Title	Addressing the discrepancy between predicted and observed local extinction of Dolly Varden charr under global warming : the roles of local environments, seasonal timing, and interspecific competition
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Degree Grantor	北海道大学
Degree Name	博士(環境科学)
Dissertation Number	甲第16225号
Issue Date	2025-03-25
DOI	https://doi.org/10.14943/doctoral.k16225
Doc URL	https://hdl.handle.net/2115/95131
Type	doctoral thesis
File Information	UEMURA_Yohsuke.pdf

Addressing the discrepancy between predicted and observed local extinction of Dolly Varden charr under global warming: the roles of local environments, seasonal timing, and interspecific competition

（温暖化による局所絶滅予測と実際の絶滅とのギャップを説明する局所環境、影響する季節、および種間競争：サケ科魚類オショロコマにおける実証）

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A PhD dissertation submitted to the Division of Biosphere Science in the

Graduate School of Environmental Science, Hokkaido University, Japan

March 2025, Sapporo

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ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to my supervisor, Dr. Itsuro Koizumi, for his support during my transition from master's to PhD studies, his patience, and his engaging discussions. His kind support and encouragement enabled me to immerse myself in some of the most enjoyable field-based "power ecology" I have ever undertaken.

I would also like to express my gratitude to the members of my PhD defense committee members, Drs. Shin-ichiro Aiba, Koh Hasegawa, and Takashi Noda for their insightful comments and constructive feedback they have provided that has been pivotal in the development of my dissertation.

I am deeply grateful to Ryota Hasegawa and Yasuhiko Otsuki for their long-term assistance in the field, and to Misaki Endo, Chiharu Furusawa, Natsuki Hara, Wei Jia, Tomoaki Konno, Hironori Mieda, Kentaro Miura, Masahiro Naka, Kosuke Negoro, Hirotake Omiya, Junya Saito, Yuma Takeuchi, and Yuki Yoshino for their invaluable support. I would also like to express my gratitude to Hideo Sakai, who kindly lent me his holiday home for my research. Makoto Tanaka, the secretary of Koizumi laboratory, supported me with administrative procedures such as applying for permission to conduct surveys and reporting research expenses. Yoshinori Taniguchi, Yoichi Kawaguchi, Kiyoshi Kasugai, Takeaki Oiso, Kazutaka Shimoda, and Hirokazu Urabe kindly shared valuable data related to this PhD dissertation. Above all, I could not have completed this dissertation research without the enriching conversations I shared with them.

I would like to thank Daisuke Aoki, Christopher G. Ayer, Adam T. Clark, Hiroki Hata, Mikio Inoue, Hinako Katsushima, Hiroyuki Matsuyama, Kentaro Morita, Yusaku Ohkubo, Otso Ovaskainen, Suvi Sallinen, Hiroaki Sumikawa, Yuuki Shimamoto, Kanzi M. Tomita, Yoko Wada, and Taihei Yamada for their insightful comments. I am also

grateful to all members of the Koizumi Laboratory, Faculty of Environmental Earth Science, Hokkaido University, for their support.

Finally, my research during this PhD course would not have been possible without the constant support of my parents, Noriko and Hirofumi Uemura. I truly appreciate their support from afar. First and foremost, I am profoundly thankful to my beloved Mizuki Uemura for her unwavering support and encouragement, whose boundless optimism has continually inspired me. All these people are integral to the basis of my philosophy.

This study was supported by JSPS KAKENHI Grant Numbers JP22KJ0130 (to me, fully), JP2J12519 (to Hasegawa, R., partially), JP23K21335 (to Koizumi, I., partially), Grant-in-Aid for Scientific Research of Lake Akkeshi and Bekanbeushi Wetland 2023 (to me, fully), and Research Fund for the Ishikari and Tokachi River by the Ministry of Land, Infrastructure, Transport, and Tourism of Japan (to Koizumi, I., partially).

Note: I have arranged the people I thanked in alphabetical order by last name, then first name, categorizing them by the relationships I have with them.

SUMMARY

Global warming has increased the risk of local extinction, and many studies have been conducted to assess these extinction risks, primarily by predicting future distribution changes. However, to the best of my knowledge, there have been few studies that compare actual local extinction with predicted distributions and assess the reliability of the predictive models. Moreover, in one of the few empirical studies, the correlation between the predicted and actual distributions was low, and the prediction of distributional changes could not adequately explain the observed changes. The discrepancy was considered to result from the failure to take proximate factors affecting species distributions into account. In the general introduction of the present dissertation, I show the importance of three factors that have not been considered in previous studies: 1) local environments, 2) seasonal timing, and 3) interspecific competition, in predicting species distributions and local extinction. In this study, I investigate whether local extinction is occurring for local populations of Dolly Varden (*Salvelinus curilus*), an endangered species of salmonid fish, across Hokkaido, for which local extinction due to global warming was predicted 30 years ago. To address the discrepancy between the predictions and actual local extinction, if any, I first investigated the effects of local environments and interspecific competition on the distribution of Dolly Varden (chapter 2). Next, I constructed a new prediction model that considers the local environmental factors, the seasonal timing of their influence, and interspecific competition. By comparing the results with the original predictions, I assessed whether its predictive power had improved and how well the models could predict observed local extinction (chapter 3).

In chapter 2, I conducted an intensive summer survey at 27 local tributary sites along the mainstem of the Sorachi River system in Hokkaido to investigate the effects of

water temperature and interspecific competition with white-spotted charr (*S. leucomaenis*) on the distribution and abundance of Dolly Varden. By examining the relative importance of local physical environmental variables, I identified water temperature as the most important explanatory variable. Next, I examined the effects of water temperature, density of white-spotted charr, and the interaction between the two on Dolly Varden abundance. The results showed moderate to strong evidence that water temperature and the interaction with competitive species density had negative effects on the abundance. Furthermore, Dolly Varden density was higher in tributaries where white-spotted charr hardly invaded. These results are consistent with the results of previous experiments. At the same time, this emphasizes the need to consider not only summer water temperature, but also interactions with competitive species, when predicting the abundance of Dolly Varden.

In chapter 3, I revisited the 141 sites in Hokkaido where Dolly Varden had been previously observed over the last 20 years and clarified the extent of local extinction. The mean annual and summer air temperature had increased at least by 0.48°C and 0.86°C since the last survey, respectively. While the previous model based on mean annual air temperature predicted that only 3.55% of the population would be extirpated, 9.22% of the population was suggested to have been extirpated. The number of sites where white-spotted charr were found increased over the past 20 years, and the number of sites where Dolly Varden and white-spotted charr co-occurred more than doubled. To explain the discrepancy between the observed local extinction and the previous predictive model, I constructed new models that incorporates the effects of microclimates, season, and the competitive species. Specifically, I constructed 42 models that considered the following factors: mean annual air temperature with local variations, mean summer air temperature with and without local variations, groundwater temperature (mean annual, summer) with locational variations, and the effect of white-spotted charr or rainbow trout (*Oncorhynchus mykiss*). After integrating multiple predictive indices for each model, the best model included the mean summer air temperature without local variation and the effect of rainbow trout. Further analysis detected the effects of rising groundwater temperatures and the presence of rainbow trout on local extinction. These results showed that past predictions based on mean annual air temperatures underestimated local extinction, and that predictive performance can be improved by considering mean summer temperatures, local groundwater temperatures, and competitive species.

This dissertation is the first to demonstrate that local extinctions of Dolly Varden are occurring more frequently than previously predicted. It identifies rising groundwater temperature, impacts of increased summer air temperature, and intensified interspecific competition due to warming as potential causes of this discrepancy. The study summarizes the current status of the endangered Dolly Varden across Hokkaido and directly tests previous predictions of local extinctions caused by global warming. Notably, no prior research has systematically analyzed the factors explaining discrepancies between predictions and observed extinctions. Since no targeted conservation measures exist for Dolly Varden, this study significantly contributes to revising current extinction assessment criteria. Therefore, these findings establish a framework for identifying local extinctions caused by global warming, a threat expected to intensify in the future.

CHAPTER 1

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General introduction

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The rise in temperature due to climate change has progressed markedly in recent decades, and its effects are significantly accelerating the loss of biodiversity across entire ecosystems (Vitousek, 1994; Thomas et al., 2004; Malcolm et al., 2006; Harley, 2011; Mahecha et al., 2022; IPCC, 2022). When species are faced with rapid environmental change on an evolutionary timescale, they are unable to adapt immediately and instead attempt to respond to the change through dispersal and niche shifts (Sinervo et al., 2010; Jezkova et al., 2016). However, for species that are particularly dependent on narrow habitats and have limited mobility, such rapid environmental changes can lead to population declines and an increased risk of local extinction (Lambers, 2015; Wiens, 2016; Roman-Palacios & Wiens, 2020; Holzmann et al., 2023). In response, the United Nations Convention on Biological Diversity has set the goal of "30 by 30," aiming to protect and conserve at least 30% of the world's oceans and land by 2030 (Dinerstein et al., 2019; CBD, 2021). This initiative has made understanding how organisms have responded to, are responding to, or are likely to respond to climate change a key focus for biodiversity conservation (Michalak et al., 2020; Stralberg et al., 2020). Therefore, for ecologists, identifying changes in the distribution and abundance of organisms across multiple timescales (i.e., past, present, and future) is one of the most fundamental and important themes (Guisan & Thuiller, 2005; Elith & Leathwick, 2009; Wolkovich et al., 2014; Valavi et al., 2022).

One of the most widely used methods for assessing the risk of population extinction due to global warming is the prediction of distribution and abundance based on correlations with environmental factors (IUCN, 2010; Urban, 2015). Furthermore, the development and spread of software tools due to recent technological innovations has accelerated this trend, and the number of studies predicting species distributions in relation to global warming continues to increase (Zurell et al., 2023). Despite this importance, very few studies have validated the performance of these predictions by comparing them to actual changes (e.g. local extinctions; Uribe-Rivera et al., 2022; but see Poloczanska et al., 2013; Sofaer et al., 2018; Piirainen et al., 2023). However, local extinction has occurred over a timescale of several decades (e.g., Chen et al., 2011; Moritz et al., 2008; Lenoir & Svenning 2015; Holzmann et al., 2023), with rising temperatures identified as a contributing factor (Román-Palacios & Wiens 2020). Therefore, it is essential to compare past predictive models with actual extinction statuses and to accumulate empirical field data to determine whether discrepancies exist.

Surprisingly, in the few empirical studies of local extinction, predictions of distribution change could hardly explain the actual changes (Sofaer et al., 2018; Piirainen et al., 2023). The factors causing the discrepancy between the predicted and the observed local extinction are thought to be largely due to limitations imposed by environmental variables, such as the failure to consider proximate factors affecting species distribution (Sofaer et al., 2018). Given these issues, how can we bridge the gap between prediction models and actual extinctions? In other words, how can we improve the predictive power of these models? Below, I discuss the background and significance of factors that have generally been underconsidered in distribution predictions to date. Specifically, there are three factors: 1) local environment or microclimate, 2) seasonal timing of impact (i.e.

selecting the meaningful season as a variable), and 3) interspecific interaction (especially, competition).

The first factor is the influence of the local physical environment. Microclimate refers to the environmental conditions that affect spatial scales of a few to hundreds of meters in ecological contexts (e.g., Lembrechts et al., 2019; Stark & Fridley, 2022), whereas variables with slightly larger spatial scales are referred to as mesoclimate (cf. Descombes et al., 2020). The interactions between different spatial hierarchies of climate also influence the formation of species-habitat associations and species diversity (Pateman et al., 2016; König et al., 2024), making the effects of the local-physical environment crucial. However, many distribution prediction studies are based on models that correlate macroclimate with species distribution records (Stanton et al., 2012), and consideration of microclimate remains a frontier in the field (Zellweger et al., 2020). In fact, focusing on microclimate is not only realistic (Potter et al., 2013) but also improves the accuracy of predictions regarding the impacts on organisms (Maclean & Early, 2023). Microclimate can explain the existence of refugia, which cannot be recognized by macroclimate (Rull, 2009; Parducci et al., 2012; Stark & Fridley, 2022). Therefore, the alignment between the spatial resolution of species distribution and abiotic predictors is a key proximate factor in species distribution prediction (Lembrechts & Lenior, 2020).

The second factor is the selection of an appropriate season. Climate varies by season, and long-term impacts, such as the rate of temperature increase, may also differ across seasons (Cleland et al., 2012; Ernakovich et al., 2014). Since the life history strategies of many organisms vary with the seasons, it is possible that climate change will have beneficial results for fitness in some critical periods, but harmful results in others (Cordes et al., 2020). Also, animals often migrate in particular seasons, so their distributions may vary depending on the season (Baker, 1978). Therefore, it is reasonable to assume that climate factors conducive to distribution during a particular season are critical. Román-Palacios & Wiens (2020) used long-term monitoring data for plants, insects, and amphibians across 538 species in 581 locations (populations) in a vast region encompassing much of Europe. These authors examined the relationship between local extinction and changes in climatic factors. Surprisingly, the sites with the greatest increase in mean annual air temperature, the most widely used indicator in distribution predictions, did not always experience local extinctions. In contrast, the sites with the greatest increase in maximum annual air temperature (i.e., in the northern hemisphere, temperatures in the second half of the summer) did experience local extinctions. This suggests that, when predicting local extinction, selecting the appropriate season is crucial, as failing to do so may lead to misleading results.

The third factor is the interaction of interspecific relationships and climate change. Species interactions influence the response of individual species and, by extension, communities to climate change (Zarnetske et al., 2012; Singer et al., 2013). Many distribution predictions have modeled the response of single species to environmental variables in isolation, but this approach has been criticized as unrealistic and insufficient for accurate predictions (Wisz et al., 2013). In fact, until the early 2010s, interspecific relationships were not explicitly incorporated into species distribution models (Chen et al., 2011; Blois et al., 2013). Since then, the development of frameworks for simultaneously estimating the distributions of multiple species (e.g., Pollock et al., 2014; Warton et al., 2015; Ovaskainen et al., 2017) has led to a gradual increase in the number of models that account for such relationships. However, it remains unclear whether including interspecific relationships improves prediction accuracy (improved:

Harris, 2015; similar: Norberg et al., 2019; Caradima et al., 2019; Zurell et al., 2020). Furthermore, to the best of my knowledge, only one study has specifically examined whether considering interspecific relationships enhances the predictive power for actual extinctions (Piirainen et al., 2023). Thus, this study is a pioneering empirical investigation that considers the effects of interaction of competition and climate change.

The southern Asian Dolly Varden charr (*Salvelinus curilus*, Dolly Varden here after in this dissertation), a native salmonid species in Hokkaido, is an excellent model for examining the factors influencing local extinction and verifying discrepancies in distribution predictions due to climate change. Many populations of Dolly Varden in Hokkaido exhibit limited sea migration, with individuals typically completing their life history in freshwater (Fausch et al., 1994; Nakano et al., 1996; Kishi & Maekawa, 2003; but see Umatani et al., 2018). As such, Dolly Varden is a valuable model organism in freshwater habitats, where the direct impacts of global warming are understudied (Collen et al., 2014; Webb & Mindel, 2015; Comte & Olden, 2017; Barbarossa et al., 2021; Román-Palacios et al., 2022). Local extinction of Dolly Varden was predicted in earlier studies (Nakano et al., 1996), and there are concerns that these populations may face extinction at the national level (Ministry of the Environment, Japan, 2013). This concern is further supported by intensive surveys in areas where Dolly Varden is concentrated (e.g., Kishi & Maekawa, 2009), which have maintained this assessment by Ministry of the Environment, Japan for at least the past decade (Ministry of the Environment, Japan, 2020). However, the current population status across Hokkaido, its temporal trends, and the accuracy of past predictions remain unclear, making it imperative to assess the actual extent of local extinctions.

Hokkaido, where Dolly Varden is distributed, is characterized by a diverse topography and geology, creating a range of habitats across different spatial scales (Ministry of Land, Infrastructure, Transport and Tourism, Japan, 2010). This results in high spatial heterogeneity in both local climate and physical environment, making it possible to design surveys that consider both regional and local habitat variations. Additionally, the interspecific relationships, in particular interspecific competition between Dolly Varden and a native conger white-spotted charr (*S. leucomaenis*) have been the subject of rigorous experiments (Taniguchi & Nakano, 2000; Watz et al., 2019), providing strong empirical evidence to support hypotheses regarding the effects of global warming on species distribution and extinction risks. Therefore, empirical research on Dolly Varden, leveraging the unique ecological and environmental context of this species, will not only expand knowledge on native species but also contribute to addressing broader ecological questions and informing conservation strategies in the face of global warming.

In my doctoral dissertation, I used data collected through a field-based approach to develop a model of local extinction for the Dolly Varden (Figure 1-1). In chapter 2, I first examined the local environmental factors influencing the abundance of Dolly Varden. I assessed the relative importance of water temperature as a local environmental factor affecting the summer abundance of Dolly Varden in the Sorachi River system. I also explored the effects of water temperature, interspecific competition, and the interactions between them. Additionally, by comparing areas where the invasion of competitive white-spotted charr were restricted, I also showed the effect of competitive species density on Dolly Varden abundance. In chapter 3, I revisited 141 sites across Hokkaido where Dolly Varden had been previously recorded to investigate actual local extinction, comparing these with predictions made by earlier models to quantify the discrepancies between predicted and actual extinctions. I used this data to confirm the past predictions of extinctions caused by global warming. Specifically, I developed new prediction models that integrated the effects of climate change and competing species, including non-native species. I then tested whether this model improved the prediction accuracy of previous models. Additionally, using the same data, I examined the direct impacts of the local physical environments on the current local extinctions of Dolly Varden. I also investigated the indirect impacts of competing species and their direct impacts on extinctions. In chapter 4, I summarized the findings from earlier chapters, estimated the mechanisms behind the local extinctions of Dolly Varden, assessed the contribution of this study to extinction predictions, and proposed directions for future research.

FIGURE

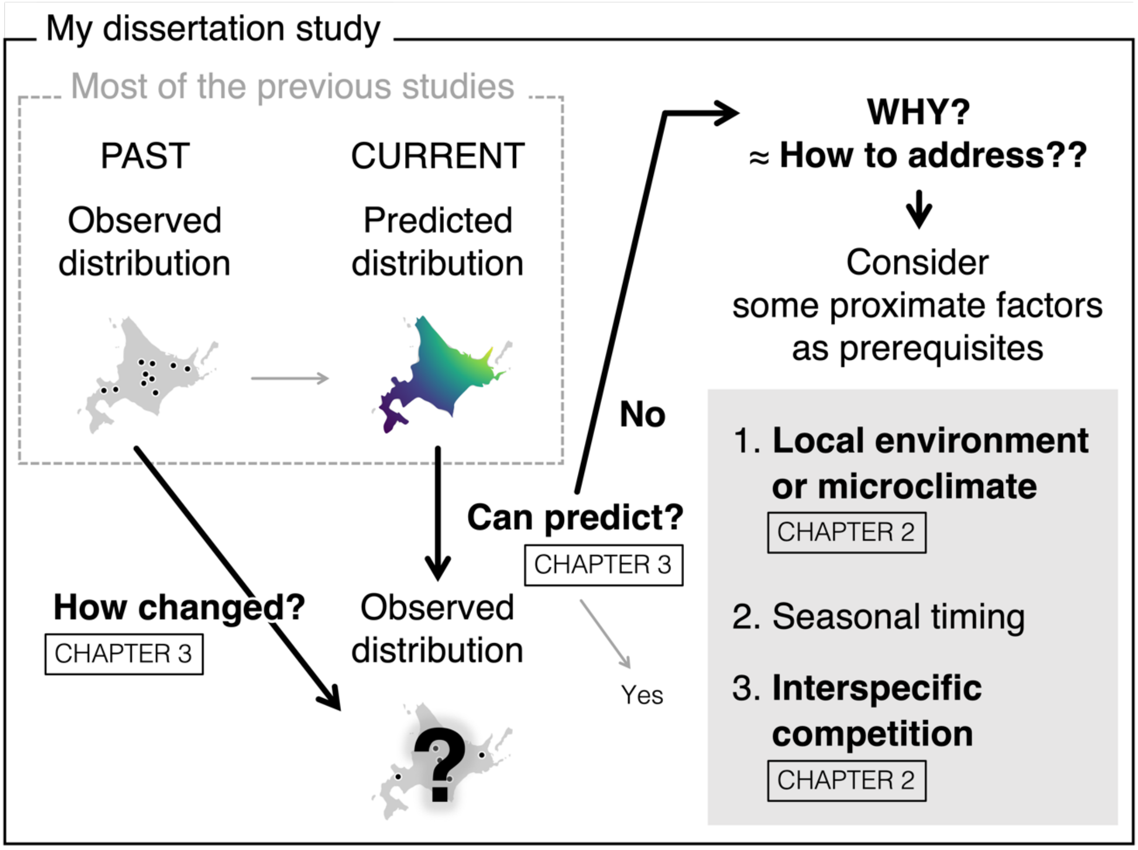

FIGURE 1-1 Conceptual diagram explaining the contents of chapters in my dissertation study.

CHAPTER 2

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Relative importance and the interaction with competitive species of local water temperature determining Dolly Varden: A field assessment

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Abstract

The rise in temperature caused by global warming influences species abundance both directly, through physiological changes, and indirectly, through species interactions. However, the previous approaches based on environmental gradients have limitations, including spatial autocorrelation and covarying variables. In this study, I evaluated the relative importance of water temperature among various local environment factors affecting Dolly Varden (*Salvelinus curilus*) abundance, employing a river-scape mosaic to avoid spatial autocorrelation. I also investigated the interaction between temperature and interspecific competition with white-spotted charr (*S. leucomaenis*), which had previously studied only by experiments. I evaluated the effects of interspecific competition by choosing areas where the invasion of the competitive species was limited. The result provides strong evidence that mean water temperature is the most significant local environment in predicting relative abundance of Dolly Varden, with a negative effect. Although the competitive species density alone did not have a significant effect, a negative impact was detected when its interaction with mean water temperature was considered. This study is the first to elucidate the relative importance of water temperature among local environments affecting Dolly Varden abundance in summer. These findings demonstrated the importance of both water temperature and the interaction with competitive species in understanding the distribution of Dolly Varden in the field.

INTRODUCTION

Rise in temperature induced by global warming has a direct physiological impact on species distribution (Deutsch et al., 2008; Alfonso et al., 2021). However, species distributions are also influenced by other environmental factors that change alongside rising temperatures or through different mechanisms (e.g., Buisson et al., 2008; Ashcroft et al., 2011; Morita et al., 2016). It is unrealistic to account for all these factors, as their relative importance varies across ecosystems. Thus, clarifying the relative contributions of these factors can provide a more plausible explanation for species distribution under global warming (Pöyry et al., 2009; Yamamoto et al., 2023).

Environmental factors can indirectly influence species distribution through interspecific interactions (Pearson & Dawson 2003; Tylianakis et al., 2008; Adler et al., 2009; Filazzola et al., 2020). These synergistic effects of global warming can accelerate the risk of extinction (Cahill et al., 2013). One mechanism for these indirect effects is condition-specific competition, where environmental factors such as temperature influence species' competitive abilities (e.g., Chesson, 1986; Danson & Travis, 1991; Taniguchi & Nakano, 2000; Chamberlain et al., 2014). Additionally, asymmetric effects on traits that govern interactions can ultimately affect species distributions (Dell et al., 2014). Empirical studies using environmental gradients revealed that the relative abundance of competing species varies along these gradients (e.g., Fausch et al., 1994; Choler et al., 2001; Hasegawa & Maekawa, 2008; Martin & Ghalambor, 2023).

