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Pink salmon productivity is driven by watershed hydrogeomorphology and can decline under a changing climate

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ABSTRACT

1. Increased flood magnitude and frequency due to climate change can reduce the population productivity of organisms such as amphibian and fish species in river and stream systems; therefore, conserving habitats that maintain high productivity under such conditions is crucial. Here, we examined the relationship between the freshwater productivity of anadromous salmonids (measured as fry migrating to the ocean per spawner) and watershed hydrogeomorphology and identified the characteristics of rivers and streams that are prone to flood disturbance.
2. We surveyed the spawner abundance and number of fry of pink salmon (*Oncorhynchus gorbuscha*) and measured environmental factors, including the average watershed slope and stream power, as characteristics of hydrogeomorphology, in 10 streams in the Shiretoko Peninsula, northern Japan. We then used generalized linear mixed models to predict the freshwater productivity of pink salmon populations in each watershed across the study region under current and future climatic conditions.
3. The productivity of pink salmon in the study region differed among the sampled watersheds and was negatively affected by the average watershed slope, stream power, and maximum daily precipitation averaged over the watershed. Namely, flood disturbance reduced the freshwater productivity of pink salmon, and salmon productivity in individual watersheds was explained by watershed hydrogeomorphology. The predicted future productivity with increased precipitation was also lower than the current productivity.
4. Our approach can be applied to other salmonids that have similar spawning behaviour to pink salmon. Highly productive watersheds under the future climatic conditions predicted by the present study should be prioritized for conservation to ensure a sustainable salmonid population.

1. INTRODUCTION

Biodiversity in freshwater ecosystems is threatened by extreme events induced by climate change (Heino, Virkkala & Toivonen, 2009; Reid *et al.*, 2019; Dudgeon, 2019). Floods are among the most crucial natural phenomena affected by climate change, and climate change enhances flood disturbance magnitude and frequency (Milly *et al.*, 2002; Arnell & Gosling, 2016). Flood disturbance reduces the recruitment and productivity of organisms such as amphibian and fish species in river and stream systems (Smith, Odenkirk & Reeser, 2005; Lowe, 2012; Kupferberg *et al.*, 2012). Hence, the increasing magnitude and frequency of flood disturbance due to climate change could lead to a decline in the productivity of organisms in river systems.

Given the increasing frequency and severity of flood disturbances resulting from climate change, conserving critical habitats that ensure high population productivity under such conditions is crucial. To achieve this, habitats that exhibit strong resistance to flood disturbance based on environmental features must be identified. Because flood disturbance is controlled by water and sediment discharge, which are determined by watershed hydrogeomorphology (Moore, Grayson & Ladson, 1991; Aalto, Dunne & Guyot, 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 population productivity of some organisms. However, few studies have examined the relationship between watershed hydrogeomorphic characteristics and population productivity. Elucidating this relationship could enable predictions of watershed productivity over wide regions without the need for field surveys, thereby contributing to the effective conservation of target species under climate change.

Anadromous salmonids are vulnerable to flood disturbance, making them an optimal model to examine the effects of hydrogeomorphology because of their well-known spawning

ecology and life cycle (Quinn, 2018). Flood disturbance causes high mortality in their egg to alevin stages by scouring redds (Holtby & Healey, 1986; Thorne & Ames, 1987; Montgomery *et al.*, 1996; Jensen & Johnsen, 1999; Waples, Pess & Beechie, 2008; Milner *et al.*, 2013). The lifetime productivity (adult offspring per spawner) of anadromous salmonids is influenced mainly by population regulation during the freshwater life stage (i.e., freshwater productivity; fry migrating to ocean per spawner) (Bradford, 1995; Morita, Ayumi & Kikuchi, 2015; Warkentin *et al.*, 2022); hence, flood disturbance is likely a key factor affecting their lifetime productivity (Greene *et al.*, 2005).

