study were steep and small, which may constrain the application of the results to other regions. Further studies examining the effect of hydrogeomorphology on pink salmon using a wider range of watershed sizes are critical to reinforce my discussion.

Dams have been built worldwide (Grill et al. 2019, Belletti et al. 2020), and 48% of the world's rivers have been affected by fragmentation, flow regulation, or both (Grill et al. 2015). Anadromous salmonids suffer from habitat fragmentation, causing loss of spawning grounds (Limburg and Waldman 2009, Nakamura and Komiyama 2010, Hilborn 2013, Watz et al. 2022). Thus, habitat restoration, such as dam removal and modification, is needed to effectively recover salmon populations (Nakamura and Komiyama 2010). However, given widespread fragmentation, these actions cannot be conducted haphazardly, and it is crucial to prioritize restoration activities. My findings in this study on the relationship between watershed hydrogeomorphology and freshwater productivity of anadromous salmonids can be applied to choose watersheds for restoration and can contribute to effective habitat restoration. Caution should be exercised, however, when considering dam removal for habitat restoration. Since the channel slope may change after removal (e.g., Burroughs et al. 2009, East et al. 2015), after identifying candidate watersheds based on my results, changes in slope after dam removal should be evaluated by hydraulic numerical simulation prior to restoration work.

Finally, my study may provide valuable information for effective habitat conservation of anadromous salmonids under a changing climate. Future climate change scenarios predict an increase in the frequency and intensity of precipitation extremes (Donat et al. 2016, Huang et al. 2020, Thackeray et al. 2022), resulting in frequent floods and increased flood risk (Milly et al. 2002, Arnell and Gosling 2016). These increases in disturbance frequency and intensity may impose high mortality on salmonids during the freshwater life stage, especially the incubation stage. Thus, it is important to build effective adaptation strategies to support the persistence of salmonid populations and implement appropriate conservation and restoration plans in watersheds with high productivity potential. This study showed that watersheds with a low average watershed slope and stream power index have high freshwater productivity; in other words, watersheds with high freshwater productivity associated with strong resistance to flood disturbance can be identified based on these watershed characteristics. Since anadromous salmonids have a homing instinct (Quinn 2018), conservation or restoration of highly productive watersheds ensures sustainable escapement. Considering that many organisms receive benefits from salmon runs and spawning (Willson and Halupka 1995, Gende et al. 2002, Schindler et al. 2003, Hocking and Reynolds 2011), conservation and restoration of anadromous salmonids based on my results will probably lead to the maintenance or improvement of watershed biodiversity under a changing climate.