The environmental gradient approach based on distribution-environment-correlation, however, has several limitations. First, as environmental conditions change in a unidirectional manner along a gradient, spatial autocorrelations can complicate analyses (Legendre, 1993; Record et al., 2013; Guélat & Kéry, 2018). This issue includes dispersal limitations, whereby a species may be unable to expand its distribution solely based on its own dispersal capabilities, rather than interspecific competition. Second, environmental gradients typically encompass multiple co-varying physicochemical factors, such as temperature and pH. Given that competing species may exhibit differential responses to these factors, this complicates the assessment of the strengths of interspecific competition attributable to each environmental factor (De Marco & Nóbrega, 2018). Third, changes in interspecific competition along gradients suggest condition-specific competition, but such observations are correlative, and the causal relationship cannot be clearly determined.

In contrast, competing species residing within environmental mosaics, rather than gradients, mitigate the first two concerns (Reif et al., 2018). In natural landscapes, distinct local habitats often emerge in a relatively stochastic manner, forming habitat mosaics. This spatial arrangement largely circumvents issues of spatial autocorrelation. Furthermore, as local habitats transition more rapidly to adjacent habitats compared to linear gradient, co-varying physiochemical factors would become more independent. The third issue can be addressed through manipulation experiments. Specifically, it is challenging to conduct such experiments on free-living organisms under natural conditions (Fausch et al., 2021). However, if a physical or biological invasion barrier exists, it may be possible to control interactions between contrasting species.

In this study, I investigated the relative importance of local environmental factors and the impact of a competing species, the white-spotted charr (*Salvelinus leucomaenis*, warm-water species), on the abundance of the endangered Dolly Varden (*S. curilus*, cold-water species) within a river landscape mosaic, using intensive field observations in contrasting habitats. The competition and coexistence mechanisms between Dolly Varden and white-spotted charr has been intensively investigated over the past five decades, encompassing distributional patterns (Ishigaki, 1969; Fausch et al., 1994; Morita, 2019), density compensation (Fausch et al., 1994), resource partitioning by behavioral (Nakano et al., 1999) and morphological changes (Nakano et al., 2020), to the inter-specific dominance hierarchies (Fausch et al., 2021), as well as condition-specific competition (Taniguchi & Nakano, 2000; Watz et al., 2019). This rich body of evidence has rendered this system a quintessential model for understating the mechanisms of interspecific competition (Begon et al., 2006; Kuwamura, 2017).

I first investigated the effects of water temperature on species relative abundance in small tributaries characterized by diverse field settings. The Sorachi River in central Hokkaido, Japan, comprises numerous small tributaries (mean stream width: ca. 1.0–3.0 m), some of which are spring-fed, whereas others derive from shallow ground water or precipitation runoff (Koizumi & Maekawa, 2004; Ishiyama et al., 2023). Consequently, during summer, water temperatures are cold in spring-fed tributaries compared to other non-spring-fed tributaries. Due to the region's volcanic geology and small geographic scale (< 50 km), spring-fed and non-spring-fed tributaries appear relatively randomly distributed along the mainstem, allowing us to consider each tributary as good replicates (i.e., minimal spatial autocorrelation). In addition, I measured a range of environmental variables that could potentially influence species interactions. Moreover, I selected two contrasting types of sites: one where the distribution of both species was not limited, and the other where one of the species was absent or present in low numbers due to physical barriers and/or local extinction, constituting a "natural experiment". The latter sites enable me to infer distributional patterns in the absence (or low abundance) of competitors. Previous studies have examined the vulnerability of Dolly Varden to water temperature (Nakano et al., 1996; Takami et al., 1997). Additionally, it has been shown that the negative effects of white-spotted charr are exacerbated at higher temperatures due to temperature-dependent competition (Taniguchi & Nakano, 2000; Watz et al., 2019). I also hypothesized that the density of Dolly Varden would be higher in the absence of white-spotted charr due to the release from competition. By integrating these findings with existing literature, I aim to elucidate the local environmental factors that affect the abundance of Dolly Varden in the wild, the effects of competitive species, and the interaction between the two.

METHODS

Study system

Dolly Varden in the Sorachi River system have been intensively studied over the past two decades (Koizumi & Maekawa, 2003; Koizumi & Shimatani, 2016). Because Dolly Varden spawn mostly in small tributaries but not in the mainstem due to their small size (ca. 100–200 mm), they form a metapopulation structure using each tributary as local habitat (Koizumi & Maekawa, 2004; Koizumi et al., 2006b, 2008; Koizumi, 2011). After hatching in tributaries, some individuals migrate to the mainstem for growth, mostly at the spring of age-1+, followed by return migration during the breeding season (Koizumi & Maekawa, 2003; Koizumi et al., 2006a; Ayer et al., 2018). While Dolly Varden can complete their entire life cycle within the tributaries, most females seasonally migrate to the mainstem (Koizumi et al., 2006a). White-spotted charr in this system exhibit a lacustrine, or lake migratory, life history: they spawn in the mainstem or lower reaches of large tributaries, followed by seasonal migration to the Kanayama reservoir for growth (Koizumi, I., unpublished data). Most females migrate to the reservoir, whereas some males remain in the mainstem or tributaries to mature. Many juvenile white-spotted charr (mostly age-0+, ca. 40–100 mm) migrate to non-natal small tributaries, the main habitat of Dolly Varden, for nursery or temporal refuge from floods (Koizumi & Maekawa, 2003; Koizumi et al., 2013). Although the spawning periods of the two species overlap (Koizumi, I., unpublished data), their spawning redds did not overlap (Uemura, Y., personal observation).

From over 100 tributaries in the Sorachi River system (Koizumi & Maekawa, 2003), I selected 27 based on factors such as temperature, location, stream size, physical barriers, and accessibility (Figure 2-1; Table S2-1). Specifically, I attempted to minimize spatial autocorrelation by selecting spring water (colder in summer) and non-spring water (warmer in summer) tributaries from various locations. In the previous experiments, temperature type (categorically high or low) has been considered as controlling factors for the interspecific competition between Dolly Varden and white-spotted charr (Taniguchi & Nakano, 2000; Watz et al., 2019), but unexpected local environmental factors may be also involved. Therefore, I measured potentially important environmental variables as comprehensively as possible (see “Environmental elements” in “METHODS”).

Within the 27 tributaries, I selected some atypical tributaries where one of the species was absent or present at low densities as contrasting habitats (Table S2-1). One type of contrasting habitat (contrasting site A) was spring-fed tributaries ($n = 3$) where Dolly Varden was absent or scarce due to potential local extinction or lack of spawning areas (Koizumi & Maekawa, 2004). In the contrasting site A, I could infer whether white-spotted charr avoid cold environment due to physiological constraints rather than interspecific competition (Taniguchi & Nakano, 2000; Twomey et al., 2008). Another contrasting habitat (contrasting site B) was non-spring-fed tributaries ($n = 5$) where white-spotted charr hardly invade due to physical barriers (natural barriers such as waterfalls) near the junction between tributaries and the mainstem. I measured these barriers and divided them into two clusters using a Gaussian mixture model, with boundaries defined by a slope > 10° or height > 50 cm (Figure S2-1). This analysis was conducted using functions *mclustBIC* and *densityMclust* in the R package *mclust* version 6.1.1 (Scrucca et al., 2023) in R version 4.4.1 (R Core Team, 2024). In these contrasting habitats, I could infer whether white-spotted charr reduce Dolly Varden density by comparing the contrasting site B to typical sites.

Fish abundance (density estimation)

Field surveys were conducted from 16 August 2020 to 6 September 2020 with permission from Hokkaido, Japan (permission ID: R02-242). Study sections (100–110 m from the confluence of each tributary) were established and blocked upstream and downstream using 5-mm-mesh seine nets. A backpack electrofisher (model 12-B, Smithroot Inc. Vancouver, Washington, USA) was used to collect fish, with all collections conducted by the same person. Fish population density ($n \cdot \mathrm{m}^{-2}$) was estimated using the 2-pass removal method (model M(b), a program CAPTURE, https://www.mbr-pwrc.usgs.gov/software/capture.html; Zippin, 1958). To minimize negative effects on fish and other aquatic animals, electrofisher settings were adjusted to DC, 200–300 V (Snyder, 2003). Over 30 minutes were allowed between passes to give uncaptured individuals time to recover. The fork length and body mass of each individual were measured to the nearest 1.0 mm and 0.1 g, respectively, after anesthesia (0.5 mL per 1.0 L of water; FA100, Bussan Animal Health Co., Ltd., Osaka, Japan). The age cohort (age 0+ and age ≥ 1+) of each fish was determined based on field observations and fork length distribution (Figure S2-2; cf. Koizumi et al., 2008). Each species was visually identified. All captured individuals were released after recovering from anesthesia at the point of capture.

I also estimated the relative abundance of juvenile (age-0+) white-spotted charr in the mainstem near each tributary to consider mass effects (i.e., more white-spotted charr migrate to tributaries when they are abundant in the mainstem). Fish were collected from confluences in the mainstem (census area: 2.0–2.5 m width × 100 m length, divided into 50 m upstream and downstream) using the electrofisher (1 pass, 300 V) for ca. 30

minutes by the same person. Each individual was anesthetized, measured, and released as the same protocol. The catch per unit effort ($n \cdot 30\ \mathrm{min}^{-1}$) of white-spotted charr in the mainstem was calculated (Table S2-2). All fish sampling followed the "Guidelines for the Use of Fishes in Research" established by the Ichthyological Society of Japan (https://www.fish-isj.jp/iin/nature/guideline/2003.html).

Environmental factors

To assess the relative importance of environmental factors in predicting fish abundance, I measured local environmental variables during the fish sampling period (Table S2-1). Transects for stream width measurement were spaced 10 m apart (0.5–2.0 times the mean stream width; cf. Grant et al., 1990; Simonson et al., 1994). Local water temperature was recorded continuously during the field period (logged hourly; HOBO UA-001, UA-002, U20L, Onset Computer Corporation, Bourne, MA, USA). As water temperature in this system did not vary significantly within a range of < 100 m (Koizumi, I., personal observation), loggers were placed centrally in each study area and shielded direct sunlight. I measured environmental variables, including stream width (cm), water depth (cm), dominant substrate type (bedrock, sand, gravel, pebbles, cobbles and boulders; cf. Wentworth 1922), cover materials area (m^2) and channel unit length (m) at each study site. Water depth and substrate type were measured at seven evenly spaced points across each transect. Substrate type was defined as the dominant substrate within a 20 cm × 20 cm quadrat at each point. Substrate roughness (mean value when considered as a rank variable) and heterogeneity (standard deviation) were calculated (Bain et al., 1985). I measured the area of woody debris, instream brush (area > 20 cm × 20 cm), undercut banks (area > 20 cm × 20 cm) and overhanging vegetation. Each study reach was divided into channel units (cascades, riffles, run and pools; cf. Kani, 1944; Hawkins et al., 1993), and the pool-riffle-sequence index (number of channel unit types within the study reach) was used as an index of channel unit complexity (Yamamoto et al., 2016). Flow velocity ($cm \cdot s^{-1}$) was measured three times at 60% of water depth at six evenly spaced points across each transect using a current meter (CR-11, f.k.a., Cosmo Riken Ltd., Osaka, Japan). Riverbed gradient between transects was measured using a laser rangefinder (TruPulse 200; Laser Tech Inc., CO, USA), while the height and slope of natural barriers near confluences (10 m from the confluence) were also measured. The elevation (m) of each confluence was determined using a digital topographic map (1:25,000; Geospatial Information Authority of Japan, GSI map: https://www.gsi.go.jp) and GPS measurements (6 decimal places) from the field survey.

Statistical analyses

Statistical significance for all analyses is presented in *p* value and the corresponding evidence strength is given in (Bland, 1986; Muff et al., 2022). All analyses were conducted using R version 4.4.1 (R Core Team, 2024).

Spatial autocorrelation of local water temperature

To examine the spatial autocorrelation of mean water temperature, I first converted the dataset into a spatial object using the *sf* package version 1.0.19 (Pebesma, 2018). Specifically, I used the *st_as_sf* function to transform the data frame into a spatial feature object, specifying the geographic coordinates (longitude and latitude) and assigning the coordinate reference system (CRS) as “EPSG:4326”. The spatial object was then converted into the *sp* format using the as function from the *sp* package version 2.1.4

(Bivand et al., 2013). Next, I constructed a spatial neighbors list based on the closest neighbors ($k = 1$) using the *knearneigh* function from the *spdep* package version 1.3.6 (Bivand et al., 2013). This function identifies the nearest neighbor for each observation in the dataset. The “neighbors” list was then transformed into a spatial neighbors list using the *knn2nb* function from *spdep* package. To quantify the spatial relationships, I created a row-standardized spatial weights matrix (style = “W”) using the *nb2listw* function from the *spdep*. This matrix was used to weight the spatial dependencies between observations during the analysis. Finally, I computed Moran’s *I* statistic for spatial autocorrelation using the *moran.test* function from *spdep*. The *moran.test* function calculates Moran’s *I* index, testing the null hypothesis of spatial randomness, using the spatial weights matrix as input. The resulting Moran’s *I* value, and its associated *p* value were used to assess the degree of spatial autocorrelation in the mean water temperature.

Local environments predicting relative abundance of Dolly Varden

I first investigated the relative abundance of both species in the tributaries, particularly focusing on water temperature. I constructed a generalized linear model (GLM, hereafter) with a logit link and binomial error distribution for 19 typical (non-contrasting habitats) tributaries. The response variable was the proportion of Dolly Varden relative to the total number of charr (Dolly Varden + white-spotted charr). Explanatory variables included mean water temperature (measured one week before and after the survey), mean tributary width, mean water depth, substrate roughness, substrate heterogeneity, mean current velocity, pool-riffle-sequence index, cover area, elevation, and catch per unit effort of age-0 white-spotted charr in the mainstem. All environmental variables were *Z*-score transformed to a mean of 0 and variance of 1. The model was constructed with the function *glm* in a default R package *stats* version 4.4.1. Multicollinearity among variables was checked using the function *check_collinearity* in the package *performance* version 0.11.0 (Lüdecke et al., 2021), based on the variance inflation factor. Overdispersion was also checked by the function *check_overdispersion* from the same package. Although the variance inflation factor was acceptable for model evaluation (Vittinghoff et al., 2012), overdispersion was detected. Therefore, the model was modulated using the *glm.binomial.disp* function in the package *dispmod* ver. 1.2 (Scrucca, 2018). I then performed model selection to check the relative importance of the explanatory variables by permutation, using the *dredge* function in the R package *MuMIn* version 1.48.4 (Bartoń, 2024). I sorted the models in order of decreasing AICc (conditional AIC) because of the small sample size (Bolker, 2008). All models with ΔAICc < 2 (Burnham & Anderson, 2002) and < 4 were considered to have good or moderate predictive power, and Akaike weights were calculated. Finally, to evaluate the importance of the selected variables in the different models, I performed model averaging using the *model.avg* function in the R package *MuMIn* version 1.48.4 (Bartoń, 2024) on the full model and the model selected by AICc (i.e., conditional model) and calculated the coefficient estimate (i.e., effect size) and statistical significance of the variables.

Interactive effect between water temperature and competitive species

I then analyzed the effects of water temperature, density of white-spotted charr, and the interaction between the two on the abundance of Dolly Varden to clarify temperature-dependent competition. I constructed a generalized linear model with a log link and negative binomial error distribution for 19 typical (non-contrasting habitats) tributaries. The response variable was the abundance of Dolly Varden. Explanatory variables included mean water temperature, density of white-spotted charr, and the interaction between mean water temperature and density of white-spotted charr, and log-transformed reach area as offset term. Mean water temperature was *Z*-score transformed to a mean of 0 and variance of 1 to prevent the collinearity of interactions that arise from differences in the numerical scale between two variables. The model was constructed with the function *glm.nb* in a default R package *MASS* version 7.3.60.2. No multicollinearity among variables was detected using the function *check_collinearity* in the package *performance* version 0.11.0 (Lüdecke et al., 2021), based on the variance inflation factor. Also, no overdispersion was detected by the function *check_overdispersion* from the same package. Conversely, the effects of water temperature, Dolly Varden density, and the interaction between the two on white-spotted charr abundance were also examined in the same manner.

Fish density in contrasting sites

To investigate the effects of temperature and white-spotted charr density on subordinate Dolly Varden, I performed an analysis of covariance (ANCOVA, hereafter) with $\log_{10}$-transformed density as the response variable, habitat type (typical sites vs. contrasting sites) as the explanatory variable, and mean water temperature as the covariate. If cold environments are stressful for white-spotted charr, a positive effect of temperature on density would be expected. I also predicted that habitat type would not affect white-spotted charr density, as they dominate over Dolly Varden (Taniguchi & Nakano, 2000; Watz et al., 2019) and should therefore not be impacted by their presence. In addition, I performed a similar ANCOVA for Dolly Varden density to examine whether the presence of white-spotted charr decreases Dolly Varden density and whether temperature negatively affects their density. In these ANCOVA, when no white-spotted charr or Dolly Varden was captured, the density ($n \cdot \mathrm{m}^{-2}$) was set to 0.001 to avoid error in log-scaling. The default *lm* function in a default R package *stats* version 4.4.1 was used for the ANCOVA.

RESULTS

I collected 2,166 Dolly Varden, and 857 white-spotted charr in this study (Table S2-2). In addition to these species, Sakhalin taimen (*Parahucho perryi*), freshwater sculpin (*Cottus nozawae*), stone loach (*Barbatula oreas*) and brook lamprey (*Lethenteron* sp.) were also caught (data not shown). In the 27 sites I investigated this time, there was no evidence of spatial autocorrelation in the mean water temperature in summer (Moran's *I* statistic standard deviate = −0.014, *p* = 0.51). Among the 10 environmental variables, mean water temperature was consistently selected in the top 10 models with the ΔAICc < 4.0 for the relative abundance of Dolly Varden (Table S2-3). In the full model, mean water temperature was selected as significant variables, whereas in the conditional model, both mean water temperature and white-spotted charr abundance were selected as significant variables (Table 2-1). As predicted, the relative abundance of Dolly Varden decreased with increasing water temperature (*p* = 0.000098). Predicted regression lines fitted to the GLM showed that charr ratio reversed at 10.85°C (Dolly Varden ratio = white-spotted charr ratio = 0.50), with the ratio rapidly decreasing from 67.49% to 32.60% as temperature from 9.85°C to 11.85°C (Figure 2-2).

There was strong evidence that mean water temperature had a negative effect on Dolly Varden abundance (offset by reach area) alone (*p* = 0.000087, AIC = 227.60; Figure 2-3a). There was no evidence that white-spotted charr density alone had an effect on Dolly Varden abundance (*p* = 0.25, AIC = 233.31; Figure 2-3b). When both water temperature and white-spotted charr density were used as explanatory variables, only the former was significant (*p* for mean water temperature = 0.00012, *p* for white-spotted charr density = 0.97, AIC = 229.60; Figure 2-3c). However, when the interaction between the two was added to the full model, there was moderate evidence that the abundance of Dolly

Varden decreased as both increased (*p* for mean water temperature = 0.0000014, *p* for white-spotted charr density = 0.51, *p* for interaction = 0.040, AIC = 228.78; Figure 2-3d).

On the other hand, contrary to expectations, there was no evidence that mean water temperature had a significant effect on the abundance of white-spotted charr (offset by reach area; *p* = 0.43, AIC = 175.40; Figure 2-4a). However, contrary to expectations, there was also moderate evidence that Dolly Varden density had a negative effect on white-spotted charr abundance, either alone (*p* = 0.010, AIC = 172.52; Figure 2-4b) or in a model with water temperature added (*p* for mean water temperature = 0.90, *p* for Dolly Varden density = 0.017, AIC = 174.50; Figure 2-4c). Furthermore, in the full model with the interaction between the two factors, there was no evidence that the interaction had an effect (*p* for mean water temperature = 0.85, *p* for Dolly Varden density = 0.027, *p* for interaction = 0.90, AIC = 176.49; Figure 2-4d)

Furthermore, in the comparison between contrasting sites, there was strong evidence that Dolly Varden density decreased with increasing mean temperature (*p* = 0.00010; Figure 2-5a), and weak evidence that density was higher when white-spotted charr were absent or in low numbers (*p* = 0.069; Figure 2-5a). On the other hand, there was no evidence that mean water temperature had a significant effect on white-spotted charr density (*p* = 0.46; Figure 2-5b), but there was a significant effect of habitat type, with moderate to strong evidence that white-spotted charr density was higher in contrasting sites where Dolly Varden were absent or scarce (*p* = 0.0030; Figure 2-5b).

DISCUSSION

The relative abundance of Dolly Varden, as compared to white-spotted charr, in the small tributaries of the Sorachi River was strongly influenced by local water temperature. This temperature effect was notable, as the proportion of the two species shifted rapidly within a narrow range (ca. 9–11°C; Figure 2-2), while other environmental factors were not significant or had weak to moderate evidence of the significance (Table 2-1). The spatial autocorrelation effect of water temperature was not significant, given the small geographic scale and diverse tributaries' locations. This temperature dependency is consistent with previous studies conducted within single streams or across altitudinal and latitudinal gradients (Fausch et al., 1994). My study, focused on a thermal mosaic within a single watershed (i.e., at meso-scale), provides additional evidence of the consistent effects of water temperature on the coexistence of these competing salmonids.

In fish, as in many other organisms, a species distribution range is often more constrained by the water temperature range than by other physiological limits (Hutchinson, 1961; Eaton et al., 1995). In the study area, the minimum and maximum water temperatures at each site ranged from 6.47–10.75°C and 8.58–17.28°C, respectively. It is difficult to explain the niche of both species in this ecosystem solely in terms of their physiological limits (e.g., mortality), since previous studies have shown that Dolly Varden experience sublethal effects only at temperatures above 20°C (Takami et al., 1997). The effect of water temperature may increase energy expenditure through behavioral changes. Salmonids, including Dolly Varden, engage in interference competition. At higher temperatures, they also increase their behavioral frequency, as shown in studies by Sakakura & Tsukamoto (1997) and Biro et al. (2010). In salmonid species, a social dominance hierarchy based on body size often develops (Fausch et al., 2021). Higher temperatures therefore could lead to increased interference behavior by larger individuals, potentially excluding smaller ones. In this water system, Dolly Varden undergoes partial migration after reaching one year of age (Koizumi et al., 2006). This results in a size-structured population in the tributaries during the summer (Figure S2-2). As a result, increased intraspecific competition may reduce the abundance of juvenile Dolly Varden, particularly the smaller individuals. On the other hand, Dolly Varden's ability to swim continuously decreases at higher temperatures (Yamada et al., 2020). Decreased swimming ability increases the risk of predation (Zaret & Suffern, 1976; Lingle & Pellis, 2002). Therefore, Dolly Varden, especially juveniles, may avoid settling in high-temperature waters where the survival cost outweighs the growth benefits.

The abundance of Dolly Varden was not explained by the density of white-spotted charr alone but was better explained by the interaction with temperature (Figure 2-3d). Watz et al. (2019) found moderate evidence that, similar to the present study, the specific growth rate of Dolly Varden is affected by the interaction between water temperature and the presence or absence of white-spotted charr, based on enclosure experiments in the Sorachi River system. However, these authors also detected a stronger negative effect from the competitive white-spotted charr alone (Table 1 in Watz et al., 2019). This weakens the interpretation of temperature-dependent competition (i.e., simple interspecific competition), though it may be due to the limited space in the enclosures, which prevented escape from interspecific competition. To address the contrasting life histories of the two species, I conducted a snapshot survey in August, focusing on the abundance that would reflect the consequences of interspecific competition mediated by the interference of Dolly Varden in the tributaries and white-spotted charr in the mainstem. Therefore, the abundance of both charr species can be interpreted as the result of dominant individuals invading and subordinate individuals moving due to temperature-dependent competition.