In this study, we examined the relationship between the total spawner abundance (males and females) and the total number of fry migrating to the ocean (hereafter total number of fry) of pink salmon *Oncorhynchus gorbuscha* and environmental factors at a watershed scale that potentially affect productivity in the Shiretoko Peninsula of Hokkaido, northern Japan. We hypothesized that watershed hydrogeomorphic characteristics drive the freshwater productivity of anadromous salmonids. In addition to hydrogeomorphology, the freshwater productivity of salmonids is influenced by other factors such as temperature and competition for suitable spawning habitat (Fukushima, Quinn & Smoker, 1998; Essington, Quinn & Ewert, 2000; Manhard *et al.*, 2017; Honkanen *et al.*, 2019); hence, we included these factors as candidate characteristics in this study. In addition, using the constructed model, we predicted the freshwater productivity of each watershed on the Shiretoko Peninsula under current and future climatic conditions. Specifically, we predicted that high watershed slope and stream power would adversely affect the productivity of pink salmon and that future productivity would be lower than current productivity as a result of increased flood disturbance caused by climate change. Pink salmon are the most abundant and widely distributed salmonid species in the northern Pacific region (Heard, 1991; Quinn, 2018) and

have a crucial ecological function as a spatial subsidy in transporting marine-derived nutrients to freshwater and terrestrial ecosystems (Koshino, Kudo & Kaeriyama, 2013; Yamada *et al.*, 2022a). Our research findings can contribute to identifying streams and rivers where conservation efforts for pink salmon should be prioritized.

2. MATERIALS AND METHODS

2-1. Study site

We selected ten streams on the Shiretoko Peninsula as our study sites (Figure 1). These streams have never been targeted for hatchery programs for pink salmon. However, fry of chum salmon (*Oncorhynchus keta*) were released in one of the streams (Mosekarubetsu). The central part of the Shiretoko Peninsula has been designated as a World Natural Heritage site since 2005 because of the close linkages between marine and terrestrial ecosystems via pink 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 $\pm$ SD and range: 210.99 ± 115.36 [range 62.6–409.1] m).

2-2. Estimation of total spawner abundance

To estimate total spawner abundance (males and females), we counted the number of adult pink salmon in the study sections every 7–11 days from mid-August until early November in 2020 and 2021, the spawning period of pink salmon (Figure S1). We walked upstream and counted all live pink salmon. Pink and chum salmon were easily distinguished based on their visual characteristics

(body size and colour and humped back). The survey was conducted only when water visibility was sufficient to see to the bottom. We determined the total spawner abundance over an entire spawning season per stream using the area under the curve (AUC) method (English, Bocking & Irvine, 1992; Bue *et al.*, 1998). This method requires "stream life" and "observer efficiency" to be defined. The former was defined as 7.85 days based on previous research conducted in the same region (Yokoyama *et al.*, 2010). To evaluate observer efficiency, we 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, we counted the fish while walking through the section (observed fish number). We defined the observed fish number/true fish number as observer efficiency. This survey was conducted 1–7 times in 6 streams (Aidomari, Osyorokko, Shoji, Kennebetsu, Funbe, and Kanayama) when 10 or more pink salmon were present in the section. We calculated the average observer efficiency for each stream and then the overall average and SD. The calculated observer efficiency was 0.92 ± 0.07 (range 0.79–1.00).

2-3. Estimation of the total number of fry

In each stream, we established a sampling point for collecting salmon fry. From April to June in 2021 and 2022, we collected pink salmon fry in each stream every week except for one survey, which was conducted at four-day intervals (Figure S2). We 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 (Hintz & Lonzarich, 2012; Yamada, Urabe & Nakamura, 2022b), at a sampling point for 15 minutes at hourly intervals (Yamada *et al.*, 2022b). Because long-term sampling with drift nets would result in higher fry mortality, we set the sampling duration to be as short as possible. We 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, Kirillova & Pavlov, 2018), and its peak was 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. We recorded the number of individuals and then immediately released all individuals. The stream discharge at each sampling point was estimated as follows: based on the depth and current velocity at $0.2 \times \text{depth}$ and $0.8 \times \text{depth}$ 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, we measured the wetted sectional area of the net and current velocity at $0.2 \times \text{depth}$ and $0.8 \times \text{depth}$ at three points (left, right, and centre) on each net. We 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 daily number of fry on each survey day D (N_D) was estimated for each stream as follows:

eq 1. $N_D = (C_D \times (S_D/F_D) \times 4)/0.899$

where C_D , F_D , and S_D are the number of fry captured, water filtered by drift nets, and stream discharge on survey day D , respectively. In the equation, “4” is the value used to convert the number of fry captured 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). We then estimated the total number of fry over an entire migrating season per stream from N_D using the AUC method (English *et al.*, 1992; Bue *et al.*, 1998). We assumed that "stream life" and "observer efficiency (i.e., collection efficiency)" were 1 day and 100%, respectively.