4-5. Appendix

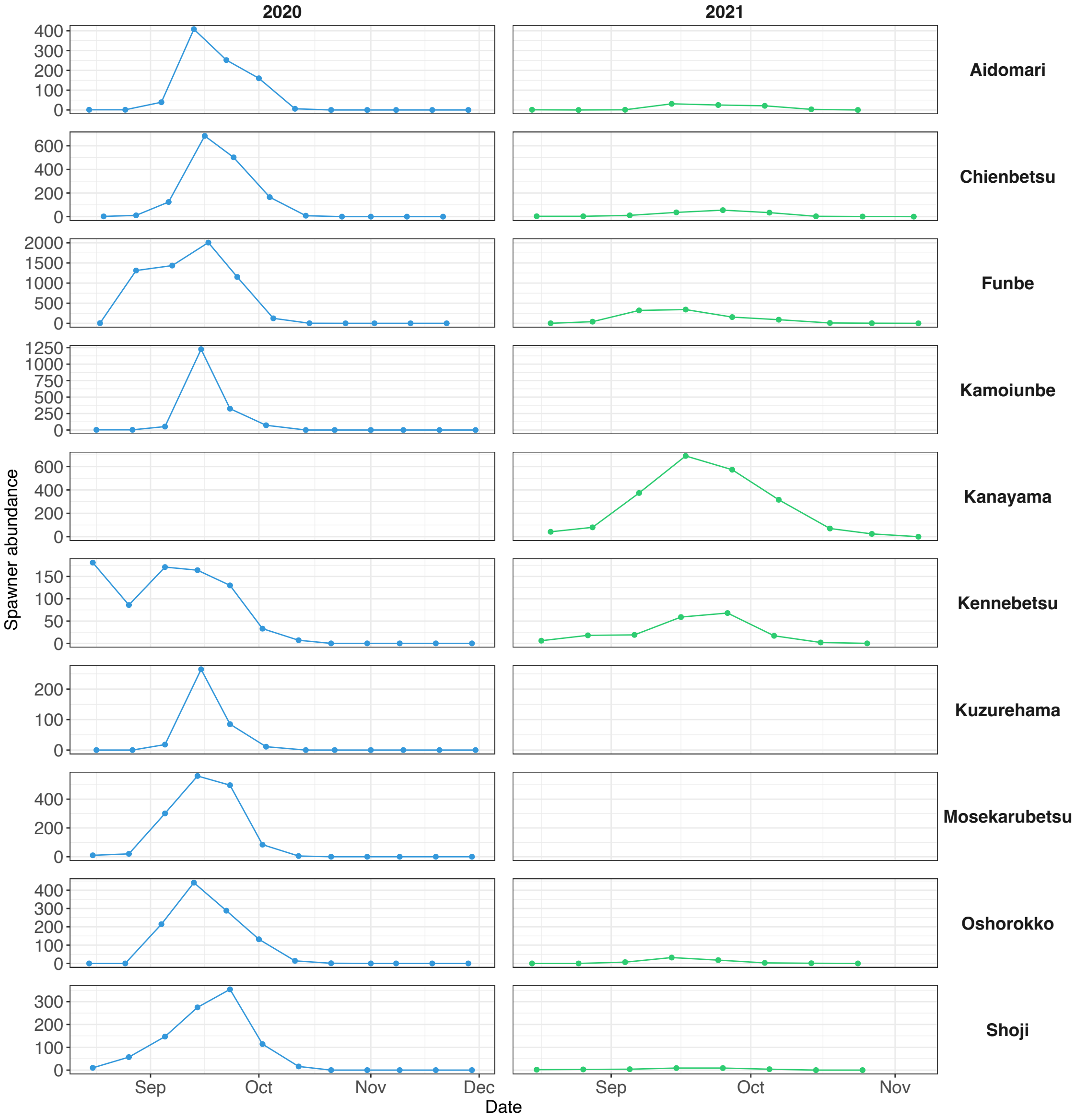

Figure A4-1 Seasonal fluctuation of spawner abundance in each stream.