One novel focus of this study was the inclusion of contrasting sites where one of the competing species was absent or present in low numbers. There was weak evidence that density of Dolly Varden was higher when white-spotted charr was scarce. For Dolly Varden, the population growth patterns in habitats less favorable for the dominant species suggest ecological release (Robertson, 1996; Kunte, 2008). This observation aligns with the previous findings showing the importance of interspecific competition in the juvenile charr populations (Taniguchi & Nakano, 2000; Watz et al., 2019). This supports the hypothesis that the competitively dominant white-spotted charr reduces the population size of Dolly Varden. The other contrasting site A, on the other hand, rejected my hypothesis: density of white-spotted charr did not decrease with declining water temperatures. This means that juvenile white-spotted charr immigrated even to cold, spring-fed tributaries, previously unsuitable or stressful due to low temperatures (e.g., Taniguchi & Nakano, 2000). Furthermore, white-spotted charr density was notably high in cold tributaries when Dolly Varden was absent. These findings are consistent with those from the sympatric sites (Figure 2-5b, Table S2-1) and suggested that Dolly Varden, despite being competitively subordinate, limited the density of white-spotted charr regardless of water temperature.

This research not only identifies factors determining the distribution of Dolly Varden but also provides insight into the long-standing question of why white-spotted charr avoid cold water. Dolly Varden is highly dependent on cold water in summer, and their populations decline as temperatures rise, even in the absence of competitors. Consequently, Dolly Varden densities are high in tributaries with cold spring-fed water, where 1.5–4.0 juveniles per square meter are commonly observed. In contrast, white-spotted charr move from the mainstem to tributaries, either as a temporary refuge or during the juvenile stage (Uemura, Y. & Koizumi, I., personal observation). While the mainstem is generally more productive than the tributaries, it also poses higher risks (e.g., energy consumption and death due to the movement; Koizumi et al., 2006a; Tsuboi et al., 2020). Given that the tributaries in this study are of similar size, white-spotted charr likely select tributaries with more food resources. In cold tributaries with high Dolly Varden densities, food resources are expected to be limited even in summer, and the rate of resource consumption is high (Kawaguchi & Nakano, 2001). The energy cost of interference behavior is predicted to increase with the density of resident Dolly Varden (Matte et al., 2021). Furthermore, this may lead to relative importance of exploitative competition, even though white-spotted charr generally dominant in interference competition (Taniguchi & Nakano, 2000; Watz et al., 2019). As a result, white-spotted charr avoid entering cold tributaries, and local coexistence based on temperature may occur in summer (Uemura et al., under review). This helps explain why the competitively dominant species does not always drive out the subdominant species, even in habitats with low stress (e.g., Twomey et al., 2008). Figueiredo & Connolly (2012) demonstrated using a mathematical model that competitive dominance and dispersal asymmetry play major roles in species coexistence. When these findings are applied to this system, several factors align, including interspecific dominance, dispersal asymmetry, and dispersal limitation (from the mainstem to the tributary). These life history differences may partially explain the extensive local and regional coexistence of these two species in Hokkaido (Fausch et al., 1994). Importantly, this coexistence is only feasible when Dolly Varden has already colonized, and the local environment is highly heterogeneous.

Considering the biological interactions between species that share overlapping habitats, such as Dolly Varden and white-spotted charr, is crucial for accurately predicting species distributions under climate change (Wenger et al., 2011; Muhlfeld et al., 2024). As river water temperatures rise due to global warming (e.g., Eaton & Scheller, 1996; Kaushal et al., 2010), the availability of suitable habitats for cold-water species, including Dolly Varden, is expected to decline. In addition, temperature-dependent competition, rather than the mere abundance of competitive species, may further reduce the population of Dolly Varden, potentially leading to their extinction. Predictions of regional Dolly Varden extinction under climate change, such as those proposed by Nakano et al. (1996), highlight a common limitation: many models rely solely on single-species analyses that consider only environmental factors. However, such models often fail to account for the complex interplay of biotic and abiotic factors. As Wisz et al. (2013) suggest, predictions based solely on these simplified approaches are insufficient when attempting to model the effects of global warming on species distributions. This study demonstrates the importance of first identifying key environmental factors and then incorporating interspecific competition and their interactions (Heinle et al., 2021; Bommersbach et al., 2024). By adopting this integrative approach, predictions of species distributions in riverine ecosystems under climate change can be made with greater accuracy and ecological relevance.

FIGURES AND TABLE

TABLE 2-1. Results of model averaging for full models and conditional models (ΔAICc < 4.00). Asterisks for each variable indicate moderate to strong evidence against the null hypothesis.

Full model average						
Variable	Estimate	Standard error	Adjusted standard error	Z-value	p (> | Z |)	Significance
(Intercept)	1.01	0.31	0.33	3.06	0.0022	**
Catch per unit effort of age-0+ white-spotted charr	−0.67	0.34	0.36	1.86	0.064	
Water temperature mean	−1.60	0.38	0.41	3.86	0.00011	***
Elevation	0.063	0.20	0.20	0.31	0.76	
Substrate heterogeneity	0.028	0.14	0.15	0.20	0.85	
Stream width mean	−0.014	0.10	0.10	0.14	0.89	
Pool-riffle-sequence index	0.015	0.10	0.11	0.13	0.89	
Substrate roughness	−0.0080	0.086	0.092	0.086	0.93	
Cover area total	−0.0076	0.089	0.10	0.079	0.94	
Water depth mean	−0.0079	0.094	0.10	0.078	0.94	
Flow velocity mean	0.0030	0.087	0.095	0.031	0.97	
Conditional model average						
Variable	Estimate	Standard error	Adjusted standard error	Z-value	p (> | Z |)	Significance
(Intercept)	1.01	0.31	0.33	3.1	0.0022	**
Catch per unit effort of age-0+ white-spotted charr	−0.71	0.30	0.32	2.20	0.028	*
Water temperature mean	−1.60	0.38	0.41	3.86	0.000113	***
Elevation	0.43	0.33	0.36	1.21	0.23	
Substrate heterogeneity	0.31	0.35	0.38	0.82	0.41	
Stream width mean	−0.19	0.31	0.33	0.57	0.57	
Pool-riffle-sequence index	0.20	0.33	0.36	0.57	0.57	
Substrate roughness	−0.12	0.32	0.34	0.36	0.72	
Cover area total	−0.12	0.34	0.36	0.33	0.74	
Water depth mean	−0.13	0.35	0.38	0.33	0.74	
Flow velocity mean	0.050	0.35	0.38	0.13	0.90	

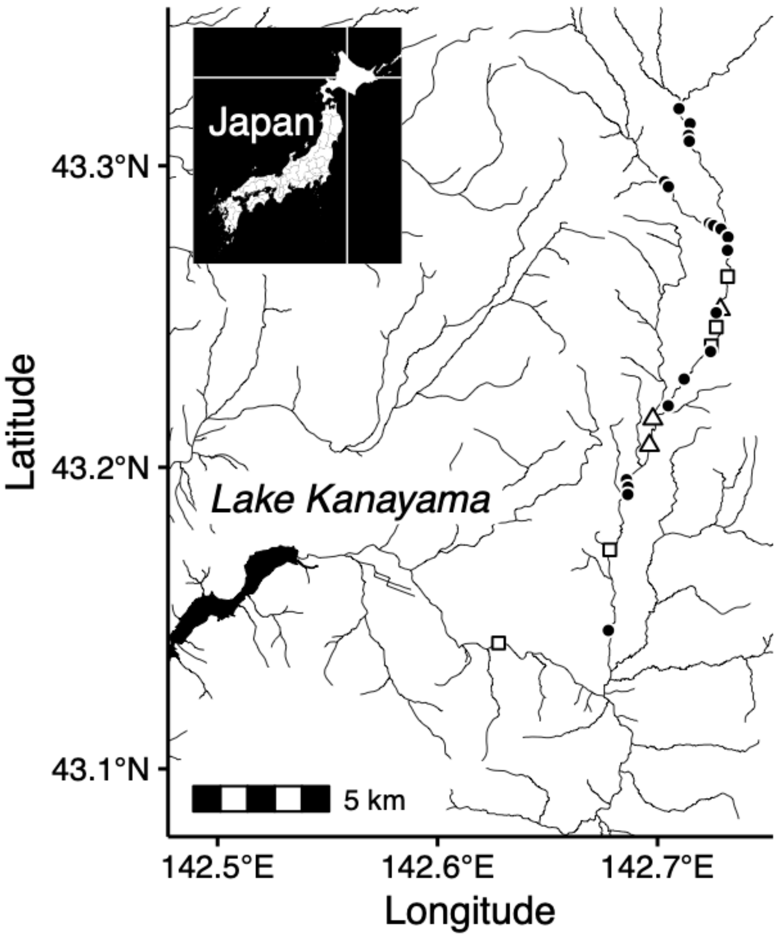


FIGURE 2-1 Map of the studied tributaries in the upper Sorachi River, central Hokkaido, Japan (inset). Black closed circles (●) represent typical tributaries, open triangles (△) indicate tributaries with few Dolly Varden (contrasting site A), and open squares (□) represent tributaries with natural barriers at confluences that obstruct the invasion of white-spotted charr (contrasting site B).

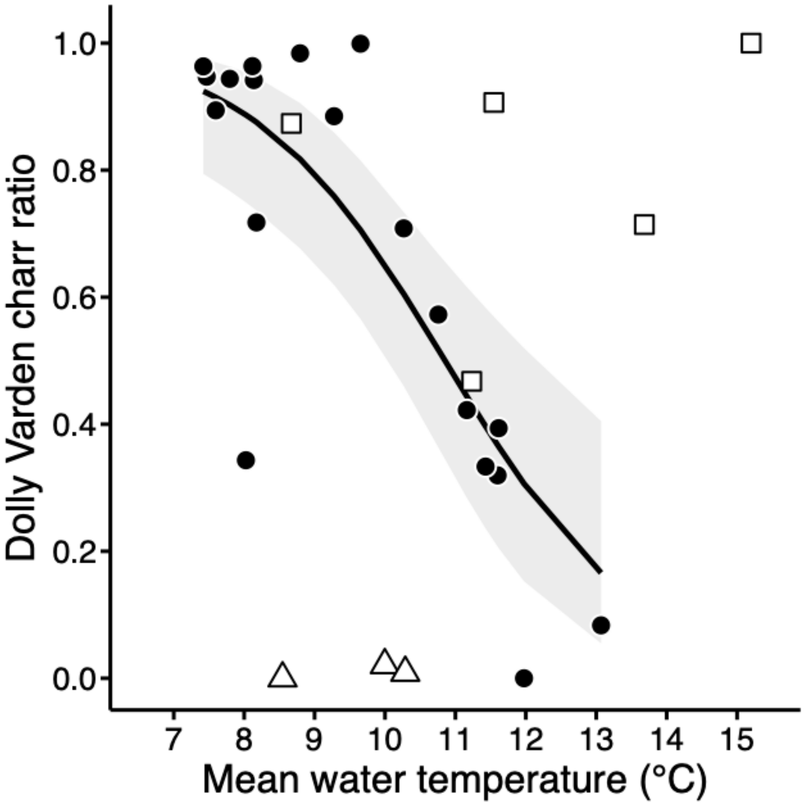
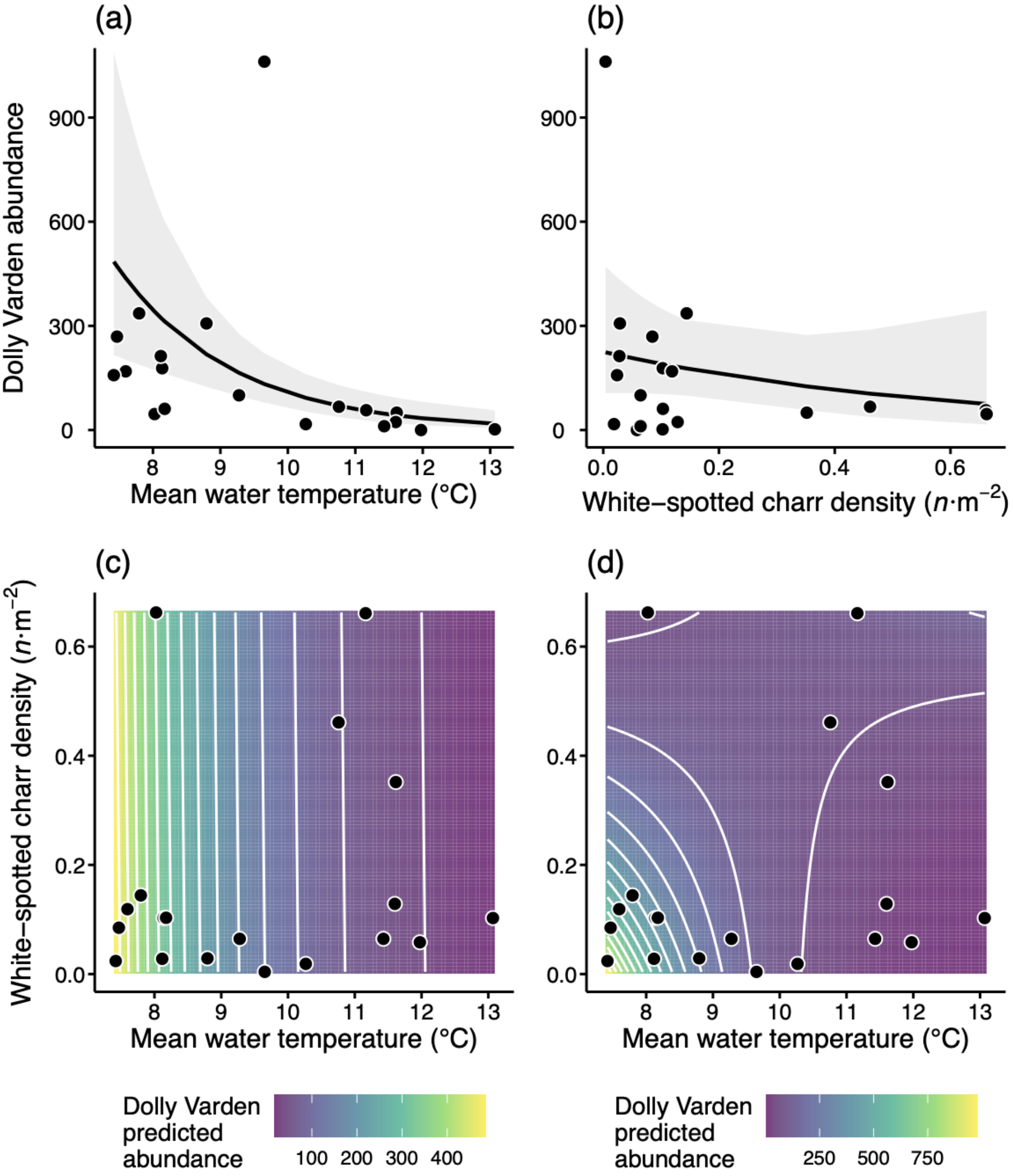


FIGURE 2-2 Relationship between mean water temperatures (°C) and the proportion of Dolly Varden in the tributaries, represented by a logistic curve (*n* = 19 typical sites, generalized linear model, family = “binomial”, link function = logit). The mean water temperature and the Dolly Varden ratio are negatively correlated (*p* = 0.000098). A 95% confidence interval is shown as a gray ribbon. Black closed circles (●) represent typical tributaries, open triangles (△) indicate tributaries with few Dolly Varden (contrasting site A), and open squares (□) indicate tributaries with natural barriers at confluences that obstruct white-spotted charr invasion (contrasting site B).



776

777 **FIGURE 2-3** The predicted abundance of Dolly Varden offset by the survey area, in

778 relation to the variables that explain it. (a) Mean water temperature (p = 0.000087), (b)

779 density of white-spotted charr (p = 0.25), (c) the combination of the two variables (p for

780 mean water temperature = 0.00012, p for white-spotted charr density = 0.97), and (d) plus

781 the interaction between water temperature and white-spotted charr density (p for

782 interaction = 0.040).

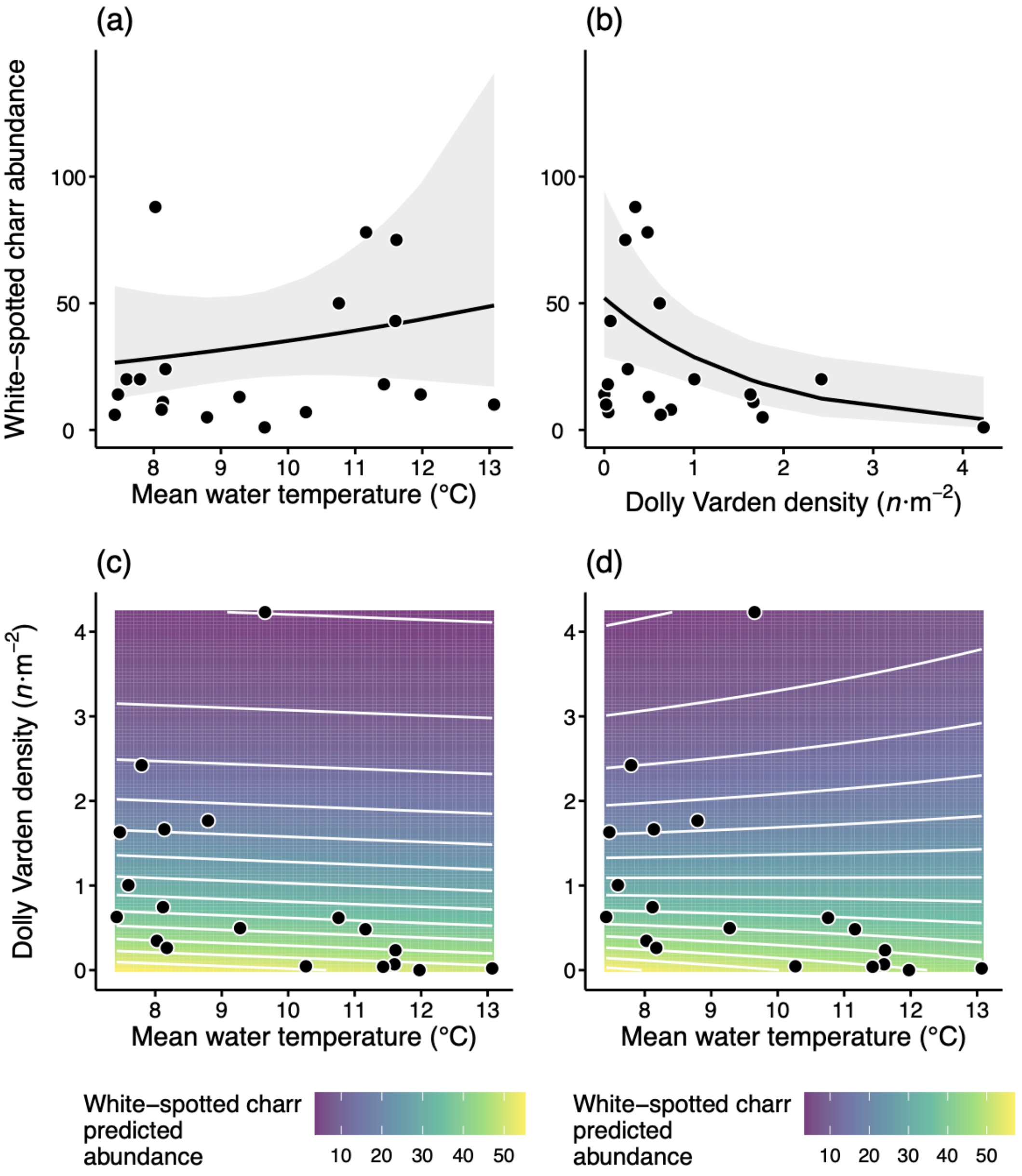


FIGURE 2-4 The predicted abundance of white-spotted charr offset by the survey area, in relation to the variables that explain it. (a) Mean water temperature ($p = 0.43$), (b) density of Dolly Varden ($p = 0.010$), (c) the combination of the two (p for mean water temperature = 0.90, p for Dolly Varden density = 0.017), and (d) plus the interaction between water temperature and Dolly Varden density (p for interaction = 0.90).

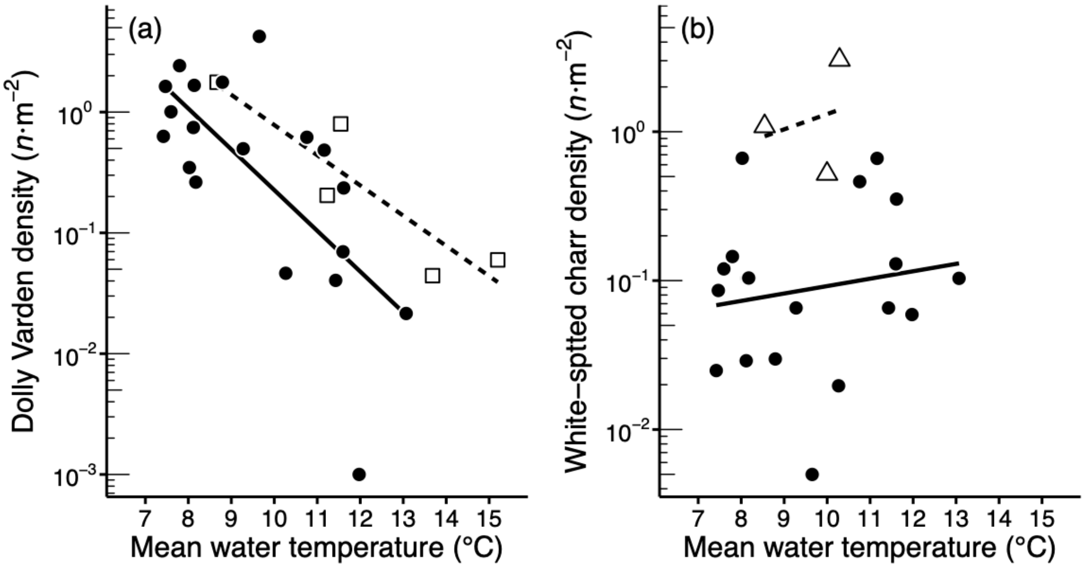


FIGURE 2-5 The effects of the habitat types on the density of Dolly Varden and white-spotted char. Black closed circles (●) represent typical tributaries, open triangles (△) indicate tributaries with few Dolly Varden (contrasting site A), and open squares (□) indicate tributaries with natural barriers at confluences (contrasting site B). (a) The effect of the habitat type on the density of Dolly Varden (n = 24). Solid lines represent linear regression for typical sites, and dashed lines for contrasting sites B. Density is marginally higher at the contrasting site (p = 0.069), with a significant negative relationship with mean water temperature (p = 0.00010). (b) The effect of habitat type on the density of white-spotted charr (n = 22). Solid lines represent linear regression for typical sites and dashed lines for contrasting sites A. Density is significantly higher at the contrasting site (p = 0.0030), with no significant relationship with mean water temperature (p = 0.46). All lines were fitted using analysis of covariance (ANCOVA).

SUPPLEMENTARY FILES

TABLE S2-1. Environmental elements measured or calculated at each tributary.