2-4. *Environmental variables*

For statistical analyses, we derived eight environmental characteristics: average watershed slope, stream power, 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 1). The description and derivation of these characteristics are provided below.

The average watershed slope and stream power (average channel slope [%] times watershed area [km²]) affect stormflow water yields, sediment yield and transport, and channel stability (Moore & 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>). We 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, the 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, we 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>). 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, we 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, we established an additional study section extending approximately 10 times the wetted width in length within each study section and caught the fish during the day 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). We 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. Afterwards, all fish were released near the capture sites. In each stream, the southern Asian Dolly Varden trout *Salvelinus curilus*, which occasionally preys on fish (Denton, Rich & Quinn, 2009), was dominant. Thus, we 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 & Strub, 1978), which is widely used to estimate population abundances from two-pass electrofishing data (Bergerot, Bret & Cattaneo, 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 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 were missing for some periods in several streams (Kamoiunbe, Kanayama, Mosekarubetsu, Oshorokko, and Shoji streams) due to machine failure or loss by floods. Therefore, missing values were estimated by generalized additive models with a gamma distribution and log-link function (Figure S3; Table S1). We 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, we calculated the average autumn temperature (September - October), average winter temperature (December - February), and average spring temperature (April - May) (Table S2). 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 freshwater productivity (Fukushima *et al.*, 1998; Essington *et al.*, 2000). Because salmonids can spawn in gravels with a median diameter up to approximately 10% of their body length (Kondolf & Wolman, 1993) and the length of returning pink salmon is generally 40–60 cm (LeBrasseur & Parker, 1964), we considered gravel (greater than 2 mm to less than 32 mm) and pebbles (greater than 32 mm to less than 64 mm) as suitable spawning grounds for pink salmon within the grain size categories usually used: bedrock, sand (<2 mm), gravel (greater than 2 mm to less than 32 mm), pebble (greater than 32 mm to less than 64 mm), cobble (greater than 64 mm to less than 128 mm), or boulder (≥ 128 mm). We identified substrate categories by visual observation and estimated the area of the streambed dominated by gravel or pebble in the fall or winter. Finally, the area available for spawning per individual was calculated by dividing the total area of suitable substrate by the total spawner abundance.

2-5. Data analysis

Before the analysis, we evaluated the correlation among explanatory variables and found that the average winter temperature had a strong negative correlation ($|r| > 0.7$, Dormann *et al.*, 2013) with the average watershed slope (Figure S4). Because the present study focused on the effect of hydrogeomorphic characteristics, the 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). The total number of fry was the response variable, study stream ID and brood year ID were treated as random intercepts, and total spawner abundance transformed to natural logarithm was included as an offset term. We built six GLMMs with the following explanatory variables: average watershed slope, stream power, average autumn temperature, average spring temperature, area available for spawning per individual, and predator density. Constructing a more complex model was difficult due to the small sample size. Only two models (average watershed slope and stream power) 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, Jones & Manley, 2018). For each GLMM, the significance of the explanatory variables was evaluated using type II Wald chi-square tests ($P < 0.05$). We 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.

2-6. Prediction of future productivity

The current (1980–1999) and future (2076–2095 under the two representative concentration pathways [RCPs; RCP2.6 and 8.5]) annual maximum daily precipitation data across Hokkaido were obtained from the Japan Meteorological Agency Regional Climate Projection Data for Japan, which was produced under the TOUGOU program. Because Hokkaido generally receives most of its precipitation during August and September (Japan Meteorological Agency; averages for the period 1991–2020), we concluded that the dataset could represent the maximum daily precipitation during the pink salmon spawning season. The dataset for current and future annual maximum daily precipitation was provided only at climate observation points, obtained using the nonhydrostatic regional climate model with a grid spacing of 2 km (NHRCM02; Murata *et al.*, 2017), which was developed by the Meteorological Research Institute (MRI). Data from a total of 93 points with high reliability in Hokkaido were used. We used the dataset to calculate an average value for each climate observation site within each condition (current and RCP2.6 and 8.5) and then calculated the average annual maximum daily precipitation for Hokkaido. We then predicted the current and future productivity of pink salmon in each watershed on the Shiretoko Peninsula, Hokkaido, northern Japan, using the model with the highest prediction accuracy, with precipitation and average watershed slope as explanatory variables (see Results).