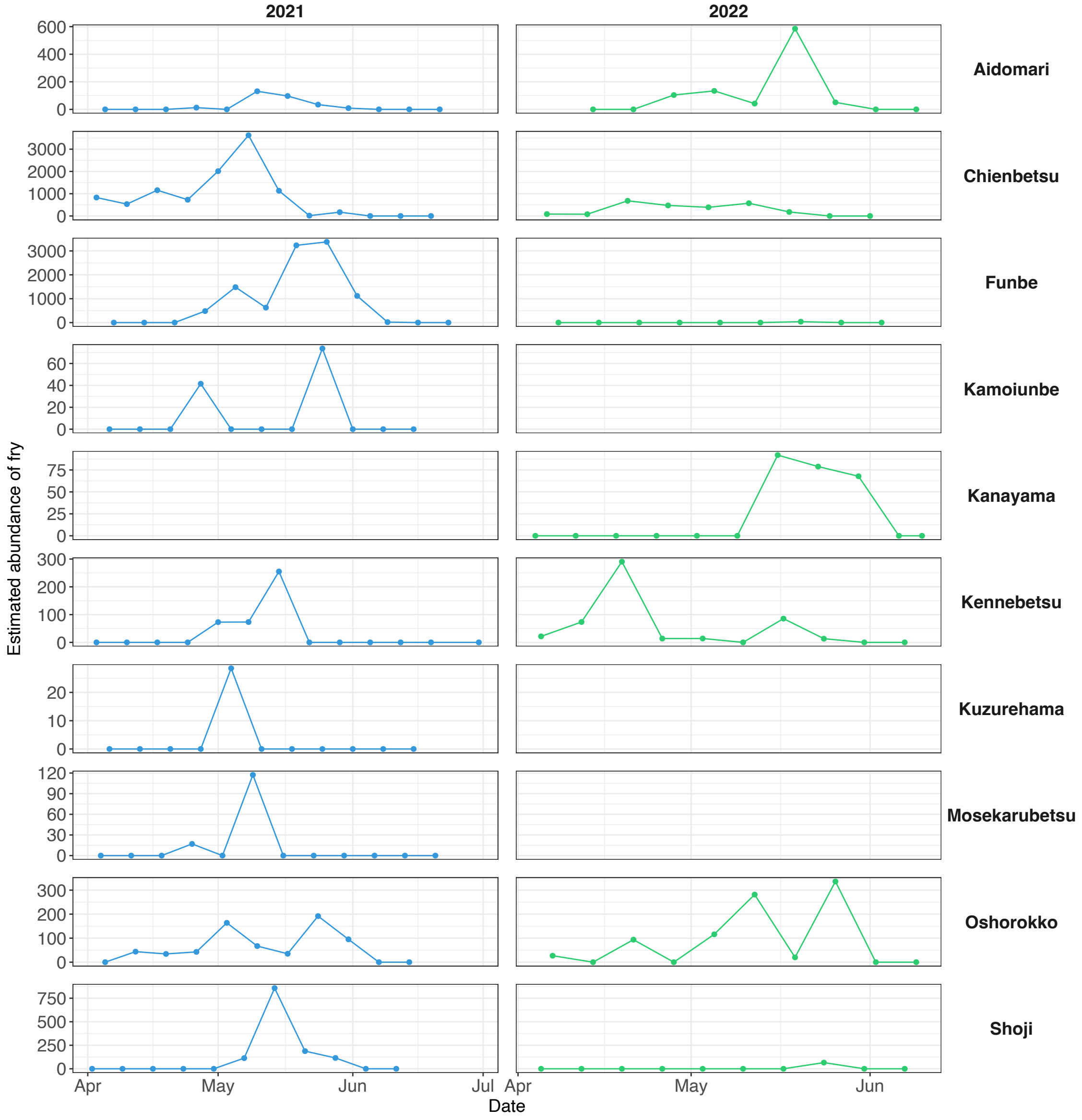

Figure A4-2 Seasonal fluctuations of estimated downstream migration of pink salmon fry in each stream.

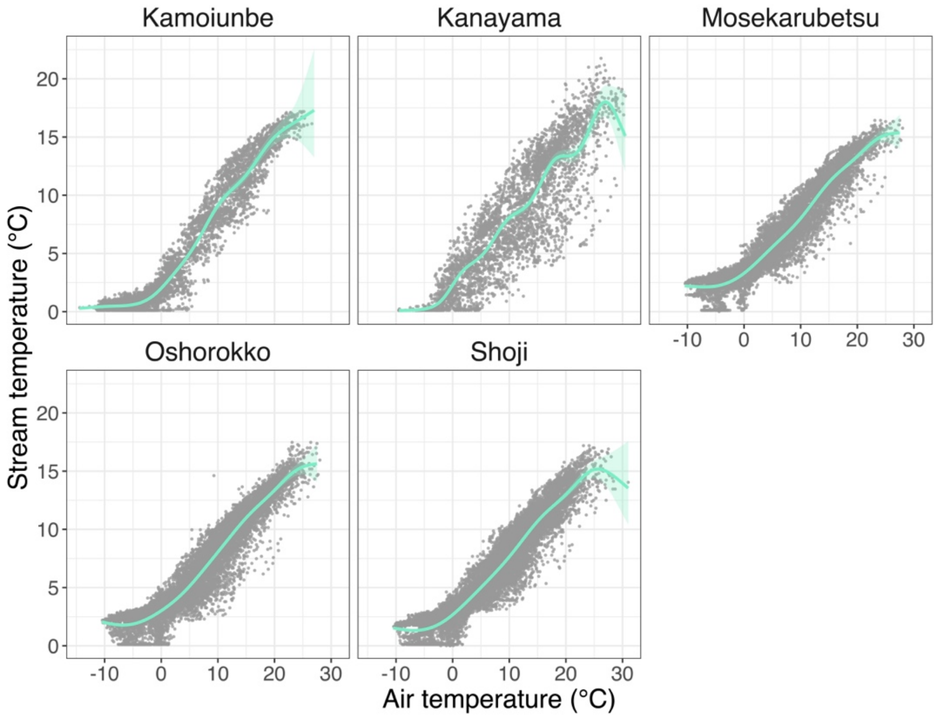

Figure A4-3 Stream temperature in relation to air temperature as predicted by generalized additive models. The shaded area indicates the 95% CI.

Table A4-1 Results of generalized additive models testing the effects of air temperature on stream temperature for each stream.