Tributary ID	Measuring date	Study reach (m)	Stream width mean (cm)	Stream width sd (cm)	Water depth mean (cm)	Water depth sd (cm)	Water temperature mean (°C)	Water temperature sd (°C)	Bedrock rate	Sand rate	Gravel rate	Pebble rate	Cobble rate	Boulder rate	Waterweed rate	Litter rate	Substrate roughness	Substrate heterogeneity	Woody debris underwater (m^2)	Woody debris overhanging (m^2)
T4	16-Aug-2020	100	105.36	38.22	8.19	4.16	10.76	0.91	0.00	0.34	0.00	0.08	0.05	0.00	0.05	0.48	2.67	1.12	4.95	2.77
T6	16-Aug-2020	100	102.27	73.50	10.27	4.39	8.14	1.02	0.00	0.35	0.00	0.03	0.06	0.00	0.05	0.51	2.56	1.13	0.18	0.00
T7	17-Aug-2020	100	245.00	77.43	12.32	12.73	9.65	0.39	0.00	0.39	0.01	0.16	0.18	0.12	0.01	0.13	3.56	1.56	0.28	0.40
T8	17-Aug-2020	100	207.73	75.34	7.69	5.17	9.28	0.72	0.00	0.29	0.00	0.04	0.18	0.05	0.05	0.39	3.49	1.59	8.292	2.26
KS	23-Aug-2020	100	117.27	33.94	7.49	4.08	11.16	1.18	0.13	0.27	0.04	0.09	0.00	0.08	0.00	0.39	2.66	1.59	1.898	0.24
T11	23-Aug-2020	100	178.18	83.13	9.10	5.27	7.60	0.58	0.00	0.40	0.06	0.06	0.05	0.03	0.00	0.39	2.74	1.21	1.66	1.14
T14	27-Aug-2020	100	298.64	132.59	10.38	6.30	8.12	0.74	0.00	0.23	0.04	0.13	0.18	0.12	0.00	0.30	3.87	1.53	3.83	6.63
T15	27-Aug-2020	100	125.17	42.62	6.51	2.90	8.02	0.64	0.00	0.52	0.04	0.08	0.14	0.00	0.00	0.21	2.80	1.22	3.2589	0.49
KU	19-Aug-2020	100	161.82	57.54	6.25	2.73	7.47	0.42	0.05	0.45	0.21	0.09	0.03	0.00	0.00	0.17	2.50	0.89	6.57	0.96
SI	19-Aug-2020	100	196.38	82.70	6.45	6.49	7.42	0.57	0.00	0.36	0.09	0.15	0.18	0.09	0.01	0.12	3.47	1.46	4.546	2.54
T16	28-Aug-2020	100	203.18	146.00	9.84	10.66	11.61	1.04	0.00	0.23	0.10	0.09	0.06	0.00	0.00	0.51	2.97	1.10	0.575	3.86
T20	23-Aug-2020	100	172.73	59.13	6.56	4.85	8.67	0.71	0.00	0.23	0.26	0.22	0.06	0.06	0.03	0.13	3.37	1.19	1.5725	3.21
T23.5	23-Aug-2020	100	178.64	132.44	8.29	6.17	10.00	1.94	0.00	0.44	0.09	0.04	0.13	0.01	0.08	0.21	2.85	1.25	1.6171	5.64
TS	22-Aug-2020	100	230.27	60.07	10.17	6.13	8.17	0.77	0.00	0.47	0.04	0.16	0.14	0.00	0.03	0.17	2.97	1.23	4.2743	1.83
T25	27-Aug-2020	100	121.82	47.24	7.13	5.65	11.55	1.72	0.14	0.26	0.21	0.05	0.05	0.01	0.00	0.27	2.52	1.21	2.039	1.72
T27.5	22-Aug-2020	100	126.73	92.35	6.51	5.13	13.68	1.56	0.14	0.48	0.00	0.00	0.05	0.04	0.06	0.22	2.24	1.30	5.1775	0.42
T28	22-Aug-2020	100	170.09	54.22	7.87	4.95	8.79	0.91	0.00	0.45	0.12	0.05	0.06	0.09	0.00	0.22	3.00	1.44	6.52	0.55
T31	25-Aug-2020	100	240.45	66.16	12.99	10.31	11.97	0.82	0.00	0.35	0.00	0.19	0.27	0.09	0.00	0.09	3.73	1.48	8.28	39.74
T38	1-Sep-2020	100	376.82	94.59	12.92	8.85	10.27	0.80	0.01	0.26	0.04	0.27	0.30	0.09	0.03	0.00	3.88	1.38	3.14	1.55
T41	24-Aug-2020	100	81.73	58.89	3.99	3.67	10.29	0.66	0.00	0.36	0.16	0.39	0.09	0.01	0.00	0.00	3.24	1.08	0.1411	0.89
T45	20-Aug-2020	100	102.36	27.50	3.49	1.94	8.54	0.44	0.00	0.77	0.05	0.01	0.00	0.00	0.00	0.17	2.09	0.34	1.4	0.85
T49	21-Aug-2020	100	340.00	94.71	9.96	7.24	11.60	0.86	0.00	0.47	0.17	0.00	0.16	0.01	0.06	0.13	2.85	1.23	2.18	0.54
T50	26-Aug-2020	100	272.73	63.65	11.31	11.46	11.43	1.03	0.00	0.17	0.03	0.17	0.29	0.04	0.00	0.31	4.00	1.30	2.1	1.66
T50.5	26-Aug-2020	100	140.00	69.25	4.57	4.16	7.80	0.22	0.00	0.36	0.09	0.22	0.13	0.03	0.01	0.16	3.23	1.26	3.86	8.00
T54	26-Aug-2020	110	157.92	92.23	10.05	15.67	11.23	1.04	0.00	0.20	0.00	0.35	0.15	0.12	0.00	0.18	3.99	1.33	0.45	1.48
T59.5	26-Aug-2020	100	95.00	27.75	6.97	4.33	13.07	1.89	0.00	0.52	0.00	0.05	0.00	0.00	0.00	0.43	2.18	0.58	1.28	0.00
KA	24-Aug-2020	100	154.55	41.98	6.21	4.42	15.20	1.17	0.00	0.03	0.03	0.32	0.29	0.29	0.00	0.05	4.82	0.99	0	0.00

Tributary ID	Measuring date	Brush (m^2)	Undercut bank (m^2)	Overhanging vegetation (m^2)	Cover area total (m^2)	Cascade rate	Riffle rate	Run rate	Pool rate	Pool-riffle-sequence index	Flow velocity mean ($cm \cdot s^{-1}$)	Flow velocity sd ($cm \cdot s^{-1}$)	Riverbed gradient mean (°)	Riverbed gradient sd (°)	Confluence height (cm)	Confluence slope (°)	Elevation (m)
T4	16-Aug-2020	3.26	0.09	12.69	23.76	0.02	0.94	0.00	0.04	3	10.08	11.64	1.74	0.51	0	1.50	700
T6	16-Aug-2020	0.63	0.09	20.77	21.67	0.22	0.66	0.00	0.12	3	6.73	7.41	2.23	1.52	31	3.65	685
T7	17-Aug-2020	50.11	0.46	5.73	56.98	0.10	0.56	0.00	0.34	3	20.25	17.68	1.58	0.85	10	1.20	673
T8	17-Aug-2020	12.79	0.39	7.80	31.52	0.06	0.78	0.00	0.16	3	7.36	10.67	2.16	1.09	19	2.60	668
KS	23-Aug-2020	4.58	0.00	4.44	11.16	0.04	0.30	0.00	0.66	3	8.18	11.07	1.37	0.77	0	2.20	650
T11	23-Aug-2020	1.96	2.34	2.40	9.50	0.04	0.16	0.08	0.72	4	6.79	8.50	1.76	1.22	23	3.70	647
T14	27-Aug-2020	0.75	0.62	40.72	52.55	0.08	0.34	0.00	0.58	3	8.50	9.83	1.45	0.94	0	2.60	608
T15	27-Aug-2020	1.58	1.47	16.34	23.14	0.02	0.44	0.00	0.54	3	10.84	8.19	1.34	1.09	14	3.00	606
KU	19-Aug-2020	13.01	9.84	9.80	40.18	0.02	0.98	0.00	0.00	2	16.40	13.86	1.48	1.10	0	4.00	599
SI	19-Aug-2020	6.04	3.51	23.24	39.86	0.56	0.33	0.05	0.07	4	23.70	26.53	6.73	3.44	34	5.00	592
T16	28-Aug-2020	6.04	2.26	3.64	16.37	0.00	0.24	0.00	0.76	2	1.11	3.54	1.13	1.24	0	0.30	586
T20	23-Aug-2020	0.84	2.32	9.04	16.98	0.08	0.66	0.00	0.26	3	19.74	19.29	2.20	1.93	160	7.30	574
T23.5	23-Aug-2020	1.12	0.66	17.27	26.31	0.06	0.44	0.00	0.50	3	9.78	11.81	1.60	1.07	0	2.40	558
TS	22-Aug-2020	4.01	3.99	11.21	25.32	0.00	0.46	0.00	0.54	2	16.09	16.30	1.16	0.66	0	1.30	557
T25	27-Aug-2020	0.70	8.76	21.88	35.10	0.00	0.34	0.06	0.60	3	8.29	9.70	3.66	2.25	52	7.70	553
T27.5	22-Aug-2020	13.98	2.78	38.34	60.70	0.18	0.22	0.00	0.60	3	2.58	4.82	2.37	3.05	2	10.30	543
T28	22-Aug-2020	7.04	14.99	7.05	36.15	0.08	0.50	0.00	0.42	3	14.58	16.22	1.91	1.94	29	7.30	545
T31	25-Aug-2020	6.87	0.72	0.80	56.41	0.00	0.40	0.00	0.60	2	9.30	14.21	1.13	0.98	0	0.60	527
T38	1-Sep-2020	0.00	5.59	2.21	12.49	0.02	0.22	0.08	0.68	4	7.57	8.20	1.05	0.85	0	1.70	516
T41	24-Aug-2020	0.70	0.24	2.10	4.07	0.00	0.21	0.60	0.19	3	5.41	9.45	4.55	2.20	0	1.20	509
T45	20-Aug-2020	7.27	0.80	16.73	27.05	0.00	0.92	0.00	0.08	2	6.86	9.11	1.23	0.48	0	1.60	499
T49	21-Aug-2020	4.44	1.72	48.33	57.21	0.08	0.44	0.00	0.48	3	12.71	12.47	1.27	1.58	15	1.50	481
T50	26-Aug-2020	0.64	38.70	1.68	44.78	0.12	0.14	0.12	0.62	4	8.29	11.30	1.11	0.80	0	2.40	479
T50.5	26-Aug-2020	0.80	1.11	3.60	17.37	0.12	0.38	0.22	0.28	4	7.67	9.36	1.94	1.91	0	6.70	476
T54	26-Aug-2020	0.00	3.00	6.34	11.27	0.05	0.49	0.00	0.45	3	16.85	22.04	1.18	2.18	65	6.20	452
T59.5	26-Aug-2020	16.42	0.32	62.50	80.52	0.00	0.68	0.00	0.32	2	8.63	10.72	1.54	0.67	0	0.70	425
KA	24-Aug-2020	4.09	0.80	3.22	8.11	0.42	0.50	0.00	0.08	3	23.87	26.87	6.70	4.45	0	17.50	380

TABLE S2-2. Population density and fork length of each species at each tributary and catch per unit effort of age-0+ white-spotted charr at mainstem near the tributary.

		Dolly Varden								White-spotted charr				
		Age 0+ (n = 1,528)				Age ≥ 1+ (n = 638)				(n = 857)				
Tributary ID	Habitat type	n of fish	Estimated population density ($n \cdot m^{-2}$)	Fork length mean (mm)	Fork length sd (mm)	n of fish	Estimated population density ($n \cdot m^{-2}$)	Fork length mean (mm)	Fork length sd (mm)	n of fish	Estimated population density ($n \cdot m^{-2}$)	Fork length mean (mm)	Fork length sd (mm)	Catch per unit effort (n in 30min)
T4	Typical	42	0.48	51.19	9.85	15	0.14	82.20	7.28	43	0.46	56.12	6.49	2.40
T6	Typical	43	1.64	54.37	4.55	2	0.02	99.00	2.83	10	0.09	62.80	4.73	34.00
T7	Typical	211	3.84	47.75	7.68	93	0.39	115.29	27.95	1	0.00	56.00	0.00	0
T8	Typical	48	0.24	48.69	7.06	37	0.26	89.32	12.77	13	0.06	61.69	5.72	9.00
KS	Typical	23	0.27	48.35	8.74	25	0.21	90.60	12.20	64	0.65	62.89	7.46	40.71
T11	Typical	43	0.39	53.63	7.80	67	0.61	97.38	22.03	14	0.12	59.64	4.68	4.29
T14	Typical	60	0.29	56.22	8.67	103	0.45	108.99	22.62	7	0.03	65.57	5.94	1.50
T15	Typical	37	0.29	60.68	3.99	7	0.05	119.57	15.99	65	0.66	63.38	5.72	58.93
KU	Typical	174	1.48	54.13	5.57	21	0.15	88.05	13.44	13	0.08	57.62	4.48	11.67
SI	Typical	108	0.57	52.08	6.20	14	0.06	88.47	6.66	5	0.02	61.50	3.87	4.29
T16	Typical	23	0.12	56.74	9.00	24	0.11	83.71	12.38	62	0.35	64.52	7.68	1.07
T20	Contrasting B	166	1.53	48.86	7.41	38	0.24	92.29	15.97	33	0.26	57.21	3.92	50.45
T23.5	Contrasting A	1	0.01	46.00	0.00	1	0.01	113.00	0.00	59	0.51	67.37	8.80	1.00
TS	Typical	22	0.12	59.14	5.92	31	0.14	102.77	13.24	20	0.10	68.30	4.69	13.24
T25	Contrasting B	39	0.35	60.03	13.45	48	0.45	99.58	19.43	10	0.08	67.30	7.27	18.53
T27.5	Contrasting B	3	0.03	49.67	4.62	2	0.02	90.00	8.49	2	0.02	54.50	0.71	0
T28	Typical	194	1.60	49.34	6.40	26	0.16	90.76	11.62	5	0.03	59.60	7.80	12.14
T31	Typical	0	0	NA	NA	0	0	NA	NA	9	0.04	73.11	10.74	2.90
T38	Typical	0	0	NA	NA	17	0.05	125.12	15.14	7	0.02	70.00	14.64	1.36
T41	Contrasting A	2	0.03	56.00	1.41	0	0	NA	NA	220	3.02	61.32	10.01	1.46
T45	Contrasting A	0	0	NA	NA	0	0	NA	NA	98	1.09	63.15	6.23	8.33
T49	Typical	0	0	NA	NA	23	0.07	129.83	20.46	22	0.13	74.27	7.30	0
T50	Typical	0	0	NA	NA	11	0.04	132.73	12.60	10	0.04	75.10	5.47	0
T50.5	Typical	266	2.35	56.65	6.46	10	0.07	101.70	24.16	20	0.14	64.35	5.58	4.05
T54	Contrasting B	23	0.14	59.87	7.60	12	0.07	133.17	23.00	30	0.18	77.13	8.52	2.40
T59.5	Typical	0	0	NA	NA	2	0.02	99.50	13.44	8	0.08	73.38	9.38	0
KA	Contrasting B	0	0	NA	NA	9	0.06	127.33	17.52	0	0	NA	NA	0

TABLE S2-3. Estimate, df, loglik, AICc, ΔAICc, and weight of abiotic or biotic elements of the best models (ΔAICc < 4.00).

Model	(Intercept)	Elevation	Catch per unit effort of age-0+ white-spotted charr	Pool-riffle-sequence index)	Cover area total	Water depth mean	Substrate roughness	Substrate heterogeneity
1	1.02	NA	−0.69	NA	NA	NA	NA	NA
2	1.00	0.43	−0.77	NA	NA	NA	NA	NA
3	1.01	NA	−0.68	NA	NA	NA	NA	0.31
4	1.05	NA	−0.79	NA	NA	NA	NA	NA
5	1.02	NA	−0.66	0.20	NA	NA	NA	NA
6	0.92	NA	NA	NA	NA	NA	NA	NA
7	1.04	NA	−0.74	NA	NA	NA	−0.12	NA
8	1.01	NA	−0.72	NA	−0.12	NA	NA	NA
9	1.05	NA	−0.73	NA	NA	−0.13	NA	NA
10	1.02	NA	−0.68	NA	NA	NA	NA	NA

Model	Flow velocity mean	Stream width mean	Water temperature mean	df	LogLik	AICc	ΔAICc	Weight
1	NA	NA	−1.65	3	−7.97	23.54	0.00	0.15
2	NA	NA	−1.50	4	−7.066	24.99	1.45	0.073
3	NA	NA	−1.61	4	−7.55	25.95	2.41	0.045
4	NA	−0.19	−1.66	4	−7.78	26.41	2.87	0.036
5	NA	NA	−1.59	4	−7.78	26.42	2.87	0.036
6	NA	NA	−1.32	2	−10.93	26.61	3.07	0.033
7	NA	NA	−1.67	4	−7.89	26.64	3.10	0.032
8	NA	NA	−1.62	4	−7.91	26.67	3.13	0.032
9	NA	NA	−1.63	4	−7.91	26.67	3.13	0.032
10	0.050	NA	−1.63	4	−7.96	26.78	3.24	0.030

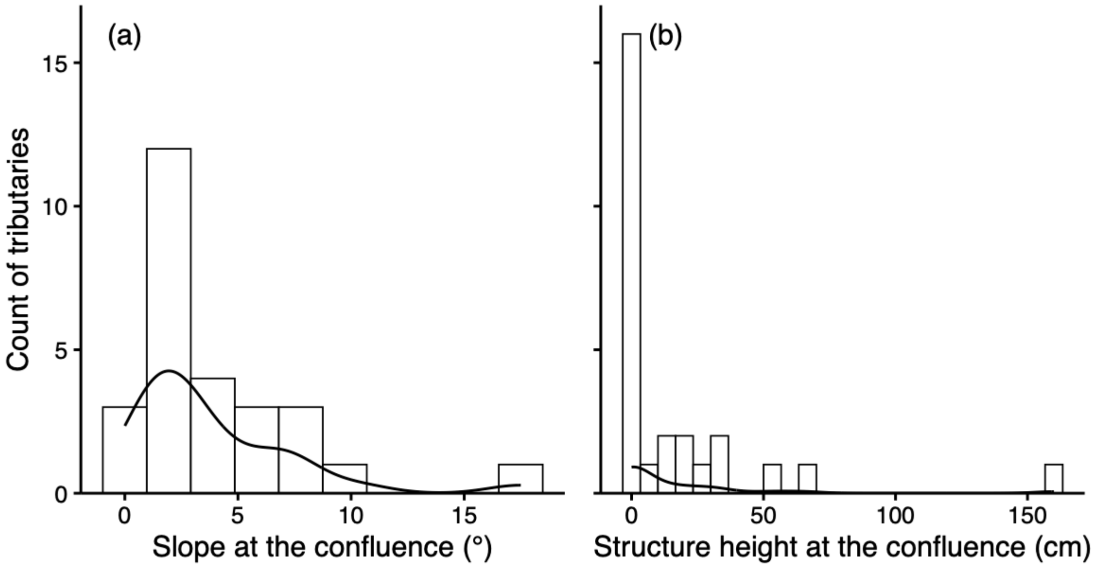


FIGURE S2-1 Histograms of the slope (a) and the height of natural physical barriers (b) at the confluences. The solid lines (density curve) are fitted by gaussian mixture model.

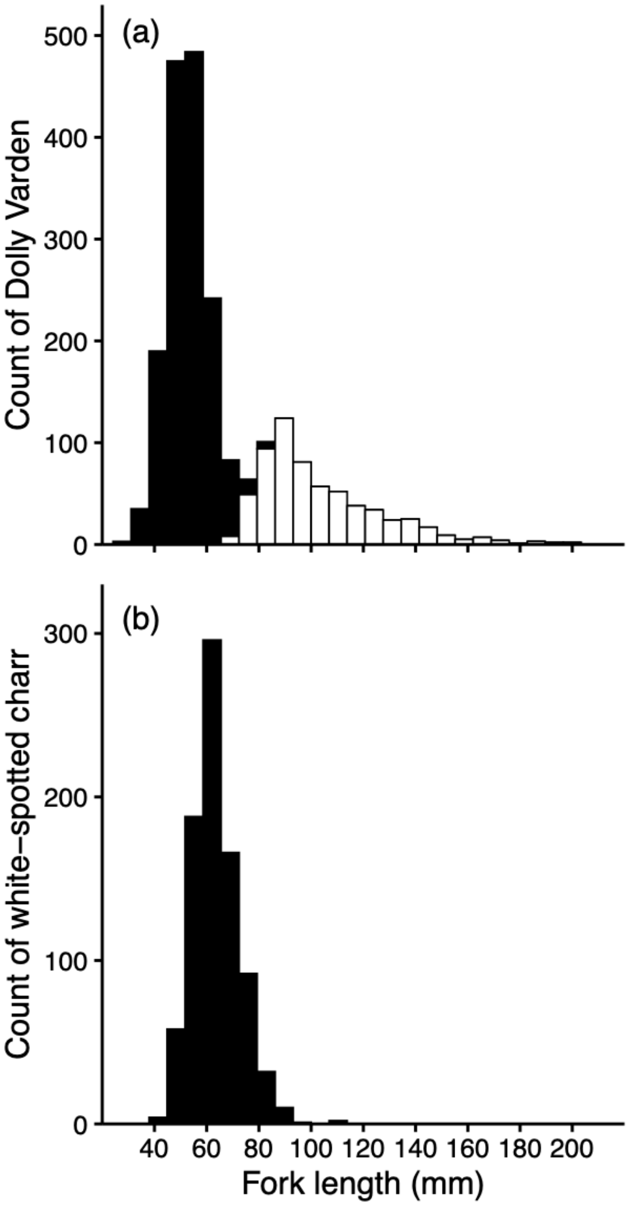


FIGURE S2-2 Size (fork length) frequency distributions of juvenile of (a) Dolly Varden and (b) white-spotted charr. Black and white bars indicate age-0+ and age ≥ 1+ fish, respectively. Age class was judged based on size frequency distribution in each tributary, as well as appearance (e.g., age-0+ tend to be skinner, age-0+ do not have red spots).

CHAPTER 3

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Validation of the past model for predicting local extinction of Dolly Varden: Do overlooked factors improve the model's predictive power?

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Abstract

Global warming is driving the rapid decline of biodiversity and heightening the risk of local extinctions. Most studies predict future species distributions but seldom assess the accuracy of these predictions in relation to actual extinctions. Few empirical studies assess prediction accuracy, with one showing a low correlation between predicted and actual distributions. This discrepancy is likely due to the neglect of proximity factors, such as local environment, seasonal timing, and interspecific competition, which influence species distributions. In this study, I investigated these overlooked proximate factors. To investigate the local extinction of an endangered salmonid, Dolly Varden (*Salvelinus curilus*), I resurveyed 141 sites in Hokkaido where the species had been confirmed up to 20 years ago. A model based on mean annual air temperature predicted an extinction rate of 3.55%, but the actual rate was 9.22%. To explain this gap, I developed a new model incorporating regional climate, temperature seasonality, and temperature-dependent competition with white-spotted charr. The best model incorporated the rise in summer temperature and another competitive species, rainbow trout. Structural equation modeling also revealed that local groundwater temperature in summer and rainbow trout was a key predictor of local extinction. In conclusion, past models may have underestimated extinctions, and incorporating microenvironments, seasonal timing, and competitive species can improve prediction accuracy.

INTRODUCTION

Climate change in recent years has increased the risk of species and population extinction (Urban, 2015; Holzmann et al., 2023) and has become a major issue in biodiversity conservation (Bellard et al., 2012; Wang et al., 2024). Rising temperatures can increase mortality rates or decrease fecundity of organisms by exceeding their physiological tolerances (Somero, 2010) or by increasing metabolic demand for oxygen (Pörtner & Knust, 2007), which ultimately leads to population extinction. Such extinction risks have been primarily assessed using distribution prediction models (Warren et al., 2018). Species distribution prediction assumes that species are in equilibrium with their environment, and models are constructed based on the correlation between the distribution information (i.e., realized niche) of a species or population and the macroclimate (Guisan & Zimmermann, 2000; Elith & Leathwick, 2009). By applying these models to current and future climate scenarios, I can illustrate environmentally suitable habitats and quantify and visualize their changes from the present to the future (≈ extinction risk). These prediction models assume the theory of the species–area relationship (MacArthur & Wilson, 1967), which posits that if the distribution area is small, population size will be small, which leads to high risk of extinction. The main objective of species distribution modelling is to identify at-risk species and populations and link them to management and conservation efforts (Guisan et al., 2013; Kujala et al., 2013). They are also used as legal criteria for endangered species (IUCN, 2010), playing a key role in political decisions (IPCC, 2022).