3. RESULTS

The average $\pm$ SD (range) across the 16 samples was 1504.25 ± 1918.32 (43–7933) for the total spawner abundance, 12316.12 ± 23181.35 (200–72374) for the total number of fry, and 18.65 ± 27.68 (0.20–84.09) for freshwater productivity. The total spawner abundance in 2020 exceeded that of 2021, consistent with recent trends in Japan of greater spawner abundance in even years based

on the two-year life cycle of pink salmon (Saito, 2021). The average watershed slope, stream power, and maximum daily precipitation had significant negative effects on freshwater productivity (Figure 2ab; Table 2). However, the maximum daily precipitation in the stream power model was nonsignificant (Table 2). The other variables had no significant effects (Table 2). In addition, the watershed slope and stream power models had the lowest and second lowest Akaike information criterion (AIC) values, respectively, with a difference of less than 2. Therefore, these models are considered plausible models in terms of model selection (Burnham & Anderson, 2002). 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 model, respectively.

The estimated annual maximum daily precipitation in Hokkaido under the current, RCP2.6, and RCP8.5 conditions was 71.07, 82.30, and 101.82 mm, respectively. The predicted productivity was lower under RCP 2.6 and RCP8.5 than under the current condition, with most watersheds predicted to have a productivity of less than 10 fry per spawner under RCP8.5 (Figure 3ab). However, several gently sloping watersheds had relatively high productivity (>100 fry per spawner) even under RCP8.5 (Figure 3ab).

4. DISCUSSION

In the present study, we 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 our 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.

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 stream power 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 and sediment yields (Aalto *et al.*, 2006; Koskelo *et al.*, 2018). The stream power is also related to sediment transport and channel stability (Moore & 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 alevins away and cause low productivity in pink salmon.

Unlike most other salmonids, pink salmon migrate to the sea immediately after emerging from the streambed (Heard, 1991). Consequently, other salmonids may be strongly affected by flood disturbance because floods have a greater impact on fish when they reside in the stream at both the egg and juvenile life stages (Neuswanger *et al.*, 2015). Alternatively, the effects of flood disturbance may be relatively less important, as salmonids other than pink salmon are expected to be more sensitive to other factors (including food and habitat availability and the presence of predators and competitors). Additional studies are needed to clarify the importance of watershed hydrogeomorphology for other salmonids.

Although several studies have indicated that competition for suitable spawning habitat, predators, and temperature affect the freshwater productivity or survival of anadromous salmonids (Fukushima *et al.*, 1998; Essington *et al.*, 2000; Manhard *et al.*, 2017; Honkanen *et al.*, 2019), we did not observe any significant effects of these variables on productivity. The average water

temperatures for each season in this study were not greatly below or above the typical temperature limits for the survival of salmon eggs (Elliott & Elliott, 2010), so we assumed that the effect was not significant. However, we note that unfortunately, we did not measure water temperature within the redds and were unable to evaluate the effects of maximum and minimum water temperatures due to the missing values, so additional evaluation taking these factors into account is needed. In addition, if temperature limits for survival are exceeded due to climate change, the freshwater productivity of salmonids will be greatly reduced. Additionally, climate change may introduce predators or alter predator density (Lawrence *et al.*, 2014), potentially affecting salmon productivity.

Regarding competition for suitable spawning habitat, the carrying capacity for spawning in pink salmon in small streams similar in size to our study streams was equivalent to a spawner density of 51.33 spawners/stream length (m) (Manhard *et al.*, 2017). We estimated a maximum spawner density of 22.78 spawners/m. Thus, our study may have been conducted below the carrying capacity, resulting in a non-significant density effect. In addition, previous studies were conducted in a single watershed, and the effects of disturbance may have been similar among the samples, leading to the effects of temperature and spawner density. Because the present study was conducted in multiple watersheds with differing disturbance intensities, the effect of disturbance may have been more distinct than others. However, our watersheds were steep and small, which may constrain the application of the results to other regions with different hydrogeomorphic characteristics.