Stream	Intercept			s(air temperature)			Adjusted R^2
	Estimate	se	*p*	edf	Ref.df	*p*	
Shoji	1.70	0.00	< 0.0001	8.50	8.90	< 0.0001	0.912
Mosekarubetsu	1.80	0.00	< 0.0001	8.08	8.74	< 0.0001	0.913
Oshorokko	1.79	0.00	< 0.0001	8.57	8.94	< 0.0001	0.920
Kamoiunbe	1.06	0.01	< 0.0001	8.49	8.92	< 0.0001	0.957
Kanayama	1.82	0.01	< 0.0001	8.93	9.00	< 0.0001	0.782

5. General Discussion

Here, I summarized the results of this study and discussed their importance for future conservation and restoration of salmonids worldwide. Furthermore, I evaluated the restoration value of watersheds for anadromous salmonids for the Shiretoko Peninsula based on the results of Chapters 2 and 4.

The main results of this study are as follows. (1) The prediction of the substrate particle size using a machine learning model achieves high accuracy. The particle size prediction model indicated that while there is a total of 40738.62 km of suitable spawning habitat for anadromous salmonids in Hokkaido, northern Japan, approximately half of it (49.84%) has not been accessed due to fragmentation by dams. (2) The diel downstream migration pattern of pink salmon fry was significantly explained by the time of day, with 89.9% of the migrations occurring between 18:00 and 23:00. (3) The freshwater productivity of pink salmon was largely explained by watershed hydrogeomorphology and precipitation (average watershed slope, stream power, and maximum daily precipitation). When considering the conservation and restoration of anadromous salmonids, careful consideration should be given to the amount of suitable spawning habitat and the hydrogeomorphology of the watershed.

Perspectives for conservation and restoration of anadromous salmonid habitat

At the 15th Conference of the Parties to the United Nations Convention on Biological Diversity (COP15), the "Kunming-Montreal Global Biodiversity Framework" was adopted, which includes a target known as "30 by 30", aimed at conserving at least 30% of land and sea by 2030. Therefore, conservation and restoration activities are expected to be active worldwide from now on. Given that disturbances in certain areas of a watershed can have an impact on the entire river network, it is crucial to prioritize such activities at the watershed scale (Moravek et al. 2023).

Previous studies have assessed the habitat for juvenile salmonid rearing based on river connectivity (Buddendorf et al. 2019) or have also been limited to assessments at scales smaller than a single watershed (Shirvell 1989, Moir et al. 2005, Goode et al. 2013, Carmichael et al. 2020). The present study is the first to simultaneously address the prediction of spawning habitat for anadromous salmonids by a machine learning model and predict the spatial variation in freshwater productivity based on environmental characteristics across watersheds. The results of this study indicated that the amount of suitable spawning habitat and freshwater productivity notably differ among watersheds. If a watershed has many suitable spawning habitats but the freshwater productivity is low, then it should be considered of low conservation and restoration value. Therefore, it is important to simultaneously assess both the amount of suitable spawning habitat and watershed-scale productivity, as was done in this study.

I succeeded in predicting suitable spawning habitats for anadromous salmonids throughout Hokkaido, northern Japan, using a machine learning model and showed that their freshwater productivity can be predicted based on the watershed hydrogeomorphology and precipitation in the Shiretoko Peninsula. However, there are some limitations. First, this study was conducted only in the whole or only part of Hokkaido. Therefore, it is not certain that the results will be consistent in other regions. Further investigation with tests in another region is required to confirm the generality of the results. In addition, the difference in spatial scale between the chapters (Chapters 3 and 4 were conducted at a smaller scale than Chapter 2) makes it difficult to directly compare the results of the chapters. In the future, the studies in Chapter 4 should be conducted in larger river systems to evaluate whether the suitable spawning habitat predicted in Chapter 2 influences salmon recruitment. Second, the present study did not consider several factors that may affect anadromous salmonid reproduction, such as forestry and nonnative species. For that reason, their relative importance to salmonid reproduction was not assessed. If the relative importance is elucidated, effective resource allocation for the conservation and restoration of anadromous salmonids could be achieved. Future studies are needed to determine the relative importance of these factors to receive sustainable benefits from anadromous salmonids.