Surprisingly, despite thousands to tens of thousands of accumulated distribution (or extinction) prediction studies (Zurell et al., 2023), there are very few studies that have subsequently tested these predictions by comparison with actual extinctions that have occurred (i.e., using independent time-series data) (Uribe-Rivera et al., 2023; but see Chen et al., 2011; Johnston et al., 2013; Rapacciuolo et al., 2014; Sofaer et al., 2018; Piirainen et al., 2023; Holzmann et al., 2023).

Is this simply because ecologists are interested only in predicting future species distributions, or is it due to a lack of sufficient datasets for verification? In some cases, after predictions and standards have been set, various conservation activities not included in the prediction scenarios have been carried out, effectively mitigating the extinction risk (Hoffmann et al., 2015). Furthermore, in the past few decades, as extinction has progressed, future climate change scenarios have also continued to evolve (O'Neill et al., 2020). In other words, these multifaceted and rapid changes may be reducing opportunities for feedback testing of distribution model performance. Therefore, it is crucial to compare past prediction models with actual extinction statuses and identify any discrepancies.

How can the discrepancies identified in the above tests be addressed? Piirainen et al. (2023) tested the predictive power of the model by comparing the predicted distribution with the actual distribution change, but the model was unable to predict most of the actual distribution change. They attribute this failure to the lack of information in the model, particularly the low resolution of environmental variables that are crucial for explaining local extinctions. In other words, the spatial variation due to meso- and microclimates was not accounted for (Zellweger et al., 2020). Another way to address these gaps and improve predictive ability is to select the critical period when the physical environment has the greatest impact on the distribution of organisms (Gardner et al., 2019). In places where local extinction observed, the increase in mean annual air temperature was smaller than in places where it did not occur, and the increase in maximum annual temperature was larger (Román-Palacios & Wiens, 2020). This suggests that, if the appropriate predictor variables and time periods are not chosen, the results could be completely opposite. Lastly, some indirect effects from other species (e.g., interspecific competition) were suggested as a cause of the discrepancy (Tylianakis et al., 2008). There are still only a limited number of studies that incorporate local environmental factors, meaningful time periods, and interspecific competition into distribution predictions (Blois et al., 2013; Zellweger et al., 2020; Essl et al., 2024). It remains an ongoing issue whether the explanatory power of distribution predictions can be improved by incorporating these factors (Slavich et al., 2014; Louthan et al., 2015; Poggiato et al., 2021).

Here, I revisited the survey sites from the previous studies of the Dolly Varden (*Salvelinus curilus*), a threatened species of salmonid fish that was predicted to become locally extinct due to global warming over 20 years ago (Nakano et al., 1996), to investigate whether it had actually become extinct. As poikilothermic fish with a narrow thermal tolerance, salmonids are among the most vulnerable species to global warming (e.g., Isaak et al., 2010; Finstad et al., 2011; Wenger et al., 2011; Isaak et al., 2012; Hedger et al., 2013; Gallagher et al., 2022). Local populations at the southern limit of their distribution are generally at high risk of local extinction (e.g., Franco et al., 2006; Cuervo & Møller, 2013), and Dolly Varden of Hokkaido is also at the southern limit of its whole distribution among Dolly Varden species or subspecies group (Whiteley et al., 2019). According to a predictive model of Nakano et al. (1996), a 1.00°C increase in mean annual temperature would cause 27.6% of the population to become locally extinct. In Hokkaido, the mean annual air temperature has risen by about 0.48°C over the past 20 years, but this increase varies locally and over time (Figure S3-1a). This is because

Hokkaido has high topographical diversity (Ministry of Land, Infrastructure, Transport and Tourism, 2010) and the local climate is influenced by topography (e.g., Elsen et al., 2020; Gentili et al., 2020; Estevo et al., 2022). Although distribution predicted by the original model is based almost entirely on summer distributions, it uses the mean annual air temperature (MAAT, hereafter), as is typical in many species distribution models. Furthermore, in Hokkaido, the native species of the same genus, white-spotted charr (*S. leucomaenis*, a warm-water species), is sympatric with Dolly Varden (a cold-water species) in some areas (Ishigaki, 1969; Fausch et al., 1994). The two species are in a competitive relationship, with white-spotted charr being the dominant species, and it has been experimentally shown that the higher the water temperature, the more dominant it becomes by measuring their fitness-related indicators (Taniguchi & Nakano, 2000; Watz et al., 2019). Moreover, the performance of Dolly Varden shows a negative correlation with water temperature and abundance and is further reduced when sympatric with high-density white-spotted charr (chapter 2; Uemura et al., under review). Therefore, in areas where white-spotted charr are present, warming is likely to accelerate the local extinction of Dolly Varden (Nakano et al., 1996), but the original model does not account for this interaction. These backgrounds of the species and regions are suitable for verifying the general issues related to the discrepancy between predictions and observed data of local extinction.

First, I confirmed how many populations were extant by re-examining 141 sites throughout Hokkaido where Dolly Varden distribution had been confirmed in the past. Dolly Varden have limited mobility, and dispersal availability differs depending on the river system, so it can be predicted that no uniform range shift will be observed. Second, I assessed how much of the current presence or absence of populations could be explained by the original model, which assumes a uniform increase in groundwater temperature based on the mean annual air temperature. In recent years, groundwater temperature has indeed risen due to global warming, but it is significantly affected by geology (Ishiyama et al., 2023; Benz et al., 2024). Geological factor was not considered in the original model. I therefore tested how well the original model and an alternative model that incorporated the following factors could explain current local extinctions: 1) local heterogeneity of temperature rise, 2) the meaningful period: annual or summer, 3) the local groundwater temperature rise, accounting for geological factors and groundwater flow. Then I compared the original model with that of the new models incorporating these factors to assess the improvement in the predictive power. I also examined both the direct effects of local environmental factors and the indirect effects via presence of other competitive species on the current local extinction of Dolly Varden.

METHODS

Fish sampling and water temperature measurement

The field surveys were conducted from 16 August to 6 September 2020, from 27 to 28 October 2020, from 29 June to 23 July 2022, on 3 November 2022, from 13 to 21 July 2023, and from 11 August to 6 September 2023, at 192 sites. The 2020s Dolly Varden census data for the 37 sites (streams) in the Shiretoko region was gathered by a collaborative study (Taniguchi, Y., & Kawaguchi, Y., unpublished data). Then I selected the 141 sites where Dolly Varden had been captured in 1968–2002 (Figure 3-1; Ishigaki, 1969; Yoshiyasu, 1973; Maekawa, 1977; Komiyama, 1982; Fausch et al., 1994; Kitano et al., 1995; Takami et al., 1995; Nakano et al., 1996; Yoshiyasu, 1996; Ishii et al., 2002; Taniguchi et al., 2002; Komiyama, 2003; Baxter et al., 2007; Kasugai, 2008; Nakano et al., 2020; Koizumi, I., unpublished data). When selecting the sites, I considered the movement patterns of Dolly Varden, ensuring the sites were sufficiently spaced apart or located in different tributaries of the same river system (i.e., considered segregated populations). These sites included sites where white-spotted charr had been captured in the past (51 sites).

A backpack electrofisher (model 12-B, Smithroot Inc. Vancouver, Washington, USA) was used to collect fish, with all collections conducted by myself. Fish population density ($n \cdot \mathrm{m}^{-2}$) was estimated using the 2–3-pass removal method (model M(b), a program CAPTURE, available from: https://www.mbr-pwrc.usgs.gov/software/capture.html; Zippin, 1958). To minimize negative effects on fish and other aquatic animals, electrofisher settings were adjusted to DC, 200–300 V (Snyder, 2003). Over 30 minutes were allowed between passes to give uncaptured individuals time to recover. The fork length and body mass of each individual were measured to the nearest 1.0 mm and 0.1 g, respectively, after anesthesia (0.5 mL per 1.0 L of water; FA100, Bussan Animal Health Co., Ltd., Osaka, Japan). The age cohort (age 0+ and age ≥ 1+) of each fish was determined based on field observations and fork length distribution (cf. Koizumi et al., 2008). Each species was visually identified. All captured individuals were released after recovering from anesthesia at the point of capture. In conjunction with fish sampling, local water temperature was recorded continuously during the field period (logged hourly; HOBO UA-001, UA-002, U20L, Onset Computer Corporation, Bourne, MA, USA).

For the following statistical analyses with past survey data, I used only the presence sites for Dolly Varden, white-spotted charr, and rainbow trout (*Oncorhynchus mykiss*). This was because the past abundance data lacked sufficient accuracy. The low accuracy resulted from issues such as many missing values, varied capture methods, inconsistent density estimation techniques, and regional biases in past and present correspondence points.

Criterion for "local extinction"

The criterion for "local extinction" in this study was defined as a location where no Dolly Varden were captured after 2–3 passes with the electrofisher removal method described above. Each survey reach was at least 50 m length, and, except for a few cases, the survey area was at least 100 m^2. Most survey reaches were tributaries that provided access for removal methods (mean river width: approximately 4–6 m; cf. Ward et al., 2015). In contrast, the capture method used in the previous study was primarily fishing, suggesting that the capture efficiency of the method used in the 2020s census is higher. For example, Morita et al. (2019) revisited a survey reach in southern Hokkaido where white-spotted charr were observed in 1999. Fifteen years later, the authors used both an electric fish collector and the eDNA detection method to define local extinction (the authors referred to it as “localized extinction”). The absence of the fish due to the electrofisher was consistent with the non-detection of environmental DNA. These findings contribute to the generalizability of the concept of “local extinction”.

Changes in the distribution elevation of Dolly Varden

To investigate whether the distribution elevation of Dolly Varden has changed over the past 20 years, I constructed a generalized linear mixed model (GLMM, hereafter) with local extinction as the dependent variable and elevation as the explanatory variable. The GLMM used a “binomial” family and a “logit” link function. The *glmer* function from the *lme4* package version 1.1.35.5 (Bates et al., 2015) in R version 4.4.1 (R Core Team, 2024) was used to fit the model. Overdispersion was assessed in the same way as in chapter 2 (see “METHODS” in chapter 2).

Air temperature rise prediction

The extent of temperature increases in Hokkaido as a whole and in specific areas over the past 20 years was assessed using data from the Japan Meteorological Agency’s database (available from: https://www.data.jma.go.jp/obd/stats/etrn/). Information was obtained for all AMeDAS observation stations (285 stations) from 1991 to 2020, and data from 153 stations with more than 28 years of continuous records were extracted for analysis. First, a linear regression model was constructed using the default *lm* function in R, with the MAAT or the mean temperature in August as the dependent variable and the year as the explanatory variable. The presence of temperature autocorrelation was tested using the Durbin-Watson test, with the *dwtest* function from the *lmtest* package version 0.9.40

(Hothorn et al., 2015) in R. If significant autocorrelation (i.e., $p < 0.05$) was detected, a regression model accounting for temporal autocorrelation was constructed using the *gls* function (correlation structure: corAR1) from the *nlme* package version 3.1-166 (Pinheiro et al., 2024) in R. The correlation coefficient of the models constructed for Hokkaido and each location was regarded as the rate of increase, and by multiplying this by 20, the rate of increase over the past 20 years was calculated (Figure S3-1). The nearest station to the fish sampling site was identified using the *nearest_station* function from the *jmastats* package version 0.2.2 (Uryu, 2024) in R, and the temperature increase at that site was defined as the temperature increase at the fish sampling site.

Groundwater temperature rise prediction

A map was created based on a model (ERA-5 model; cf. Benz et al., 2024) that estimates groundwater temperature and its increase (from 2000 to 2100), taking into account groundwater flow and geothermal models (available from: https://susanneabenz.users.earthengine.app/view/subsurface-temperature-profiles). By plotting the GPS coordinates of each fish sampling location, I estimated the subsurface water temperatures over the past 20 years for each of the four seasons: January, April, July, and October. The annual average and summer increase rate were calculated in the same manner as for air temperature. The groundwater temperatures were not obtained for 16 out of the 141 sites because the groundwater could not be estimated well on the website and was not displayed on the map.

A model for estimating groundwater temperatures to determine local extinction

The original model used in Nakano et al. (1996) was adopted for estimating past groundwater temperatures (Equation 1).

Past groundwater temperature

$$= 56.364 - 1.120 \times \text{latitude} - 0.005 \times \text{elevation} \quad \text{———————————— Equation 1}$$

In Nakano et al. (1996), the current estimated groundwater temperature is calculated by adding the rate of increase in groundwater temperature caused by the increase in MAAT (0.939 × the increase in MAAT, uniform across Hokkaido) to the estimated past groundwater temperature (Equation 2, Model-01). If the current groundwater temperature exceeds 8.00°C, it is considered an indication of local extinction (Nakano et al., 1996).

Current groundwater temperature

$$= \text{Past groundwater temperature} + 0.939 \times \text{the increase in MAAT} \quad \text{——————————— Equation 2}$$

In this study, the temperature added to the estimated past groundwater temperature was the increase in MAAT which varies by location, the increase in mean August air temperature (uniform across Hokkaido or varying by location), and the increase in groundwater temperature calculated using a refined model, which also varies by location (Table S3-1).

Furthermore, in areas where white-spotted charr were recorded before 2000 or caught in current surveys, it is estimated that temperature-dependent competition from white-spotted charr negatively impacts Dolly Varden populations (Nakano et al., 1996;

Taniguchi & Nakano 2000; Watz et al., 2019; chapter 2). Therefore, I also created models where the temperature increase was multiplied by 1.05: small effect, 1.10: moderate effect, and 1.50: strong effect (Table S3-1). Rainbow trout were also caught in this survey as a competitive species for Dolly Varden (e.g., Sahashi & Morita, 2016). Hence, models were constructed under the assumption that rising temperatures would have a stronger effect at sites where rainbow trout had been caught, either in the past or present, similar to white-spotted charr. The effects of masu salmon (*O. masou masou*) were not included in the models because no clear density compensation (resulting patterns of interspecific competition pattern) with Dolly Varden was identified in the present sites (Figure S3-2).

Model performance evaluation

First, for each groundwater prediction model, a confusion matrix (true positive, true negative, false positive, false negative) was created by comparing actual local extinctions (local extinction = 1, no local extinction = 0) identified through fish sampling with the local extinctions predicted by each regional water temperature model (local extinction = 1, no local extinction = 0).

The following metrics were calculated as indicators of model performance (cf. Stehman, 1997):

Accuracy = (true positive + true negative) / (true positive + false positive + true negative + false negative)

Sensitivity = (true positive / true positive + false negative)

Specificity = (true negative / true negative + false positive)

Precision = (true positive / true positive + false positive)

F-score = 2 × true positive / (2 × true positive + false positive + false negative).

Each metric ranges from 0 to 1, and a model with a value of 1 is considered a good model. The error rate, false negative rate, and false positive rate were then calculated as the values obtained by subtracting accuracy, sensitivity, and specificity from 1.

Next, a GLMM (family = “binomial”, link = “logit”) was constructed using the *glmer* function in *lme4* package version 1.1.35.5 (Bates et al., 2015) in R, with observed local extinction (local extinction = 1, no local extinction = 0) as the dependent variable, and local extinction predicted by each of the groundwater prediction models (local extinction = 1, no local extinction = 0) as the explanatory variable. River ID was included as a random effect. The AIC was calculated to evaluate the predictive performance of each model (the smallest value indicates the best model; Burnham & Anderson, 2002).

Finally, to evaluate the model’s performance while considering bias between negative and positive values, I used the F-score and AIC for ranking. For all the models (42 models), I assigned a score of 42 to the best model for each metric and a score of 1 to the worst. Then, I calculated the total of each score and evaluated as the overall index (the higher the number, the better the model).

Structural equation modeling

The direct effects of 9 local climatic or environmental variables (local MAAT in 2020, local mean summer temperature in 2020, local MAAT rise in the past 20 years, local mean summer temperature rise in the past 20 years, annual mean local groundwater temperature, summer local groundwater temperature, annual mean local groundwater temperature rise, summer local groundwater temperature rise, and observed river water temperature in 2020) on the observed local extinction of Dolly Varden, as well as the indirect effects of sympatry with white-spotted charr, rainbow trout (before 2000 or at present), or masu salmon (present) were examined using structural equation modeling (SEM). Although the current density (or presence) of masu salmon may not have a significant effect as noted above, its long-term impact on the local extinction of Dolly Varden is important and cannot be overlooked (e.g., Morita, 2022); I therefore treated the presence of masu salmon as a variable in this model. SEM was constructed using the *piecewiseSEM* package version 2.3.0 in R (Lefcheck et al., 2016).

The SEM model was constructed with two components. First, local extinctions (local extinction = 1, no local extinction = 0) were set as the response variable, with sympatry with white-spotted charr, rainbow trout, or masu salmon (sympatry = 1, not sympatry = 0) and the local climate or environments as explanatory variables. Second, sympatry with white-spotted charr, rainbow trout, or masu salmon was treated as the response variable, while increases in the local climate or environments and river ID were used as an explanatory variable and a random-effect, respectively. For this analysis, a GLMM with a "binomial" family and a "logit" link function was employed. The *glmer* function from the *lme4* package in R (Bates et al., 2015) was used.

RESULTS

Dolly Varden was collected at 128 of the 141 sites, indicating that local extinction occurred at 13 sites (local extinction rate: 9.22%; Figure 3-2). No evidence was found that elevation had an effect on local extinction ($p = 0.22$; Figure 3-3). According to the groundwater prediction model by Nakano et al. (1996), 5 out of the 141 sites were predicted to be extirpated (3.55%), meaning the actual extinction rate was more than twice as high as the predicted rate.

According to the model scoring results, the best model considered the increase in summer temperatures and the strong effect of rainbow trout (Table 3-1). Similarly, the top five models included those accounting for warming amplification due to rainbow trout or white-spotted charr in summer.

Among the 9 SEM models considering sympatry with white-spotted charr, the model incorporating the summer local groundwater temperature rise using the ERA-5 model had the lowest AIC (Figure 3-4h). Strong evidence suggested that the summer rate of groundwater temperature rise positively affected the local extinction of Dolly Varden. For the four SEM models considering sympatry with rainbow trout, strong evidence indicated that the presence of rainbow trout positively affected the local extinction of Dolly Varden in all models (Figure 3-5). Even when rainbow trout were considered, the model including the summer local groundwater temperature using ERA-5 had the lowest or second lowest AIC (Figures 3-5f and 3-5h). No direct effect of masu salmon on Dolly Varden was detected in any model (Figure 3-6). The model with the lowest AIC strongly indicated that a local increase in groundwater temperature in July significantly increased the occurrence of Dolly Varden's local extinction, as well as the sympatric state with masu salmon (Figure 3-6h).

DISCUSSION

Local extinction of Dolly Varden

In this study, I investigated whether Dolly Varden had become extinct, as predicted by Nakano et al. (1996). Previous studies on animal distribution predictions emphasize that failures often occur because the data set does not adequately cover the potential distribution range of the species (Sofaer et al., 2018; Piirainen et al., 2023). Possible responses to warming include niche shifts and local extinctions. However, in birds, range shifts are more common due to their high mobility (e.g., Sekercioglu et al., 2008; Hällfors et al., 2024; Zurell et al., 2024). This highlights the importance of understanding the basic life history of the target species when designing a sampling strategy for prediction. Based on previous literature on Dolly Varden, I ensured that sampling covered the entire range of the species, including both the southernmost and northernmost populations. Additionally, because rivers vary in elevation, I incorporated elevation in the analysis. These approaches revealed that the cause of Dolly Varden’s local extinction was not due to uniform range shifts.

Extensive re-surveys of 141 sites in Hokkaido revealed 9.22% of local extinctions of Dolly Varden (Figure 3-2). In general, the distribution ranges of wildlife often shift northward or to higher elevations in response to warming climate (e.g., Warren & Robert, 2013; Freeman et al., 2018). However, species with low mobility or strong dependence on local ecosystems may fail to adapt to the pace of warming, resulting in local extinction (Chevin et al., 2010; Maclean & Wilson, 2011). In this study, no significant differences were observed in the altitudinal distribution of Dolly Varden populations between the past and present (Figure 3-3). This finding supports that Dolly

Varden likely falls into the latter category, unable to keep pace with environmental changes.

A previous study on brown trout in southern Europe reported a decrease in density at lower altitudes due to climate change (Almodóvar et al., 2012). However, another study suggests that no significant changes in distribution have occurred (Comte & Grenouillet, 2013). These findings indicate that even within the same species, distributional changes can vary depending on regional or water system characteristics. Therefore, surveying the entire distribution range is crucial to evaluate changes in species distribution and assess the risk of local extinction (Owens et al., 2013). This study is among the few to quantitatively analyze long-term changes in the distribution of a specific salmonid fish.

In most of the study sites, dams were found to restrict the upstream or downstream movement of individuals (Uemura, Y., personal observation). At the three sites where extinction occurred, crossing structures were also present upstream or downstream. In these sites, fish were absent, and summer river flow was nearly nonexistent, limiting habitable space from the outset. The narrow temperature tolerance typical of salmonids may have amplified the negative effects of physical barriers, making escape from habitat warming more difficult (Nakano et al., 1996). Additionally, the extinct sites were located in the upper reaches of tributaries. In such narrow habitats, rapid environmental changes may have accelerated extinction more than in other broad areas.

Meaningful season

This study found that local extinctions occurred more frequently than predicted by Nakano et al. (1996) based solely on MAAT. To investigate the cause of this discrepancy, I developed a model incorporating multiple realistic proximate factors. Among these, the model that best predicted the observed local extinctions included the synergistic effect of the average temperature increase in August and the presence of rainbow trout (Table 3-1). Model performance results also indicated that summer temperature was the factor best explaining the local extinctions of Dolly Varden, rather than the annual average temperature.

All sampling was conducted during the summer (see “METHODS”), as the summer environment significantly affects the growth, competition, migration, and final distribution of juvenile salmonids (e.g., Winkowski & Zimmerman, 2018; Skoglund et al., 2024). Summer river water temperature closely follows changes in air temperature with a short time lag (e.g., Rosencranz et al., 2021), and this effect is intensified during periods of low flow (van Vliet et al., 2011). Dolly Varden spawn and settle in small streams (Nakano et al., 1996; Koizumi & Maekawa, 2003), and their limited migration range makes it difficult for them to escape rising summer temperatures. For these reasons, summer is considered a “critical period” for the local extinction of Dolly Varden.

When I examined models with a high false negative rate, i.e., models that predicted extinction for many sites where extinction actually did not occur, all of the top-ranked models included the annual average values of MAAT and groundwater (Table S3-2). As used by Nakano et al. (1996), many distribution prediction models use MAAT as an environmental variable in the base model. However, it has been pointed out that MAAT is often of low importance, or even meaningless, as a predictor (Austin, 2002; Gardner et al., 2019). Based on this, I conclude that caution is warranted when using MAAT in predictions.

Effects of competitive species

The temperature effect was stronger in areas where rainbow trout were present, and this model best explained the extinction of Dolly Varden (Table 3-1). SEM results provided evidence of local extirpation of Dolly Varden in sympatry with rainbow trout, regardless of the type of temperature increase (Figure 3-5). Additionally, there was strong evidence of sympatry with rainbow trout in areas with rising summer temperatures. This led to the estimation of a path in which summer temperatures indirectly affect local extirpation of Dolly Varden through the presence of rainbow trout (Figure 3-5b). The spawning season for rainbow trout occurs in spring, and juvenile hatching takes place in early summer (Aoyama et al., 1999). Hence, the timing of flooding is considered strongly related to the increase in hatched juveniles and young fish, as well as their establishment, than to global warming (Fausch et al., 2001). However, strong evidence shows that rising summer temperatures positively affect the presence of rainbow trout (Figure 3-5b). This suggests that warmer summer temperatures promote the rapid growth and survival of rainbow trout.

The result that the presence of rainbow trout explains the local extinction of Dolly Varden is consistent with an earlier study reporting a negative correlation between the density of rainbow trout and native species, including Dolly Varden (Sahashi & Morita, 2016). The occurrence of rainbow trout and their new invasions can reduce Dolly Varden density (Misawa et al., 2007) and even lead to their exclusion (Baxter et al., 2007). Redd superimposition is considered the most critical factor affecting Dolly Varden juvenile abundance (Taniguchi et al., 2000). Rising temperatures generally alter the breeding season of organisms (e.g., Møller et al., 2010; Mingozzi et al., 2022). Thus, warming may delay Dolly Varden spawning while advancing that of rainbow trout. As a result, Dolly Varden eggs and fry may die before sufficient growth due to the disruptive impact of rainbow trout spawning behavior.

