Watershed hydrogeomorphology drives freshwater productivity of anadromous salmonids: Implications for habitat conservation and restoration

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Abstract

Considering the spatial omnipresence of the threat to biodiversity and limited resources and time for conservation and restoration, it is crucial to prioritize conservation and restoration activities to maximize benefits. By transporting marine-derived nutrients to freshwater and surrounding ecosystems, anadromous salmonids contribute greatly to biodiversity maintenance; however, their abundance has been decreased by human activities in many regions. Salmon populations are mainly governed by their productivity in the freshwater life stage; therefore, freshwater productivity, namely, the number of juveniles migrating to the ocean per reproducing parent, should be investigated to maintain healthy populations. Given that productivity decreases dramatically in response to flooding, the flood disturbance intensity controlled by hydrogeomorphology at a watershed scale may strongly influence the freshwater productivity of salmonids. In this study, we evaluated the effect of watershed hydrogeomorphology on the productivity of pink salmon (*Oncorhynchus gorbuscha*). We surveyed the escapement and number of fry migrants of pink salmon and measured environmental factors, including the average watershed slope and stream power index, as parameters of hydrogeomorphology. The freshwater productivity of pink salmon differed among the streams investigated and was negatively affected by average watershed slope, stream power, and average watershed maximum daily precipitation. These results indicated that flood disturbance reduces the freshwater productivity of pink salmon and that salmon productivity in an individual stream can be predicted by watershed hydrogeomorphology. Our approach can be applied to other anadromous salmonids that have spawning behaviour similar to that of pink salmon, which bury eggs in gravel. Predicting highly productive habitats based on the present study can contribute to planning and prioritizing habitat conservation and restoration for anadromous salmonids.

1. INTRODUCTION

Biodiversity is threatened by anthropogenic activities across our planet (Barnosky et al., 2011; Cardinale et al., 2012; Dudgeon, 2019; Johnson et al., 2017; Reid et al., 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 (T. M. Brooks et al., 2006). While several reproductive statuses, such as productivity and recruitment, are often included in the index for prioritization (Cruz et al., 2015; Waples & Hendry, 2008), 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. They affect the abundance and distribution of other organisms and the structure of biological communities by transporting marine-derived nutrients to freshwater and terrestrial ecosystems as a resource subsidy (Field & Reynolds, 2011; Hocking & Reynolds, 2011; Yamada, Katahira, et al., 2022); therefore, they are often regarded as keystone species (Willson & Halupka, 1995). In addition, they are also important organisms providing ecosystem services (Holmlund & Hammer, 1999; Watz et al., 2022) as valuable fishery and recreational resources (Quinn, 2018). However, declines in anadromous salmonid abundance have been observed in various regions worldwide (Mills et al., 2013; Nicola et al., 2018; Ruckelshaus et al., 2002; Ward et al., 2015). The declines in anadromous salmonid abundance can be explained by several anthropogenic activities (Gillson et al., 2022; Thorstad et al., 2021). For example, the hatchery programs that have been conducted around the world for the conservation and enhancement of salmonids (Kitada, 2018, 2020; Laikre et al., 2010; Morita, Morita, et al., 2006; Morita, Saito, et al., 2006; Naish et al., 2007) negatively affect salmonid population persistence by decreasing fitness and reproductive success and increasing competition between fish of wild and hatchery origin (Araki et al., 2007; Christie et al., 2012; Ohlberger et al., 2022; O'Sullivan et al., 2020; Terui et al., in press; Willoughby & Christie, 2019). Moreover, the natural reproduction of anadromous salmonids has been hindered by habitat fragmentation (Hilborn, 2013; Limburg & Waldman, 2009; Nakamura & Komiyama, 2010; Watz et al., 2022). Therefore, conservation of wild populations and restoration of their habitats for reproduction are needed.

The lifetime productivity (adult offspring per parent) of anadromous salmonids, which utilize diverse habitats throughout their lifetime, is influenced mainly by population regulation during the freshwater life stage (Bradford, 1995; Morita et al., 2015). Therefore, freshwater productivity (the number of juveniles entering the ocean per reproducing parent) 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 (Anderson & Topping, 2018; Essington et al., 2000; Fukushima et al., 1998; Honkanen et al., 2019; Jensen & Johnsen, 1999; Manhard et al., 2017; Warkentin et al., 2022). In particular, flood disturbance causes high mortality in the egg to alvine stage by scouring redds (Carline & McCullough, 2003; Greene et al., 2005; Holtby & Healey, 1986; Milner et al., 2013; Montgomery et al., 1996; Seegrist & Gard, 1972; Thorne & Ames, 1987; Waples et al., 2008, 2009). Since flood disturbance is controlled by water and sediment discharge, hydrogeomorphic characteristics at a watershed scale (e.g., Aalto et al., 2006; Koskelo et al., 2018; Moore et al., 1991) may reflect the intensity of flood disturbance in a basin and therefore regulate the freshwater productivity of salmonids. However, few studies have examined the relationship between watershed hydrogeomorphic characteristics and salmonid productivity. If we can elucidate this relationship, we 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, we examined the relationship between the number of total escapes and emergent fry of the pink salmon *Oncorhynchus gorbuscha* and environmental factors at a watershed scale that potentially affect productivity in the Shiretoko Peninsula of Hokkaido, northern Japan, based on the hypothesis that watershed hydrogeomorphic characteristics drive the productivity of anadromous salmonids. Specifically, we predicted that watershed slope and stream power would negatively affect the 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, Katahira, et al., 2022). Our research findings can contribute to selecting streams and rivers where conservation and restoration efforts for pink salmon should be prioritized.