Additionally, we caution that we did not consider certain environmental conditions such as watershed geology and land use; in fact, our constructed models did not fully explain the variation in the productivity of pink salmon. Watershed geology influences flow regimes, such that watersheds containing more permeable bedrock experience a reduction in flood runoff (Musiake,

Takahasi & Ando, 1981). Watershed land use also affects flood peak discharge (Saghafian *et al.*, 2008; Olang & Fürst, 2011). Hence, these factors potentially affect the freshwater productivity of salmonids by affecting the flood disturbance intensity. In addition, watershed geology governs the transport of fine sediment (Bond, 2004). High transport rates for fine sediment can reduce the survival rate of embryos by decreasing the permeability of the streambed (Julien & Bergeron, 2006; Yamada & Nakamura, 2009), suggesting that watershed geology may impact salmonid productivity. Similarly, land-use conversion in watersheds (including urban, rural-residential, and vineyard areas) can result in an increase in fine sediment inputs (Lohse *et al.*, 2008). However, because the present study was conducted in volcanic and forested watersheds, we were unable to investigate the effects of watershed geology and land use. Consequently, further studies examining the effect of hydrogeomorphology on pink salmon using a wider range of watershed sizes and types will be critical to evaluate our results.

Future climate change scenarios predict an increase in the frequency and intensity of precipitation extremes (Donat *et al.*, 2016; Huang, Swain & Hall, 2020; Thackeray *et al.*, 2022), resulting in heavy and frequent floods and increased flood risk (Milly *et al.*, 2002; Arnell & Gosling, 2016). These increases in disturbance frequency and intensity may impose high mortality on salmonids during the freshwater life stage, especially the incubation stage. Indeed, our predictions indicated that the future productivity of pink salmon (2076–2095 under RCP8.5) is likely to decline. Thus, effective adaptation strategies are needed to support the persistence of salmonid populations. Given that some basins are predicted to exhibit high productivity under future conditions, these watersheds should be prioritized for conservation. In addition, removing dams in these watersheds to improve connectivity and increase spawning and rearing habitat (Nakamura & Komiyama, 2010; Forget *et al.*, 2018; Ramos & Ward, 2023) may serve as an effective adaptation strategy. Geospatial

data regarding climate and geomorphology are widely available. Hence, this approach may be useful for predicting the effects of climate change on salmonid productivity in many regions across the globe, contributing to the conservation of salmonid habitat.

Pink salmon are declining in Japan (Saito, 2021). However, they are expanding their distribution as an invasive species in northern Europe, raising concerns about their impact on native salmonids (Sandlund *et al.*, 2019; Lennox *et al.*, 2023; Skóra *et al.*, 2023). Our results provide insights into watersheds that may be highly productive for invasive pink salmon. By prioritizing monitoring in watersheds with a lower slope and a lower stream power, invasions by pink salmon could be more effectively managed.

Anadromous salmonids hold significant ecological and commercial importance because they transport marine-derived nutrients to freshwater and terrestrial ecosystems (Willson & Halupka, 1995; Gende *et al.*, 2002; Schindler *et al.*, 2003; Hocking & Reynolds, 2011), and they provide valuable ecosystem services as fishery and recreational resources (Quinn, 2018; Watz *et al.*, 2022). Nevertheless, declines in their abundance have been observed in many regions of the world (Mills *et al.*, 2013; Ward *et al.*, 2015; Nicola *et al.*, 2018). Serious negative impacts on ecosystems and economies could result if we do not prevent further declines in salmon populations due to climate change. The conservation of anadromous salmonids based on our findings can contribute to ensuring sustainable populations under a changing climate.

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AUTHOR CONTRIBUTION STATEMENT

Conceptualisation, writing: TY, HU, FN. Developing methods: TY, HU. Conducting the research, data analysis, data interpretation, preparation of figures and tables: TY.

DATA AVAILABILITY STATEMENT

The datasets supporting this article are available at the Figshare repository: DOI.

Only for peer review: <https://figshare.com/s/ef5cd902a98de1c144a3>

CONFLICTS OF INTEREST STATEMENT

None declared.

ETHICS STATEMENT

All animal handling in the surveys was conducted in accordance with the Act on Welfare and Management of Animals and the regulations for animal experiments of Hokkaido University. No fish were sacrificed, and no surgical procedures were performed in this study. All fish collection was legally conducted in accordance with the permit from the Hokkaido Government (no. 170).