The results of the new model were consistent with the assumption that white-spotted charr has a temperature-dependent negative effect on Dolly Varden (Table 3-1; Taniguchi & Nakano, 2000; Watz et al., 2019). The patterns of local extinction and distribution changes I identified support this. In the Shiretoko area, where white-spotted charr are almost absent (Morita, 2019), Dolly Varden showed almost no extirpation (Figure 3-2). Moreover, in rivers where the two species coexist, the frequency of coexistence more than doubled over the two decades (Figure S3-3). These observations suggest that white-spotted charr have begun to invade Dolly Varden's habitat over the past 20 years. Considering that the current average water temperature (mean: 12.67°C, standard deviation: 3.11°C, range: 7.30–19.88°C; Figure S3-4) has not yet exceeded the lethal threshold for Dolly Varden (26°C; cf. Takami et al., 1997), it is likely that the reduction in Dolly Varden's realized temperature niche, due to the increasing density of white-spotted charr, is gradually negatively impacting the species (chapter 2; Uemura et al., under review).

Interestingly, these patterns are consistent with results from studies on other cold-water species, such as the distribution prediction model for Arctic charr (*Salvelinus alpinus*), which belongs to the same genus as Dolly Varden. This model predicts that the competitive impact of predators like brook trout and northern pike will intensify due to global warming, leading to more severe negative effects (Bommersbach et al., 2024; Muhlfeld et al., 2024). Additionally, long-term fishery censuses have shown that Arctic char are being replaced by warmer-water species, such as brown trout (Svenning et al., 2022). These findings suggest a synergistic effect of sympatric species on the impact of warming on cold-water salmonids.

In this study, no direct impact of masu salmon on Dolly Varden was detected (Figure 3-6). However, there was a negative correlation between the density of Dolly Varden and masu salmon (Figure S3-2). A report indicates that the number of rivers where masu salmon have established new local populations has been increasing due to river improvements and the securing of upstream migration routes (Sahashi et al., 2018). Additionally, the number of masu salmon caught in coastal areas has been rising (Hasegawa et al., 2022). Theoretical predictions suggest that continued masu salmon stocking under current fisheries policies negatively impacts native species through interspecific competition (Terui et al., 2023). Although no direct impact on Dolly Varden extinction was detected, the influence of masu salmon cannot be ignored as an independent extinction factor alongside global warming.

Local groundwater temperature in summer

Although not the best model, one that considered the local increase in groundwater temperature during summer (ERA-5 model) outperformed the original model (Table 3-1). Strong evidence also supports the positive and significant effect of local summer groundwater temperature on local extirpation (Figures 3-4, 5). Dolly Varden often inhabits tributaries formed by groundwater seeping to the surface (Nakano et al., 1996; Koizumi & Maekawa, 2003; Uemura, Y., personal observation). Therefore, the increase in summer groundwater temperature is considered one of the proximate causes of Dolly Varden’s extinction.

In this study, I used actually measured air temperature and predicted groundwater temperature as alternative indicators because historical river water temperature data were unavailable. Surprisingly, the correlation between these variables and the measured water temperature was low (Figure S3-5). Furthermore, the results of the SEM indicated that summer groundwater temperature, rather than measured water temperature, was a better predictor of the local extinction of the Dolly Varden. Arismendi et al. (2012) found that air temperature increases do not explain the rise in river water temperature, based on long-term data spanning several decades. Interestingly, I observed a negative correlation between summer air temperature increases and measured river water temperatures (Figure S3-5). Although this may seem counterintuitive, increased summer air temperatures often lead to greater vegetation around rivers. Vegetation, including forests and grasslands, blocks sunlight, reducing the exposure of river water to direct sunlight. Shade from riparian vegetation is widely recognized as a major factor in the heat budget of rivers (dan Moore et al., 2005; Arismendi et al., 2012). Additionally, high summer temperatures increase evaporation, which can lower water temperature (Kadlec, 2006). Arismendi et al. (2012) also emphasized that the length and timing of time series are crucial when assessing the impact of climate change on river water temperature. In this study, the correlation coefficients between static variables and between dynamic variables (i.e., changes) were moderate to large (Figure S3-5).

However, the low correlation between the local air temperature rise and the groundwater temperature rise suggests that different mechanisms underlie local extinction caused by rising temperatures (Figure S3-5; Kurylyk et al., 2015; Ishiyama et al., 2023; Benz et al., 2024). The absolute value of groundwater temperature may not be the only important factor at a given time. For example, slight fluctuations in summer groundwater temperature can increase respiration and metabolism of fish (Riedel, 2019). If these demands are not met by food intake, energy deficiency, stunted growth, and increased mortality may occur. Conversely, many spring-fed water sources do not freeze in winter and are sometimes relatively warmer than non-spring-fed sources. In such cases, overwintering survival may be enhanced (Koizumi et al., 2017). Therefore, rising groundwater negatively affects survival in summer but positively affects it in winter. These opposing seasonal effects may cancel out on average over the year. As this study demonstrates, this could explain why local extinction effects were not detected. This study is the first to quantitatively clarify the role of groundwater in predicting salmonid distribution and extinction, from both hydrological and thermodynamic perspectives.

Conclusion

Research on global warming predictions began in the 1990s, meaning that the predicted "futures" have not yet arrived. Thus, comparing these predictions with current conditions remains challenging. However, in this study, sufficient time has passed since the original prediction (Nakano et al., 1996), which allowed for an evaluation of its long-term impact.

To my knowledge, no study has yet integrated the multiple factors explaining discrepancies between predictions and actual extinctions. Local environmental changes directly affect the physiological responses of individuals, and even minor changes can impact populations within a short period. Since Dolly Varden are cold-water fish with a narrow temperature tolerance, small temperature increases can significantly influence their abundance (chapter 2; Uemura et al., under review). A rise of less than 1.0°C could determine their survival or extinction. Furthermore, summer is a crucial period for juvenile growth and survival. The alignment of global warming effects with the species' life history likely improves prediction accuracies.

Past scenarios in Nakano et al. (1996) did not consider the distribution of rainbow trout as a factor related to future global warming. However, this variable better explains the local extinction of Dolly Varden, as SEM detected a direct rather than an indirect impact of rainbow trout. The factors identified in this study that contributed to local extinction will likely play a key role in revising extinction assessment criteria for Dolly Varden. These findings underscore the importance of accounting for co-occurring species and their ecological changes, which may be linked to or parallel with global warming, when assessing extinction risks due to climate change.

TABLE

TABLE 3-1. Ranks of groundwater temperature prediction models based on AIC and F-score (in descending order). Factors considered in each model are shaded in dark gray. The original model by Nakano et al. (1996) is shaded in gray and the text is in bold.

Model	AIC (by GLMM)	F-score	Total rank score	Macro (uniformity)	Local (variety)	Air temp annual	Air temp summer	ERA-5 annual	ERA-5 summer	WSC comp weak (× 1.05)	WSC comp moderate (× 1.10)	WSC comp strong (× 1.50)	RT comp weak (× 1.05)	RT comp moderate (× 1.10)	RT comp strong (× 1.50)
m33	67.08	0.44	82	■			■								■
m32	69.45	0.45	79	■			■							■	
m13	72.93	0.43	70	■			■			■					
m31	72.93	0.43	70	■			■						■		
m14	74.18	0.42	65	■			■				■				
m03	76.43	0.41	60	■			■								
m15	74.76	0.38	60	■			■					■			
m16	79.45	0.38	51		■		■			■					
m17	79.45	0.38	51		■		■				■				
m34	79.45	0.38	51		■		■						■		
m35	79.45	0.38	51		■		■							■	
m30	80.90	0.38	48		■	■									■
m42	81.27	0.38	46		■				■						■
m36	81.40	0.35	43		■		■								■
m09	82.93	0.34	40	■		■						■			
m04	82.51	0.34	39		■		■								
m18	82.64	0.33	37		■		■					■			
m22	83.66	0.32	35		■				■	■					
m23	84.31	0.31	32		■				■		■				
m24	84.61	0.31	32		■				■			■			
m27	85.37	0.26	25	■		■									■
m40	85.90	0.25	21		■				■				■		
m41	86.29	0.24	20		■				■					■	
m11	86.10	0.20	15		■	■					■				
m29	86.10	0.20	15		■	■								■	
m12	86.88	0.21	15		■	■						■			
m06	87.03	0.17	10		■				■						
m01	**85.86**	**0.13**	**7**	■		■									
m05	86.40	0.13	5		■			■							
m19	86.40	0.13	5		■			■		■					
m20	86.40	0.13	5		■			■			■				
m37	86.40	0.13	5		■			■					■		
m38	86.40	0.13	5		■			■						■	
m02	86.65	0.12	4		■	■									
m07	86.65	0.12	4	■		■				■					
m08	86.65	0.12	4	■		■					■				
m25	86.65	0.12	4	■		■							■		
m26	86.65	0.12	4	■		■								■	
m21	86.87	0.12	3		■			■				■			
m39	86.87	0.12	3		■			■							■
m10	87.11	0.11	2		■	■				■					
m28	87.11	0.11	2		■	■							■		

FIGURES

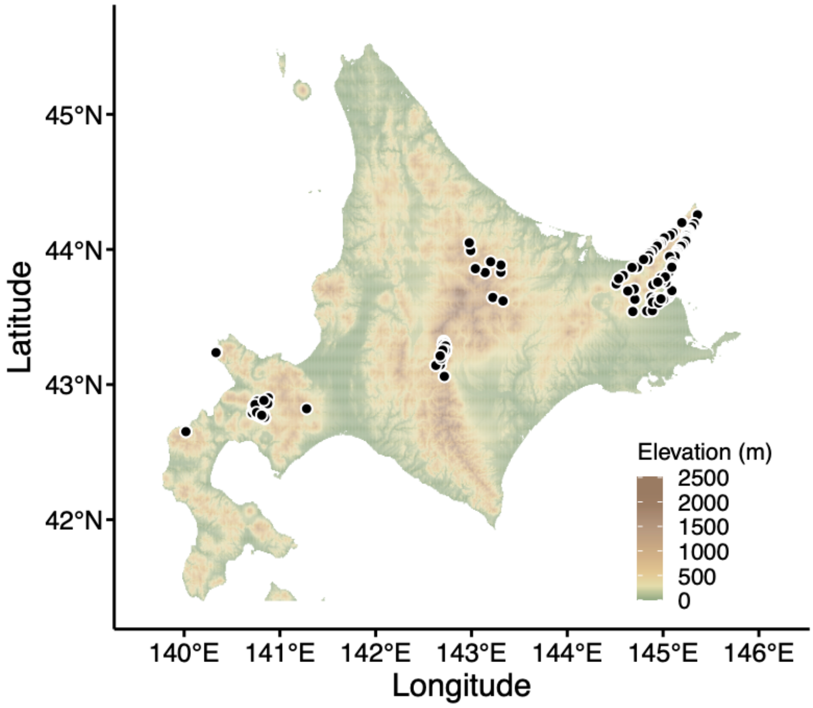

FIGURE 3-1 Map of the 141 sites where Dolly Varden were caught over 20 years ago and resurveyed during this study (see "METHODS").

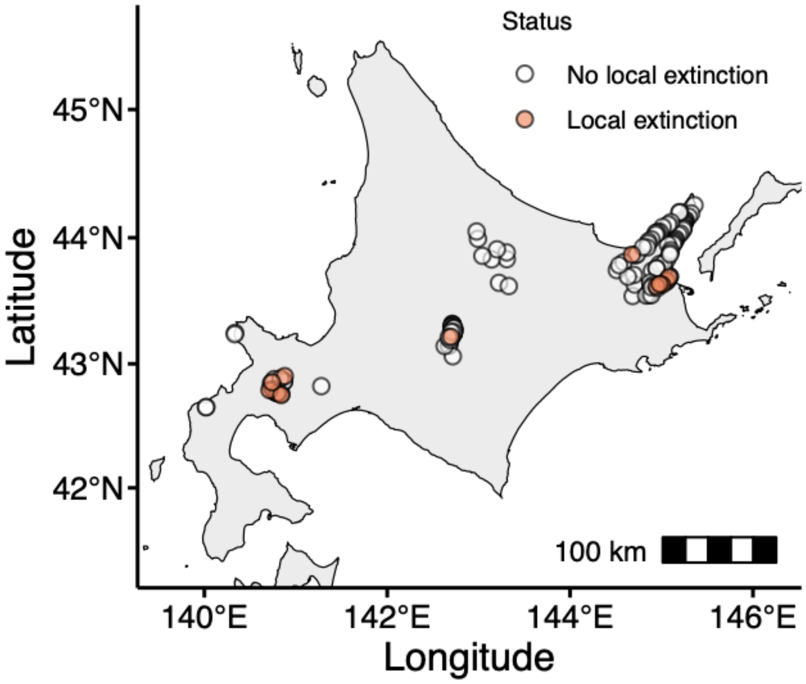

FIGURE 3-2 Map showing areas where Dolly Varden have become locally extinct (filled by orange) and areas where they have not been extinct (filled by white).

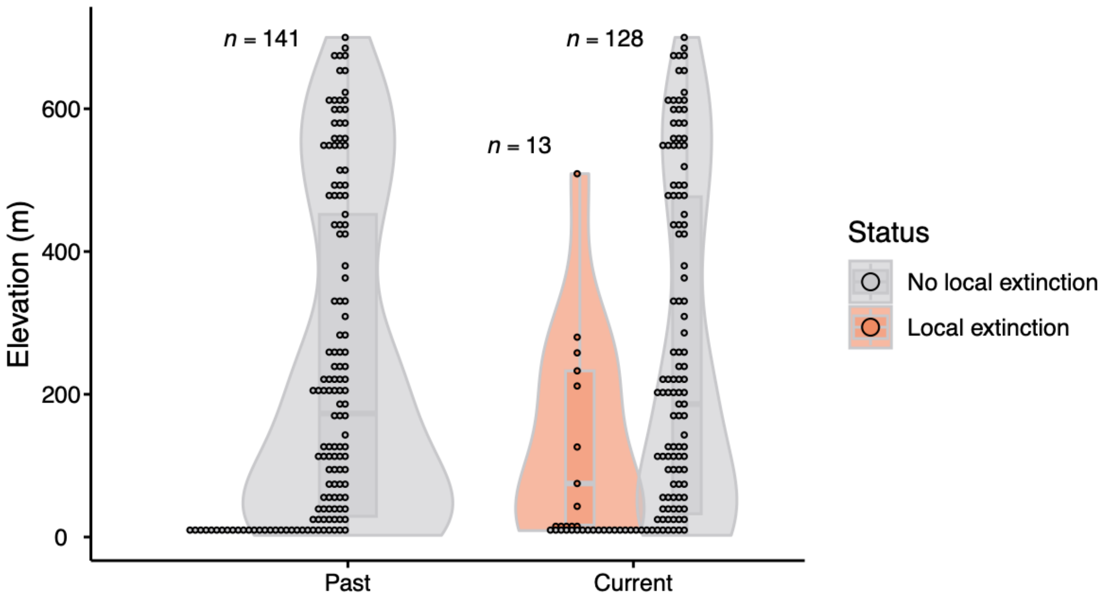

FIGURE 3-3 Local extinction of Dolly Varden (present) and changes in the elevation of their distribution over the past 20 years.

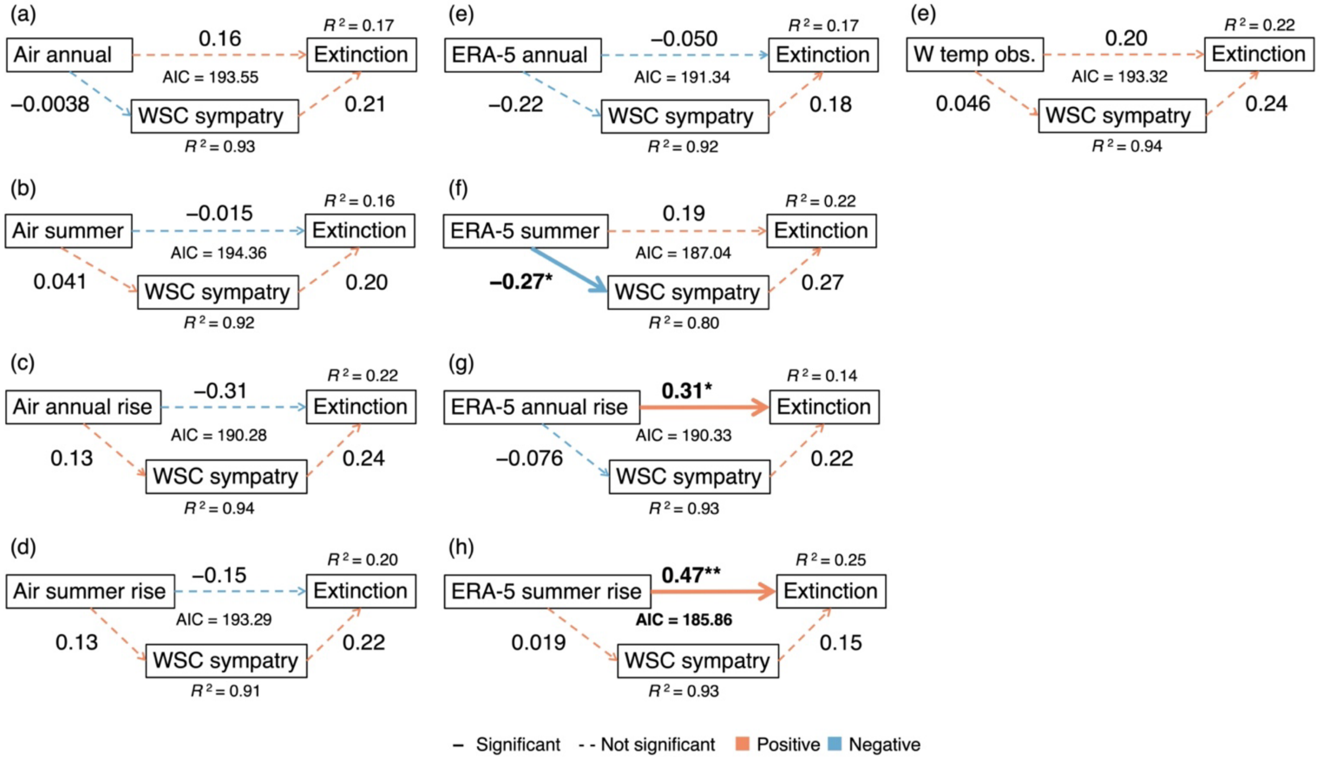

FIGURE 3-4 Direct effects of temperature increase on the local extinction of Dolly Varden, indirect effects via the co-occurrence with white-spotted charr (WSC), and direct effects of co-occurrence with white-spotted charr. Numbers shown alongside the paths are standardized estimates. The asterisks indicate the significance of the paths: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. These were estimated using structural equation modeling (see “METHODS”).

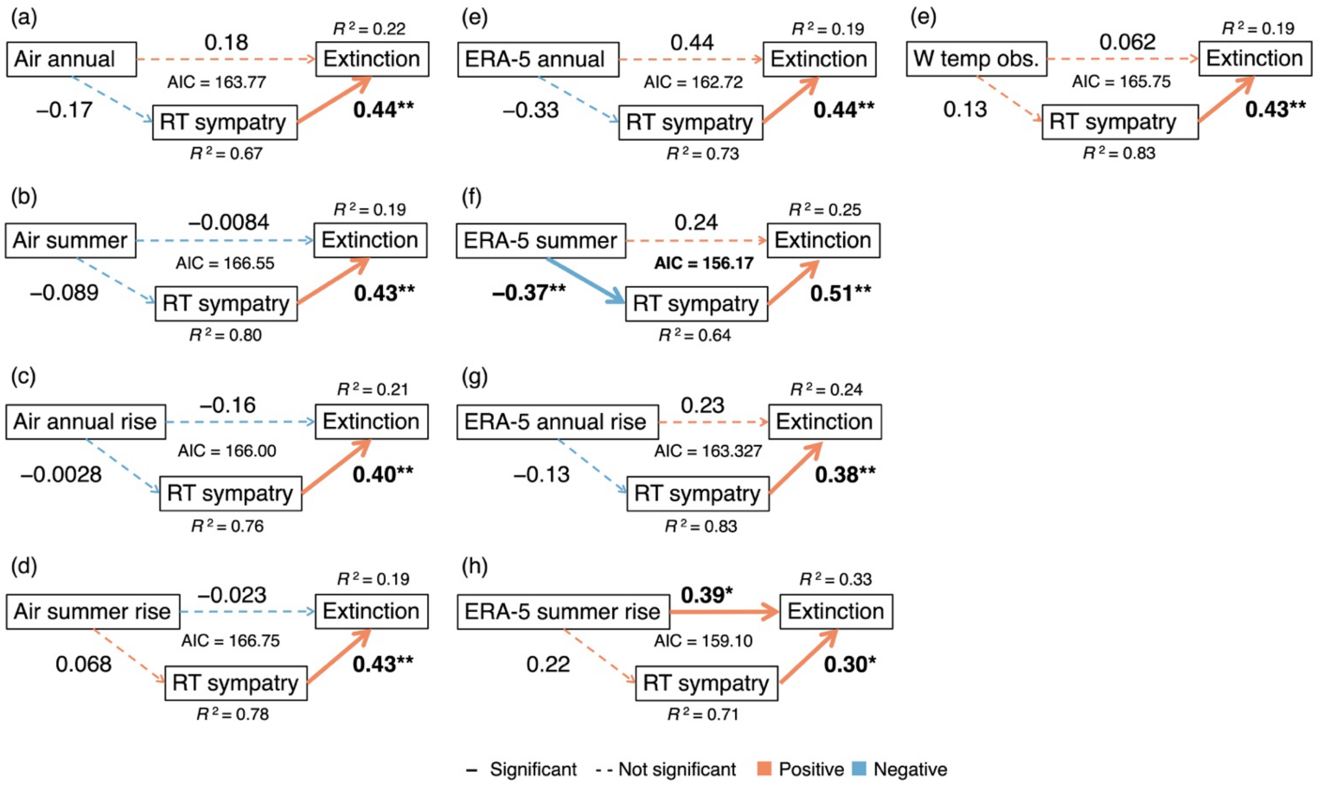

FIGURE 3-5 Direct effects of temperature increase on the local extinction of Dolly Varden, indirect effects via the co-occurrence with rainbow trout (RT), and direct effects of co-occurrence with rainbow trout. Numbers shown alongside the paths are standardized estimates. The asterisks indicate the significance of the paths: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. These were estimated using structural equation modeling (see "METHODS").