Watershed-scale assessment for habitat restoration of anadromous salmonids: Lessons from the Shiretoko Peninsula

Here, I evaluated the restoration value of each watershed in the Shiretoko Peninsula as an example that has more than 330 check dams (Takahashi et al. 2005) based on a series of results of this thesis. On the Shiretoko Peninsula, organisms across various taxonomic groups, such as brown bear, red fox *Vulpes vulpes schrencki*, Blakiston's fish owl *Ketupa blakistoni*, white-tailed eagle *Haliaeetus albicilla*, brown dipper *Cinclus pallasii*, gulls genus *Larus*, Dolly Varden, and aquatic macroinvertebrates, receive benefits from spawning migration of anadromous salmonids. The Shiretoko World Natural Heritage Site is recognized for this close relationship between the marine and terrestrial ecosystems maintained by the migration of anadromous salmonids (IUCN 2005). To preserve this valuable ecosystem, natural restoration activities should be implemented effectively.

To evaluate the restoration value of each watershed, I extracted the watersheds where check dams exist (dam data: GSI Vector Tile Experiment, https://maps.gsi.go.jp/vector/). Here, I considered watersheds with longer fragmented reaches and higher freshwater productivity to be more valuable for restoration. In addition, spawner abundance was incorporated into the assessment because of its importance to the ecosystem and fisheries. The restoration value (RV) was calculated for each watershed, W, as follows:

Eq. 5-1. $$\boldsymbol{RV_W = H_W \times P_W \times A_W}$$

where H_W, P_W, and A_W are the unavailable suitable spawning habitat, freshwater productivity, and spawner abundance in watershed W, respectively. The unavailable suitable spawning habitat was predicted by the constructed particle size prediction model (Chapter 2), and then the freshwater productivity of each watershed was predicted using the average watershed slope model (Chapter 4). The spawner abundance was predicted based on watershed area. A previous study showed that the average size of annual salmon runs was positively correlated with watershed area (Kim and Lapointe 2011). Based on a previous study, a relationship between spawner abundance and watershed area was estimated by fitting a GLMM assuming a negative binomial distribution with a log link function, considering stream ID and brood year ID as random intercepts, and a positive correlation was confirmed ($p < 0.0001$). All predicted values were normalized (min = 0, max = 1); thus, the theoretical minimum and maximum restoration values are 0 and 1, respectively. As a result, the Shunkarikotan Stream, Rikushibetsu Stream, and Iwaobetsu Stream had high restoration values within the watersheds of the Shiretoko Peninsula (Figure 5-1). Therefore, these watersheds should be prioritized for restoration.

There are several measures for restoration from dam-induced fragmentation: complete removal of the dam for hydropower, irrigation, and flood and sediment control (Garcia de Leaniz 2008, Fjeldstad et al. 2012, Birnie-Gauvin et al. 2018, Ishiyama et al. 2018), partial removal of the check dam (Nakamura and Komiyama 2010), and installation of the fishway (Naughton et al. 2007, Kiffney et al. 2009, Katopodis and Williams 2012, Landsman et al. 2018, Brito-Santos et al. 2021). Fishways often stop working when objects such as logs and/or gravels become jammed. Furthermore, in some cases, even if the fishway was working, the fish would not pass it due to higher water velocity and turbulence (Hinch and Bratty 2000). Additionally, passage of the fishway reduces the survival of adult salmon (Roscoe et al. 2011). In addition, the alteration of sediment regimes by check dams cannot be improved by the installation of the fishway. Check dams alter sediment regimes, reduce the amount of drifting prey, and ultimately reduce fish carrying capacity (Urabe et al. 2014). Thus, other measures (i.e., complete or partial removal of the dam) are better than installing fishways. To decide which measure should be used, consideration must be given to ensure that human safety is not threatened, as check dams were constructed with the aim of reducing the effects of a natural disaster. In view of the drastic decrease in the human population in Japan, complete removal can be actively chosen in the underpopulated area, including the Shiretoko Peninsula.

The salmon stock management in the Shiretoko Peninsula has been conducted solely through hatchery releases, despite it having negative impacts on wild salmon populations: decreasing reproductive success and increasing competition between fish of wild and hatchery origin (Araki et al. 2007, Christie et al. 2012, Willoughby and Christie 2019, O’Sullivan et al. 2020, Ohlberger et al. 2022, Terui et al. 2023). In addition, hatchery release may have a stronger negative impact under climate change because the interactive effects of ocean climate and competition could affect salmon productivity (Ohlberger et al. 2022). Promoting habitat restoration based on this study could contribute to reducing the reliance on hatchery releases by contributing an increase in the number of returning salmon and eventually could contribute to population persistence under a changing climate.