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TABLES

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

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

Table 2. Results of GLMMs testing the effects of six explanatory variables and a covariate (maximum daily precipitation) on freshwater productivity. The χ^2 and p values were derived from the type II Wald chi-square tests. AIC, Akaike information criterion; R2m, marginal R^2 ; R2c, conditional R^2 .

Model	Estimate	se	χ^2	p	AIC	Δ AIC	R2m	R2c
Intercept	2.22	0.60			325.7	0.0	0.478	0.597
Watershed slope	-0.78	0.24	10.58	0.0011				
Maximum precipitation	-1.20	0.36	11.06	0.0009				
Intercept	2.29	0.52			327.3	1.6	0.357	0.447
Stream power	-1.14	0.39	8.55	0.0035				
Maximum precipitation	-0.16	0.78	0.04	0.8388				
Intercept	2.65	0.51			332.5	6.8	0.068	0.126
Predator density	0.57	0.34	2.83	0.0923				
Intercept	2.69	0.65			333.5	7.8	0.032	0.154
Spring temperature	0.40	0.31	1.65	0.1990				
Intercept	2.77	0.54			333.8	8.1	0.215	0.216
Available area	1.18	0.86	1.88	0.1698				
Intercept	2.77	0.51			334.3	8.6	0.026	0.076
Autumn temperature	-0.37	0.39	0.87	0.3519				