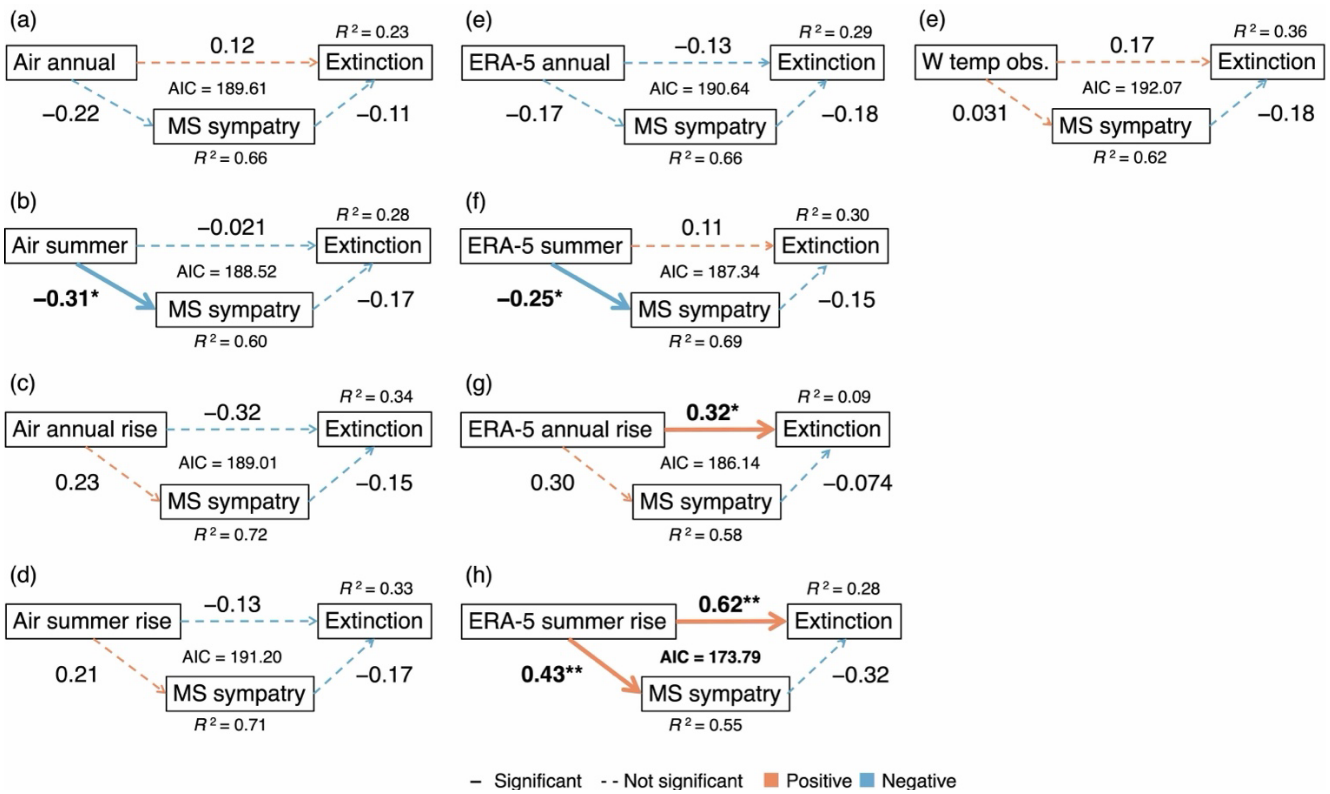

FIGURE 3-6 Direct effects of temperature increase on the local extinction of Dolly Varden, indirect effects via the co-occurrence with masu salmon (MS), and direct effects of co-occurrence with masu salmon. Numbers shown alongside the paths are standardized estimates. The asterisks indicate the significance of the paths: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. These were estimated using structural equation modeling (see "METHODS").

SUPPLEMENTARY FILES

TABLE S3-1. The formula for predicting the current groundwater temperature for each model.

Model							
01	Past groundwater temperature	+	0.939	×	MAAT		
02	Past groundwater temperature	+	0.939	×	MAAT (locally different)		
03	Past groundwater temperature	+	0.939	×	mean summer air temperature		
04	Past groundwater temperature	+	0.939	×	mean summer air temperature (locally different)		
05	Past groundwater temperature	+	0.939	×	ERA-5 (locally different) mean annual		
06	Past groundwater temperature	+	0.939	×	ERA-5 (locally different) summer		
07	Past groundwater temperature	+	0.939	×	MAAT	×	1.05 (negative-weak interaction with white-spotted charr: WSC)
08	Past groundwater temperature	+	0.939	×	MAAT	×	1.10 (negative-moderate interaction with white-spotted charr)
09	Past groundwater temperature	+	0.939	×	MAAT	×	1.50 (negative-strong interaction with white-spotted charr)
10	Past groundwater temperature	+	0.939	×	MAAT (locally different)	×	1.05
11	Past groundwater temperature	+	0.939	×	MAAT (locally different)	×	1.10
12	Past groundwater temperature	+	0.939	×	MAAT (locally different)	×	1.50
13	Past groundwater temperature	+	0.939	×	mean summer air temperature	×	1.05
14	Past groundwater temperature	+	0.939	×	mean summer air temperature	×	1.10
15	Past groundwater temperature	+	0.939	×	mean summer air temperature	×	1.50
16	Past groundwater temperature	+	0.939	×	mean summer air temperature (locally different)	×	1.05
17	Past groundwater temperature	+	0.939	×	mean summer air temperature (locally different)	×	1.10
18	Past groundwater temperature	+	0.939	×	mean summer air temperature (locally different)	×	1.50
19	Past groundwater temperature	+	0.939	×	ERA-5 (locally different) mean annual	×	1.05
20	Past groundwater temperature	+	0.939	×	ERA-5 (locally different) mean annual	×	1.10
21	Past groundwater temperature	+	0.939	×	ERA-5 (locally different) mean annual	×	1.50
22	Past groundwater temperature	+	0.939	×	ERA-5 (locally different) summer	×	1.05
23	Past groundwater temperature	+	0.939	×	ERA-5 (locally different) summer	×	1.10
24	Past groundwater temperature	+	0.939	×	ERA-5 (locally different) summer	×	1.50

TABLE S3-1. The formula for predicting the current groundwater temperature for each model (continuation of the previous page).

Model							
25	Past groundwater temperature	+	0.939	×	MAAT	×	1.05 (negative-weak interaction with rainbow trout: RT)
26	Past groundwater temperature	+	0.939	×	MAAT	×	1.10 (negative-moderate interaction with rainbow trout)
27	Past groundwater temperature	+	0.939	×	MAAT	×	1.50 (negative-strong interaction with rainbow trout)
28	Past groundwater temperature	+	0.939	×	MAAT (locally different)	×	1.05
29	Past groundwater temperature	+	0.939	×	MAAT (locally different)	×	1.10
30	Past groundwater temperature	+	0.939	×	MAAT (locally different)	×	1.50
31	Past groundwater temperature	+	0.939	×	mean summer air temperature	×	1.05
32	Past groundwater temperature	+	0.939	×	mean summer air temperature	×	1.10
33	Past groundwater temperature	+	0.939	×	mean summer air temperature	×	1.50
34	Past groundwater temperature	+	0.939	×	mean summer air temperature (locally different)	×	1.05
35	Past groundwater temperature	+	0.939	×	mean summer air temperature (locally different)	×	1.10
36	Past groundwater temperature	+	0.939	×	mean summer air temperature (locally different)	×	1.50
37	Past groundwater temperature	+	0.939	×	ERA-5 (locally different) mean annual	×	1.05
38	Past groundwater temperature	+	0.939	×	ERA-5 (locally different) mean annual	×	1.10
39	Past groundwater temperature	+	0.939	×	ERA-5 (locally different) mean annual	×	1.50
40	Past groundwater temperature	+	0.939	×	ERA-5 (locally different) summer	×	1.05
41	Past groundwater temperature	+	0.939	×	ERA-5 (locally different) summer	×	1.10
42	Past groundwater temperature	+	0.939	×	ERA-5 (locally different) summer	×	1.50

TABLE S3-2. Ranks of groundwater temperature prediction models based on false negative rate (in descending order). Factors considered in each model are shaded in dark gray. The original model by Nakano et al. (1996) is shaded in gray and the text is in bold.

Model	False negative rate	Macro (uniformity)	Local (variety)	Air temp annual	Air temp summer	ERA-5 annual	ERA-5 summer	WSC comp weak (× 1.05)	WSC comp moderate (× 1.10)	WSC comp strong (× 1.50)	RT comp weak (× 1.05)	RT comp moderate (× 1.10)	RT comp strong (× 1.50)
m01	**0.92**	■		■									
m05	0.92		■			■							
m19	0.92		■			■		■					
m20	0.92		■			■			■				
m37	0.92		■			■					■		
m38	0.92		■			■						■	
m02	0.92		■	■									
m07	0.92	■		■				■					
m08	0.92	■		■					■				
m25	0.92	■		■							■		
m26	0.92	■		■								■	
m21	0.92		■			■				■			
m39	0.92		■			■							■
m10	0.92		■	■				■					
m28	0.92		■	■							■		
m11	0.85		■	■					■				
m29	0.85		■	■								■	
m06	0.85		■				■						
m27	0.77	■		■									■
m40	0.77		■				■				■		
m41	0.77		■				■					■	
m12	0.77		■	■						■			
m22	0.69		■				■	■					
m23	0.69		■				■		■				
m30	0.62		■	■									■
m09	0.62	■		■						■			
m24	0.62		■				■			■			
m42	0.54		■				■						■
m04	0.46		■		■								
m16	0.38		■		■			■					
m17	0.38		■		■				■				
m34	0.38		■		■						■		
m35	0.38		■		■							■	
m36	0.38		■		■								■
m18	0.38		■		■					■			
m03	0.31	■			■								
m13	0.23	■			■			■					
m31	0.23	■			■						■		
m14	0.23	■			■				■				
m32	0.15	■			■							■	
m15	0.15	■			■					■			
m33	0.08	■			■								■

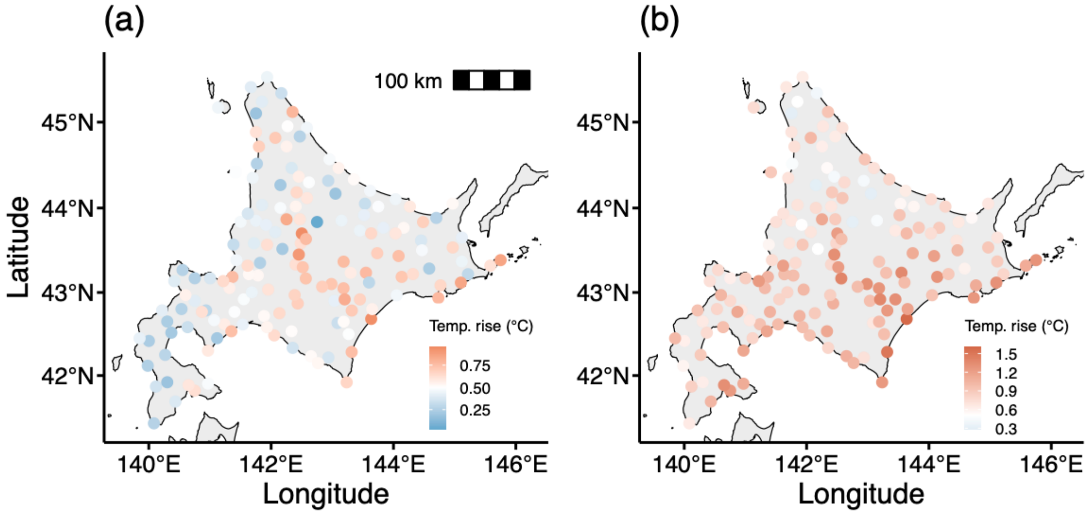

FIGURE S3-1 The increase in (a) mean annual air temperature and (b) mean summer (August) air temperature at 153 meteorological observation stations in Hokkaido over the past 20 years.

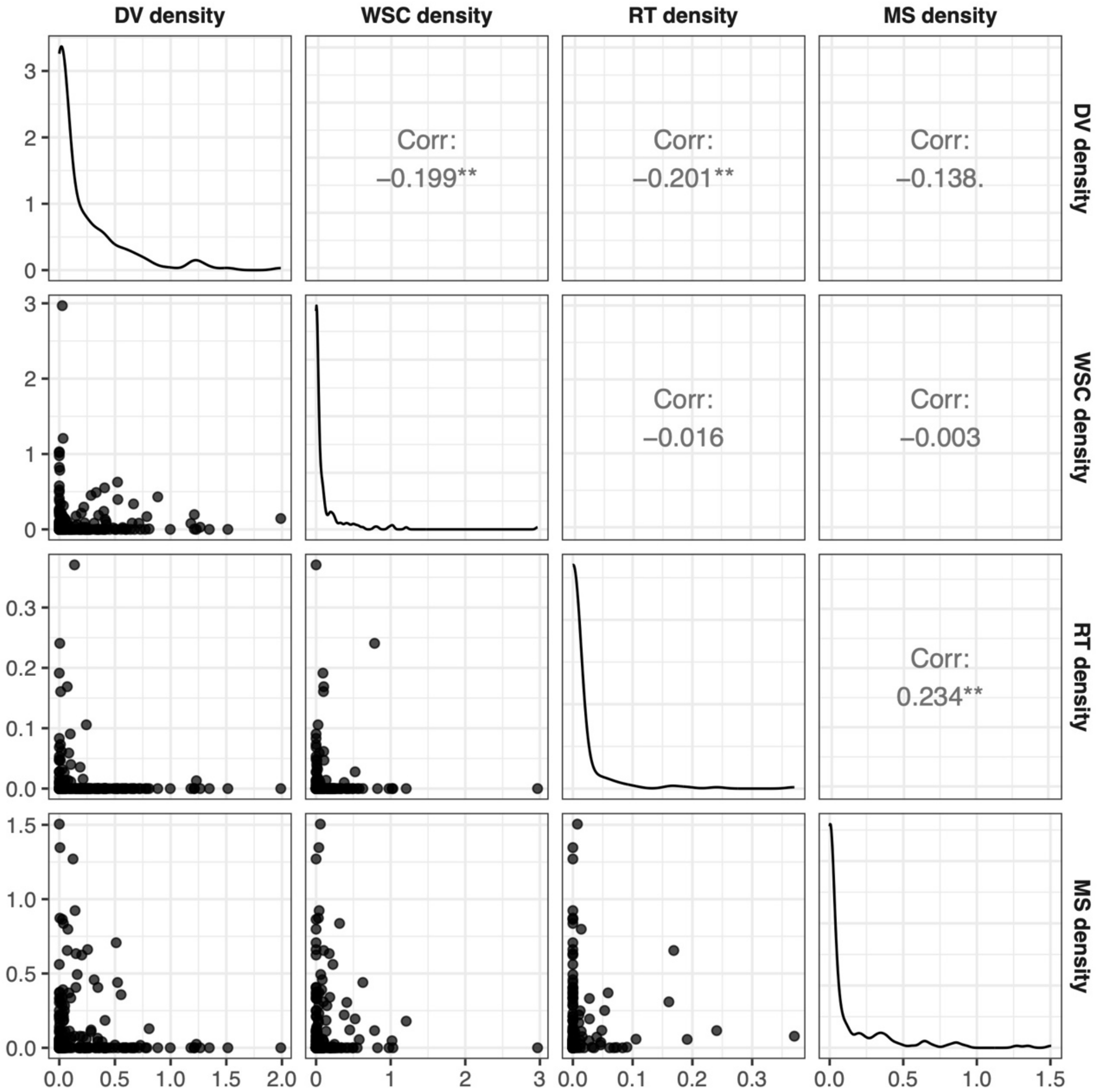

FIGURE S3-2 Correlation matrix between densities of salmonid species. DV indicates Dolly Varden, WSC indicates white-spotted charr, RT indicates rainbow trout, and MS indicates masu salmon, respectively. The Spearman's rank correlation coefficient and its significance are shown in the upper right of all the figures. The asterisks indicate the significance of the paths: . $0.05 \leq p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

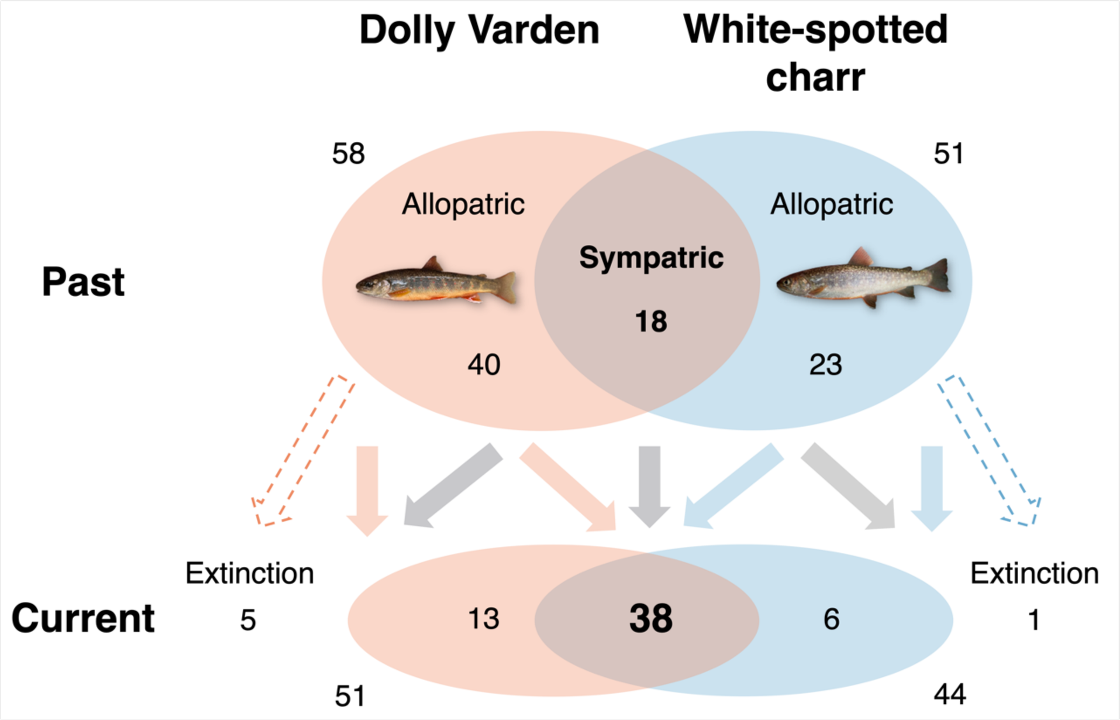

FIGURE S3-3 Changes in the number of allopatric and sympatric sites where Dolly Varden and white-spotted charr co-occurred over time.

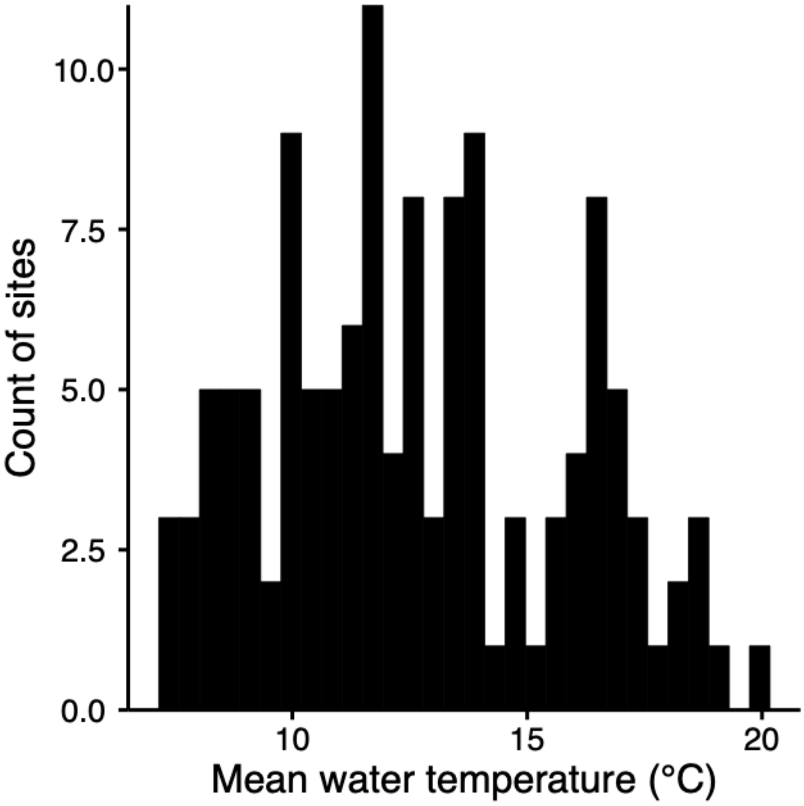

FIGURE S3-4 Histogram showing the mean stream water temperatures measured during the summer (i.e., survey period) using HOBO’s water temperature loggers and handy thermometer (see “METHODS”).

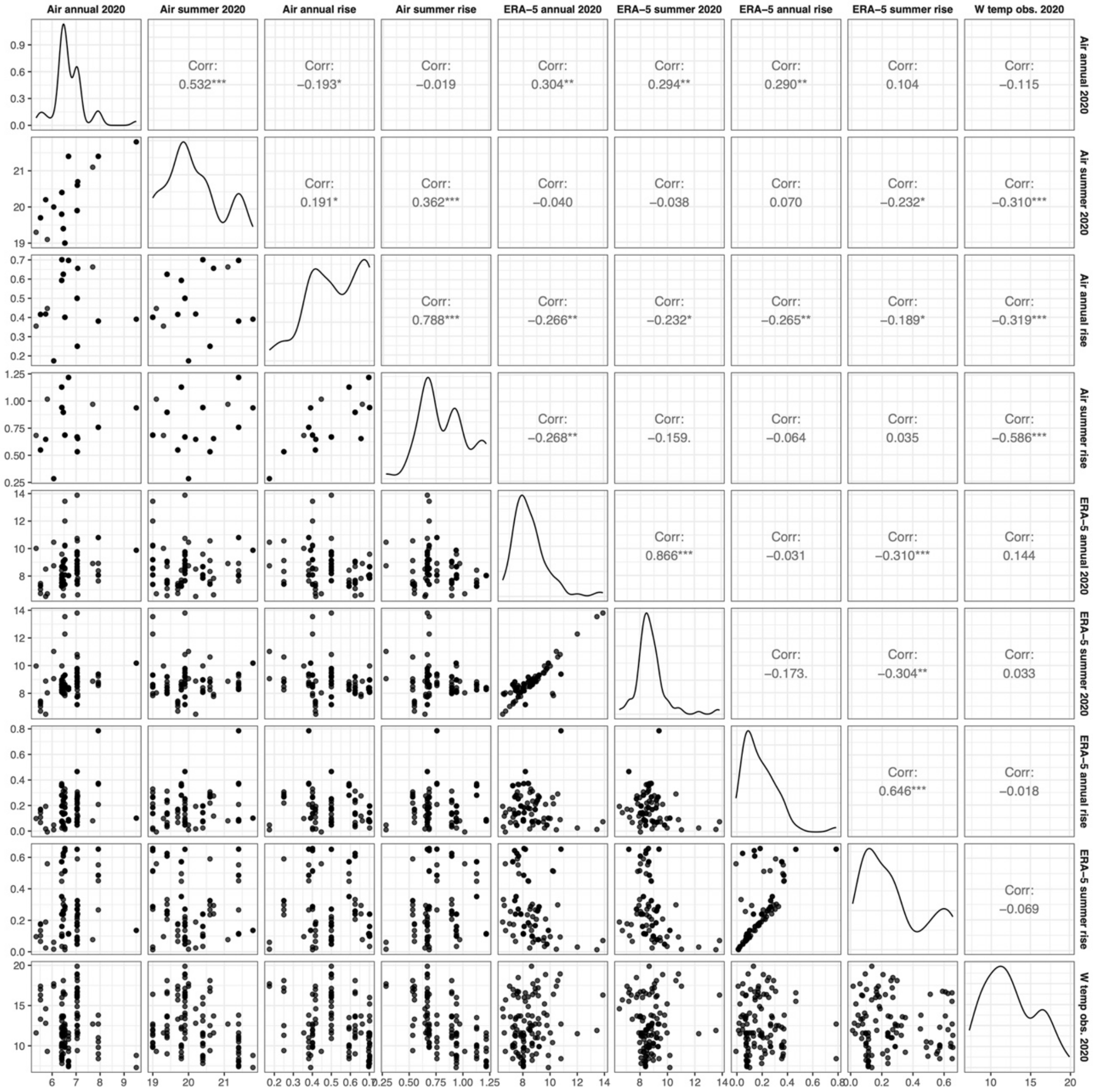

FIGURE S3-5 Correlation matrix between mean annual air temperature in 2020 and rise, and mean summer air temperature in 2020 and rise, mean annual groundwater temperature predicted by ERA-5 in 2020 and rise, summer groundwater temperature predicted by ERA-5 in 2020 and rise, and observed stream water temperature (W temp obs.). The Pearson's correlation coefficient and its significance are shown in the upper right of all the figures. The asterisks indicate the significance of the paths: . $0.05 \leq p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

CHAPTER 4

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General discussion

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Summarizing the results of this study, I first consider the reasons for the scarcity of empirical research on extinction. Next, I explain the primary factors contributing to local extinction identified in this study, with a focus on differences in temporal and spatial scales. I then address the study's limitations. Finally, I position this research within the broader context of species conservation. The main findings of this study are as follows:

(1) Mean water temperature was the most critical local environmental factor for predicting relative Dolly Varden (*Salvelinus curilus*) abundance as compared to potentially competing white-spotted charr (*S. leucomaenis*). Species composition shifted rapidly with just a 1.0°C increase in temperature. Dolly Varden density showed a significant negative correlation with water temperature. Although white-spotted charr density did not independently affect Dolly Varden density, an interaction with water temperature negatively influenced Dolly Varden abundance. Weak evidence suggested slightly lower Dolly Varden densities in areas where the two species coexisted compared to areas where white-spotted charr invasion was physically prevented. This finding highlights that local water temperature plays a crucial role in determining Dolly Varden populations during summer. Additionally, temperature-dependent competition with white-spotted charr limits Dolly Varden abundance, as the presence of white-spotted charr amplifies the negative effects of temperature.