Here, I proposed a framework for prioritizing habitat restoration for anadromous salmonids on the Shiretoko Peninsula based on the models I constructed. To test the effectiveness of this framework, it is important to monitor the reproduction of salmonids in several streams after restoration. Furthermore, to avoid further expansion of the adverse effects of fragmentation, it is important to protect watersheds that are currently of high value for salmonid reproduction (i.e., watersheds with many available spawning habitats and high freshwater productivity and spawner abundance) from damming.

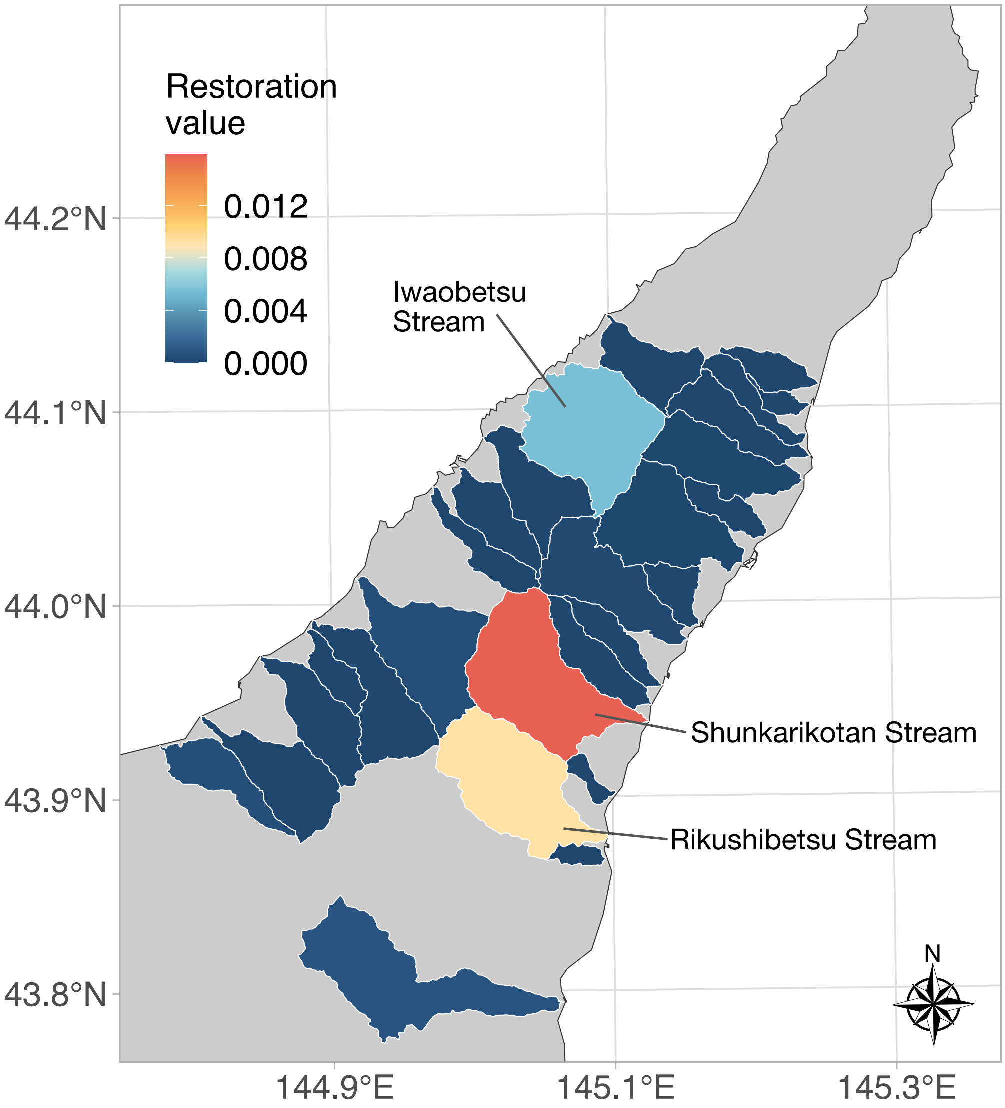

Figure 5-1 Map of the estimated restoration value for the spawning habitat of anadromous salmonids in the Shiretoko Peninsula, Hokkaido, northern Japan. The coloured bar indicates the range of restoration values.

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