2. MATERIALS AND METHODS

2-1. Study site

We selected ten streams on the Shiretoko Peninsula as the study streams (Figure 1; Table 1). These streams have never been targeted for hatchery programs for pink salmon. However, in only one stream (Mosekarubetsu Stream), fry of chum salmon (*Oncorhynchus keta*) 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).

2-2. Estimation of total escapement

To estimate total spawners, we counted the number of 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. We walked upstream and counted all live pink salmon. The survey was conducted only when water visibility was good enough to see to the bottom. We determined the total number of spawners per stream using the area under the curve (AUC) estimation method (Bue et al., 1998; English et al., 1992). 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, 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 Stream, Osyorokko Stream, Shoji Stream, Kennnebetsu Stream, Funbe Stream, and Kanayama Stream) when there were 10 or more pink salmon in the section. We 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).

2-3. Estimation of the total number of fry migrants

In each stream, we 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, we collected pink salmon fry in each stream every week except for one survey, which was conducted at a four-day interval. 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; T. A. Johnston, 1997; Yamada, Urabe, et al., 2022), at a sampling point for 15 minutes at hourly intervals (Yamada, Urabe, et al., 2022). Since 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 (Kirillov et al., 2018; Neave, 1955), and its peak was found at approximately 20:00 in this study area (Yamada, Urabe, et al., 2022). 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. 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, we 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. 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 total number of migrants per hour (T) was estimated for each stream each day, D, as follows:

eq 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, Urabe et al. (2022). We also determined the total number of pink salmon fry during the sampling period per stream using the AUC estimation method (Bue et al., 1998; English et al., 1992). 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 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 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 (e.g., Aalto et al., 2006; Koskelo et al., 2018; Moore et al., 1991; Moore & Burch, 1986). 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, 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 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). 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. After that, 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 et al., 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 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 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 S1; 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). 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 (Essington et al., 2000; Fukushima et al., 1998). Since 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 (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). We 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.

2-5. Data analysis

Before the analysis, we 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. We 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 (R. Johnston et al., 2018). For each GLMM, the significance of the explanatory variables was evaluated using type II Wald chi-square tests ($P < 0.05$). 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 (M. E. Brooks et al., 2017) for GLMM fitting and "MuMIn" v. 1.47.1 (Bartoń, 2022) for marginal and conditional R^2 calculations.

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 2; Figure 2). However, maximum daily precipitation in the stream power index model was nonsignificant (Table 3). The other variables had no significant effects (Table 2; Table 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.

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. 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 et al., 1991; Moore & Burch, 1986). 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.

Although several studies have indicated that competition for suitable spawning habitat and temperature affect the freshwater productivity of anadromous salmonids (Essington et al., 2000; Fukushima et al., 1998; Honkanen et al., 2019; Manhard et al., 2017), no significant effects of these parameters on 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 & 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 our discussion.

Dams have been built worldwide (Belletti et al., 2020; Grill et al., 2019), 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 (Hilborn, 2013; Limburg & Waldman, 2009; Watz et al., 2022). Thus, habitat restoration, such as dam removal and modification, is needed to effectively recover salmon populations (Nakamura & Komiyama, 2010). However, given widespread fragmentation, these actions cannot be conducted haphazardly, and it is crucial to prioritize restoration activities. Our 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 our results, changes in slope after dam removal should be evaluated by hydraulic numerical simulation prior to restoration work.

Finally, our 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 (Arnell & Gosling, 2016; Milly et al., 2002). 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 stream 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 (Gende et al., 2002; Hocking & Reynolds, 2011; Schindler et al., 2003; Willson & Halupka, 1995), conservation and restoration of anadromous salmonids based on our results will probably lead to the maintenance or improvement of watershed biodiversity under a changing climate.

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TABLE

Table 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
Average stream slope (%)	29.81 ± 5.65	22.35–38.35
Average 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

Table 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 R^2; R2c, ConditionalR^2.

Variable	**Estimate**	**se**	p	**AIC**	**R2m**	**R2c**
Intercept	2.22	0.60	0.0002	325.7	0.478	0.597
Average 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 3 Results of the type II Wald chi-square tests for each model.

Variable	**$\chi 2$**	p
Average 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

FIGURE LEGENDS

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

Figure 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.