FIGURES

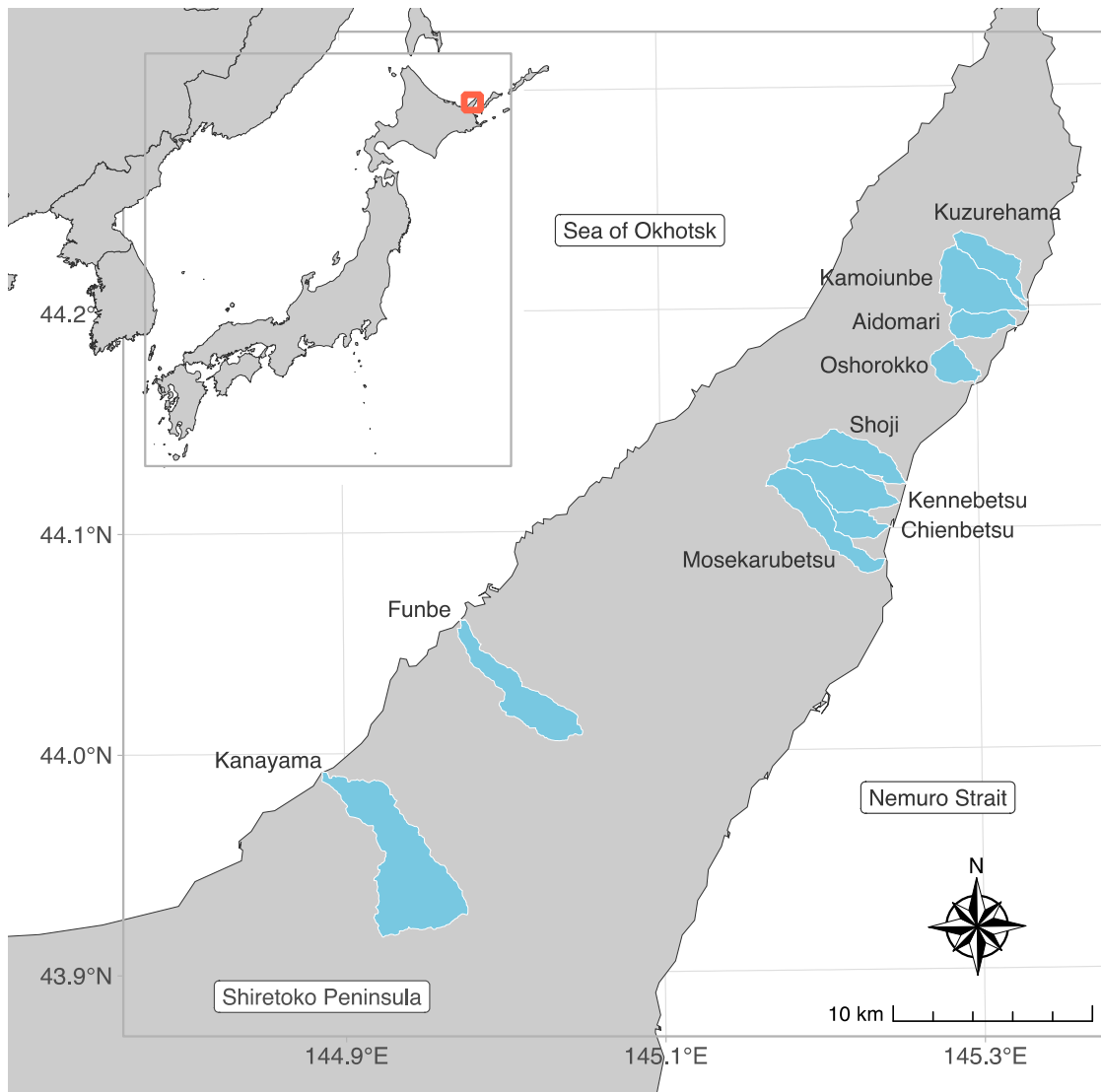
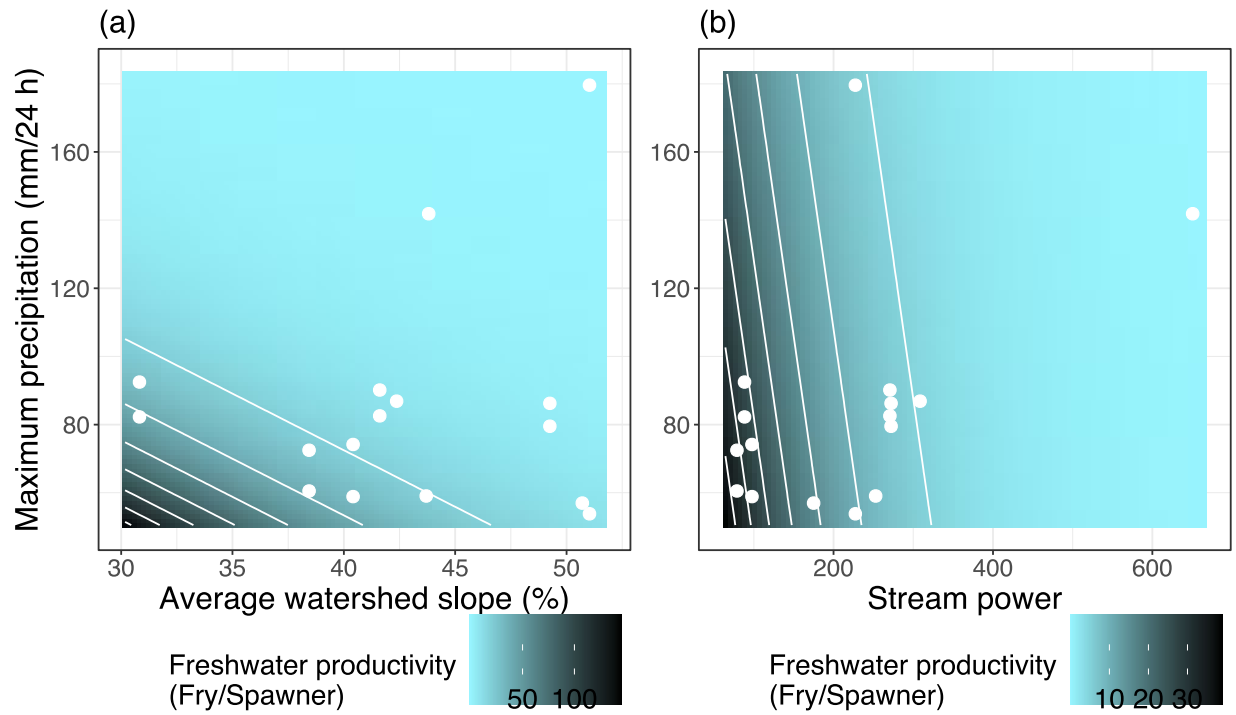


Figure 1. Map of the study area. Blue areas represent each watershed. The inset map shows the location of the study area (represented as an open orange square) in the Shiretoko Peninsula, northern Japan.

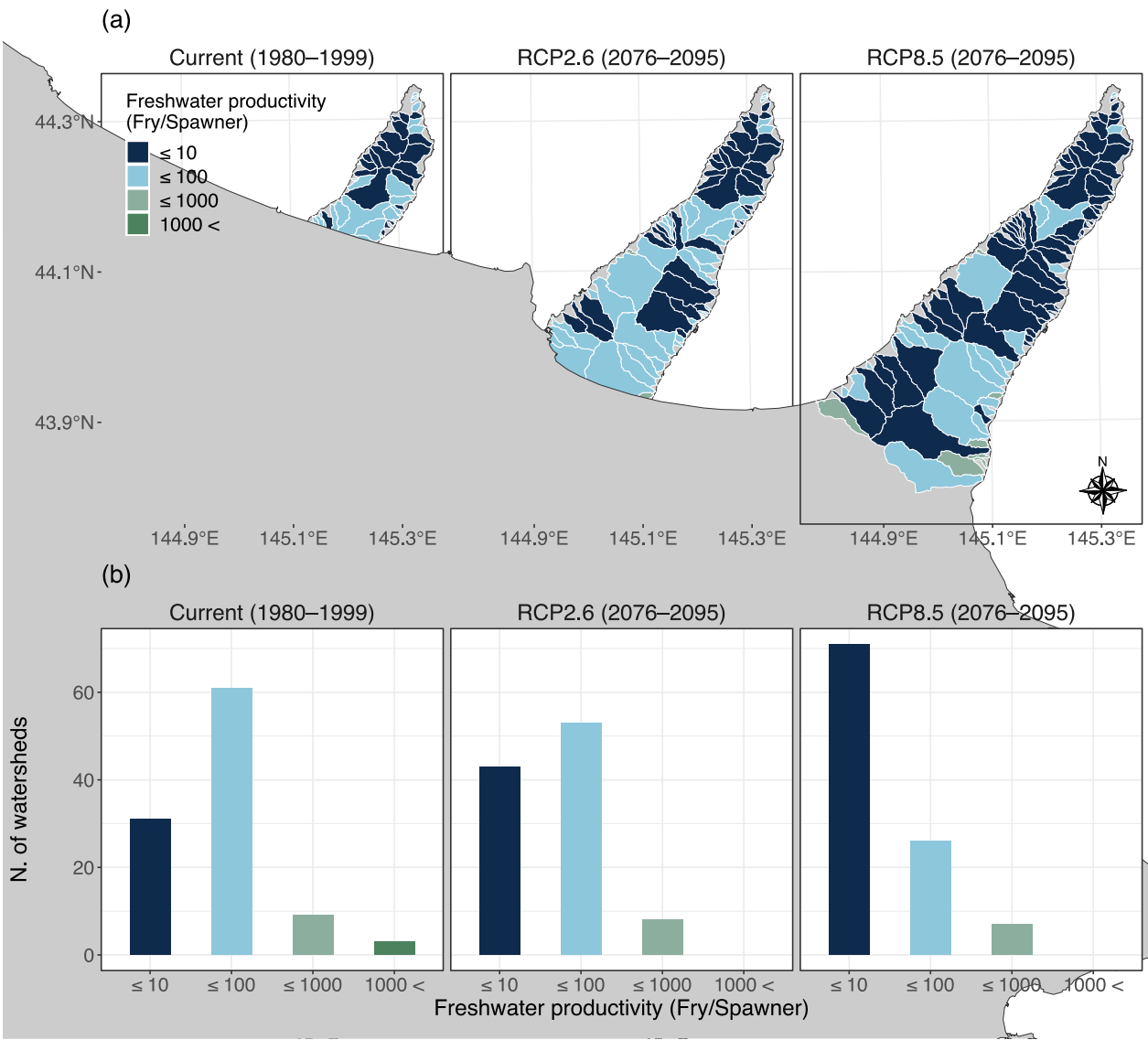
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684 **Figure 2.** Effects of the (a) average watershed slope and (b) stream power on freshwater
685 productivity at different levels of maximum daily precipitation. Coloured bars indicate the range
686 of values for estimated freshwater productivity. White circles denote each observation condition.

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690 **Figure 3.** (a) Current and future freshwater productivity of each watershed for pink salmon on the
691 Shiretoko Peninsula, Hokkaido, northern Japan. Predictions are shown for each condition (current
692 [1980–1999] and RCP2.6 and RCP8.5 [2076–2095]). (b) Number of watersheds per grade of
693 freshwater productivity predicted for each condition.