(2) Dolly Varden have gone locally extinct at 13 of 141 sites in Hokkaido, about twice the number predicted by the previous model of Nakano et al. (1996). To investigate this discrepancy, I developed a model incorporating three new factors: local environmental conditions (air and groundwater temperatures), affecting timing (annual and summer mean temperatures), and interspecific competition. This model predicted local extinctions more accurately than the previous models. Direct and indirect effects of rising local temperatures and interspecific competition were then examined. I found that increased summer groundwater temperatures and the presence of non-native rainbow trout (*Oncorhynchus mykiss*) positively influenced local extinctions. In conclusion, Dolly Varden is disappearing faster than earlier predictions. Understanding this discrepancy requires addressing the meaningful period, local environmental changes (particularly groundwater warming), and interspecific competition.

Background of the lack of empirical research of local extinction

Why are there still so few empirical studies on prediction models? The primary reason seems to be challenges stemming from limitations in data sampling and processing methods.

In the former case, the effects of global warming are often predicted 50 to 100 years into the future based on climate scenarios (e.g., RCP8.5: Riahi et al., 2011; IPCC, 2008; Lee et al., 2023). Since research on ecological predictions of global warming began in the 1980s and 1990s (Parmesan, 2006; Zurell et al., 2023), these predicted futures have not yet been reached, making comparisons with the current situation difficult. In this study, I verified long-term effects using the early predictions of Nakano et al. (1996). This demonstrates that empirical studies in this field can contribute to validating long-term climate models. One reason for the scarcity of empirical studies is the limited extent of species distribution changes observed so far (e.g., Piirainen et al., 2023). Additionally, in many areas, local extinction has not yet occurred (Bolam et al., 2021), making it challenging to detect the impacts of climate change. These challenges may also apply to this study. Furthermore, past predictions have supported conservation efforts (Armstrong & Seddon, 2008; Naujokaitis-Lewis et al., 2021) and may have mitigated extinctions (IUCN, 2019; Bolam et al., 2021, 2023). Consequently, the risk of extinction may have decreased (e.g., Hoffmann et al., 2015). However, these assessments depend on species-specific traits, such as tolerance and resilience to warming, and may involve biases (Howard & Bickford, 2014; Barbarossa et al., 2021).

With regard to the latter, it is crucial to ensure that the number and spatial distribution of data points used in forecasts are not biased. However, endangered species often have small distribution areas, and rare species may be absent from suitable locations due to ecological and historical factors (Gogol-Prokurat, 2011). This absence can lead to model over-fitting (Vaughan & Ormerod, 2005; but see Breiner et al., 2015), complicating the estimation of potential distributions and future projections (Botts et al., 2013; Galante et al., 2018). Additionally, the rapid development of climate models tailored for future predictions may contribute to inconsistencies in past forecasts (O'Neill et al., 2020). As a result, earlier predictions are frequently updated. However, the probabilistic validity of climate models is often not evaluated (Sarofim et al., 2024). Future distribution predictions can vary significantly depending on the climate model used, necessitating careful selection (Ruiz-Diaz et al., 2024). Moreover, some studies suggest that climate models may overestimate global warming (Hausfather et al., 2022; Voosen, 2022). Therefore, improving the accuracy of these models and validating their predictions are essential for reliable future projections.

In other words, both climate and distribution models require constant evaluation and improvement to enhance their versatility for environmental and biological predictions. However, the demand for expanded research applications may often limit opportunities for performance verification. To the best of my knowledge, no research currently integrates and validates the factors explaining discrepancies between predictions and actual extinctions. This study identifies the key factors contributing to local extinction and emphasizes their significance for improving prediction models.

Importance of summer as a critical period

The local extinction of Dolly Varden was best explained by summer temperatures rather than annual mean temperatures. Dolly Varden in Hokkaido typically spawn in October and November, with juveniles emerging in February and March (Ishigaki, 1969). Their summer distribution is influenced by juvenile growth, competition, and subsequent migration or mortality. Therefore, the summer distribution reflects the outcomes of these processes. As a result, the relationship between Dolly Varden abundance and water temperature varies by season, even within the same water system (Yamada et al., 2023).

River temperatures in summer are influenced by air temperatures with a slight time lag (e.g., Rosencranz et al., 2021). When summer flow rates are restricted, the impact becomes more pronounced (van Vliet et al., 2013). Juvenile salmonids generally exhibit limited mobility (e.g., Roy et al., 2013) but migrate to avoid rising summer water temperatures (Dugdale et al., 2015). However, Dolly Varden has low migration ability and spawns and settles in relatively small tributaries (Nakano et al., 1996; Koizumi & Maekawa, 2003). Consequently, their movement range is limited for both juveniles and adults. Summer, therefore, represents a critical period due to its impact on life history and vulnerability to global warming.

At first glance, the predictions in the Sorachi River system (in chapter 2) that rising summer temperatures reduce Dolly Varden abundance appear consistent with whole Hokkaido (in chapter 3). However, local extinction has hardly occurred in the Sorachi River system. This discrepancy may result from differences in temperature variation due to spatial scale. The Sorachi River system, located at a higher altitude, experiences smaller temperature fluctuations and lower maximum water temperatures than other river systems in Hokkaido (Uemura, Y., unpublished data). If Dolly Varden extinction is determined by a physiological threshold (i.e., an absolute temperature limit) due to rising temperatures (e.g., Takami et al., 1997), the cooler temperatures in the Sorachi River system likely prevent extinction. On the other hand, the probability that temperature exceeds the threshold is high in other river systems of Hokkaido, suggesting earlier extinction elsewhere. However, a simple comparison is challenging because chapter 2 employs static data to predict distribution-environment relationships, whereas chapter 3 uses dynamic analyses of distribution and environmental changes (Essl et al., 2024).

Importance of local groundwater temperatures

In chapter 3, the analysis of the direct impact of local extinction emphasized the importance of rising groundwater temperatures in summer, based on groundwater flow and heat transport theory. On the contrary, the explanatory power of local extinction based on observed river water temperatures was weak. Although the underlying mechanism remains unclear, summer groundwater temperature increases more significantly than the annual average, like air temperature trends (Figure S3-5 in chapter 3).

Rising groundwater temperatures not only reduce oxygen saturation but also lower pH, causing acidification (Riedel, 2019). These changes accelerate the onset of physiological limits to habitation (Munday et al., 2012; Jellyman & Herding, 2014). In some cases, rising groundwater temperatures result from shallow groundwater aquifers. These temperatures are influenced by air temperature and groundwater discharge, which may lead to water depletion (Condon et al., 2020). Therefore, increases in groundwater temperature may reflect not only seasonal effects but also other groundwater properties.

In Hokkaido, many rivers are spring-fed regardless of altitude (e.g., Koizumi & Maekawa, 2003; Sakai et al., 2023; Watz et al., 2019), and many Dolly Varden habitats are near spring-fed areas (Nakano et al., 1996; Koizumi & Maekawa, 2004). Therefore, water temperature is influenced not only by air temperature but also by groundwater temperature, with a short time lag. Although temperature varies with spatial scale, groundwater temperature is initially low and changes little, so significant variation is unlikely. Therefore, the abundance or occurrence probability of Dolly Varden decreases as temperature rises. This pattern is common to both the Sorachi River system (chapter 2) and Hokkaido as a whole (chapter 3), particularly near spring-fed waters.

A unique aspect of this study is that, although the local extinction of Dolly Varden was closely related to groundwater temperature and its seasonal rise, current river water temperature, considered the most proximate factor, had a low explanatory power. In chapter 3, I examined the correlation between river water temperature, air temperature, and groundwater temperature. Surprisingly, river water temperature and groundwater temperature were not correlated.

One possible reason is the complex mechanisms by which groundwater temperature influences river water temperature. In this study, the distance from the point where river water temperature was measured to the groundwater inflow varied (Uemura, Y., personal observation). As this distance increases, river water temperature becomes more susceptible to external influences (Woessner, 2020). Additionally, temperature effects were complex. A significant negative, not positive, correlation was observed between river water temperature and air temperature (Figure S3-5 in chapter 3). This could result from two mechanisms: direct cooling from the heat of vaporization at the water surface (Kadlec, 2006) and indirect cooling from riverbank vegetation, which blocks sunlight and reduces heat input (Arismendi et al., 2012).

As distance increases, these mechanisms can either weaken or amplify the warming effect of rising air temperature, making river water temperature harder to predict. In fact, river water temperature changes rapidly, even within a few tens of meters from a groundwater spring (Iwasaki et al., 2024). In Hokkaido, river water and groundwater temperatures were almost uncorrelated (Figure S3-5 in chapter 3). However, in the upper reaches of the Sorachi River system, where many spring-fed points exist and river size is small, a positive correlation was found (Figure S4-1). This suggests that distance from the groundwater source delays the influence of groundwater and that river size and flow rate also affect groundwater contributions to river water temperature. Thus, while river water temperature may serve as a temporary habitat factor for many organisms, its high variability and sensitivity to external influences make it an unreliable predictor of long-term effects such as local extinction.

Complex effects of interspecific competition

In chapter 2, I detected an interactive effect between the density of the competitive species, white-spotted charr, and temperature on abundance of Dolly Varden in the Sorachi River system. Across Hokkaido, intensifying warming in areas where white-spotted charr occur improved the accuracy of local extirpation predictions, but no direct effect of white-spotted charr on local extirpation was observed. In contrast, there was strong evidence that the presence of rainbow trout influenced the local extinction of Dolly Varden (Figure 3-5 in chapter 3).

In general, the explanatory power of biological factors for distribution decreases with increasing spatial scale (Cohen et al., 2016; Leach et al., 2016). This is based on the assumption that the distribution has reached an equilibrium state. In the case of the target species, the native white-spotted charr has coexisted with Dolly Varden for a long time (Yamamoto et al., 2014), making this assumption applicable. Thus, recent warming was not large enough to shift the equilibrium state, and the direct impact of white-spotted charr on Dolly Varden may not have been detected in the structural equation modeling in chapter 3. Rainbow trout are widely distributed across Hokkaido, irrespective of global warming (Hasegawa, 2020), but their history of coexistence with Dolly Varden is shorter than that of native species, making it unlikely that their distribution has reached an equilibrium state. Therefore, the general rule does not apply to rainbow trout, and their strong effect on the local extinction of Dolly Varden throughout Hokkaido was detected.

The mechanisms behind the local extinction of Dolly Varden likely differ for white-spotted charr and rainbow trout. Based on the results of chapters 2 and 3, the relationship between white-spotted charr and temperature appears to be a key factor in explaining the distribution and changes in the distribution of Dolly Varden across spatial scales. Previous studies, such as those by Taniguchi & Nakano (2000) and Watz et al. (2019), have demonstrated temperature-mediated interspecific competition between both charr species, but this study is the first to demonstrate the importance of the interaction between competition and temperature in the wild populations. Therefore, the reliability of the path through which interference competition—caused by rising temperatures in white-spotted charr—affects the distribution and distribution change of Dolly Varden, via growth or survival, has increased. On the other hand, the model in which rainbow trout enhance the effect of temperature better explains the local extinction of Dolly Varden, which likely differs from that of white-spotted charr. Rainbow trout reduce Dolly Varden density (Misawa et al., 2007; Sahashi & Morita, 2016) and can drive their extinction (Baxter et al., 2007). Additionally, this is not limited to specific competitive species, but interspecific competition for resources may lower the temperature tolerance of more vulnerable species, reducing their temperature threshold for extinction (Walberg, 2024).

Although interspecific interaction primarily occurs in summer as a form of competition, its effects in other seasons, such as reproductive interference, cannot be ignored (Hasegawa, 2020). In this study, rainbow trout showed only a weak interaction with river water temperature, yet their co-occurrence with Dolly Varden directly influenced local extinction, independent of temperature effects. Thus, rainbow trout may negatively impact Dolly Varden in other seasons as well. Dolly Varden spawn in fall to winter, while rainbow trout spawn in spring (Kitano, 2004; Hasegawa, 2020). When rainbow trout invade Dolly Varden habitats, they cause redd superimposition (Taniguchi et al., 2000). This overlap likely threatens the survival of Dolly Varden eggs, fries, and juveniles.

Native masu salmon (*O. masou masou*) did not directly cause the local extinction of Dolly Varden (Figure 3-6 in chapter 3), but they can exert both positive and negative indirect effects on Dolly Varden. Masu salmon have a competitive advantage over white-spotted charr (Nakano, 1995), leading to habitat segregation and food-resource partitioning (Miyasaka et al., 2003; Morita et al., 2016). This advantage may indirectly benefit Dolly Varden by weakening the effect of white-spotted charr, creating a situation like the “enemy of my enemy is my friend” effect (Sabelis et al., 2001; Morita et al., 2023).

On the other hand, the density of masu salmon was positively correlated with rainbow trout density in this study (Figure S3-2 in chapter 3). Masu salmon can coexist with rainbow trout, even in areas where rainbow trout are already present (e.g., Shimoda et al., 2016; Hasegawa, 2018). The underlying mechanism of this coexistence remains unclear, but it may involve reach-scale niche partitioning (Hasegawa, 2020) or variations in habitat use due to migratory behavior. This coexistence could disadvantage Dolly Varden by indirectly enhancing the negative effects of rainbow trout. The recent expansion of masu salmon populations is noteworthy (Sahashi et al., 2018; Hasegawa et al., 2022; Morita, 2022). Complicating matters, this expansion is also influenced by artificial stocking, which is driven by policy decisions. Theoretical predictions suggest that continuing the current artificial stocking policy may negatively affect the habitats of other native fish species, including salmonids, through density-dependent competition (Terui et al., 2023).

These findings suggest that spatial scale, species composition, and interspecific competition contribute to the local extinction of Dolly Varden through complex direct and indirect effects.

Limitations of this study

The verification of local extinctions of Dolly Varden across Hokkaido relies on the presence-absence data at two time points: past and present. However, this approach limits the ability to quantitatively evaluate local extinctions at the region scale. With only two data points, it is impossible to determine when the extinction occurs during the time interval. To improve predictions, it is crucial to account for incomplete detection in sufficiently long time series data (e.g., Koshkina et al., 2017; Devarajan et al., 2020; Holderegger & Spillmann, 2022; Doser et al., 2023).

Analysis based on abundance data can provide more comprehensive insights (e.g., Howard et al., 2014; Ehrlén & Morris, 2015; but see Waldock et al., 2022). In the Appendix, I conducted an analysis using 18 years of long-term time series data from 22 sites in the Sorachi River system. This analysis showed that increases in water temperature led to increases in white-spotted charr populations (Figures A-1b, 2b in Appendix). However, no direct effect of water temperature on Dolly Varden was detected. Although Dolly Varden abundance temporarily decreased, it later recovered, displaying random dynamics (Figure SA-1 in Appendix). This may be because Dolly Varden in this system form a metapopulation (Koizumi et al., 2006b). Due to the limitation in the quality of the historical data, I was unable to use abundance data in this study. However, for understanding the mechanisms of extinction in detail, it is important to have a wide range of quantitative data.

In this study, I examined the effects of global warming, but I could not assess the impacts of concurrent land-use changes. This limitation arose from the lack of sufficient time-series data of land use to quantify these changes. Land-use changes can significantly alter natural landscapes, such as rivers, and affect biodiversity, including species distribution and local extinction (e.g., Feeley & Silman, 2010; Powers & Jetz, 2019; Milanesi et al., 2020). At a broader spatial scale, the impact of land use within a watershed on the local environment and species distribution is substantial. For example, deforestration increases the incoming solar radiation to rivers and raises river water temperatures (Dugdale et al., 2017). In regions where Dolly Varden inhabits, summer temperatures have risen due to deforestration (Kishi et al., 2004). Moving forward, once quantifiable data is available, it will be crucial to evaluate the relative importance of climate change, land-use change, biological factors, and their interactions.

To improve the accuracy of this research, it is essential to consider carryover effects on population dynamics caused by global warming (Ryo et al., 2019). Carryover effects are classified into the two following types: accumulative type) it occurs when short-term, successive events accumulate over time (e.g., marine heatwaves repeatedly damage intertidal communities: Ishida et al., 2023) and interactive type) it occurs when the impact mechanism changes over time (e.g., metabolic shifts: Jutfelt, 2020, changes in reproductive traits: Hasegawa et al., 2021, and the development of thermal tolerance: Minuti et al., 2022). This study examined the effects of long-term temperature changes on Dolly Varden' local extinction. Short-term, strong negative impacts of rapid temperature change likely contribute to population dynamics, although these were not considered in this study, as they were averaged out. For freshwater fish species, sharp temperature increases over short periods can cause local extinction, regardless of species-specific critical temperatures (Tye et al., 2022). This is an example of an accumulative carryover effect. In contrast, experiments suggest that brown trout (*Salmo trutta*), a salmonid species can reduce their metabolism when exposed to warmer environments

(González-Ferreras et al., 2023). This exemplifies an interactive carryover effect. Although unverified, these may also apply to Dolly Varden.

To investigate the accumulative carryover effects, it is essential to identify past events of strong negative impacts (e.g., temperatures exceeding critical thresholds) and use them as an explanatory variable. For the interactive carryover effects, changes in traits, such as temperature tolerance, could serve as response variables. A tank experiment to test critical water temperature thresholds for Dolly Varden was conducted over 30 years ago (Takami et al., 1997). Further investigation into the relationship between river water temperature and air temperature could reveal the air temperature threshold for Dolly Varden's survival, making it possible to count past threshold-exceeding events. Additionally, reconstructing the experiment with the same Dolly Varden population could assess changes in water temperature tolerance. By investigating and experimenting with these factors in the future, I will be able to gain a deeper understanding of the impacts of global warming on the local extinction of Dolly Varden and its underlying mechanisms.

Conservation implication

A major challenge in implementing conservation is the gap between the data needed for informed decision-making and the data currently available, which limits the ability to develop and communicate effective conservation strategies (Pennisi, 2010; Stephenson & Stengel, 2020). Although many historical distribution records exist for Dolly Varden, they are not always digitized or organized into comprehensive databases (see "METHODS" in chapter 3 for past distribution records). This complicates their use in research and conservation efforts. In this study, I revisited populations that had not been studied for a long time and collected data on population size, individual condition, and local habitat status. This process will not only increase the available data but also help reorganize and integrate past research (Kempel et al., 2020). These efforts will significantly advance conservation of salmonid fishes in Hokkaido, particularly focusing on Dolly Varden.

Dolly Varden is widely distributed in Hokkaido (Fausch et al., 1994; Morita, 2019), and long-term monitoring is being carried out in some areas (Koizumi & Shimatani, 2016; Hokkaido Regional Forest Office, Forestry Agency, Japan, 2023). Despite this, there are currently no conservation activities targeting this species, such as reintroduction programs. Conservation of endangered species typically focuses on preserving populations in key locations (Geldmann et al., 2013), but with rapid climate change, there is growing recognition that landscape-level conservation is more important than site-specific management (Donaldson et al., 2019).

How will the Dolly Varden population change in the future, and what can I do to prevent this? Here I estimated local extinction over the 20 years later, assuming the same rate of increase as in the past 20 years (see “METHODS” in chapter 3). The best model, which considered the negative effects of rising summer temperatures and rainbow trout presence, predicted a 63.83% local extinction rate compared to 20 years ago (approximately 60.16% compared to the present; Figure 4-1). In contrast, the original model by Nakano et al. (1996) predicted a 31.21% decline (24.22% compared to the present; Figure 4-1), less than half of the revised estimate. At first glance, predictions of such a decline may seem extreme. However, in recent years, significant population declines in salmonids have been observed over several decades. For example, between 2021 and 2022, catches of Chinook salmon (*O. tshawytscha*) and coho salmon (*O. kisutch*) in multiple rivers of western Alaska reached record lows. These catches were ca.

81% and 92% lower than the 30-year average, respectively (Schoen et al., 2023). The contributing factors are thought to be related to the river environment. These include restricted adult fish migration due to rising water temperatures and reduced river flow (Howard & von Biela, 2023) and reduced juvenile fish numbers due to increased rainfall (Murdoch et al., 2023). Furthermore, these declines are also thought to be influenced by interspecific interactions, such as competition with other species (Feddern et al., 2023; Ruggerone et al., 2023). Considering these observations and the underlying causes, the future predictions for Dolly Varden may fall within the expected range.

In chapter 3, I considered the effects of interspecific competition for the prediction, which best explains the current local extinction, though this was not possible in the past. Over the next 20 years, new threats may emerge for Dolly Varden' local extinction. However, even the conventional Nakano et al. (1996)'s model, which does not account for these threats, predicts a significant decrease in coming 20 years. Therefore, the conservation of Dolly Varden remains an urgent priority.

Effective conservation against invasive species requires identifying factors that determine their presence or absence (Rahel & Olden, 2008). Therefore, I additionally examined the relative importance of local air temperature, groundwater temperature, river water temperature, and physical river conditions: water depth (mean), water flow velocity (mean), substrate roughness, channel unit (pool-riffle-sequence index), and water surface coverage area, for the occurrence of rainbow trout. Specifically, I constructed a generalized linear mixed model with rainbow trout presence or absence as the response variable, the above environmental elements as explanatory variables, and River ID as a random effect. I then assessed the relative importance of these factors using model averaging based on models with ΔAIC < 2.00, following the AIC-based selection approach described in chapter 2. The results identified water flow velocity as the strongest positive predictor of effect size (estimate; Table S4-1). The second most influential factor was the mean water temperature. These findings highlight the importance of monitoring both water temperature and flow velocity for rainbow trout management. Climate change affects not only temperature but also river flow, with increased discharge already observed (e.g., Nilawar et al., 2019). If this trend continues, rainbow trout may expand their range, increasing the local extinction risk for Dolly Varden. Also, considering climate change factors other than warming may help prevent non-native species invasions.

The all data I have collected in this study can play a crucial role in determining conservation priorities at both the population and watershed levels. By assessing the current status of Dolly Varden populations, tracking changes over time (including local extinctions), and evaluating environmental factors that affect distribution, such as summer water temperature, I can develop more targeted and effective conservation strategies. Furthermore, the results of this research will help establish future evaluation criteria for Dolly Varden's local extinction (e.g., domestic Red List), providing policymakers with the necessary information to make informed decisions.

In summary, this research with Dolly Varden can provide a comprehensive understanding of the causes of local extinction and offers a quantitative framework for species conservation. By covering the species' entire distribution range and applying ecological focus to both basic (e.g., quantifying individual/population characteristics) and applied research (e.g., prediction considering abiotic and biotic factors), it contributes to developing more effective and feasible conservation strategies preventing local extinction.

FIGURE

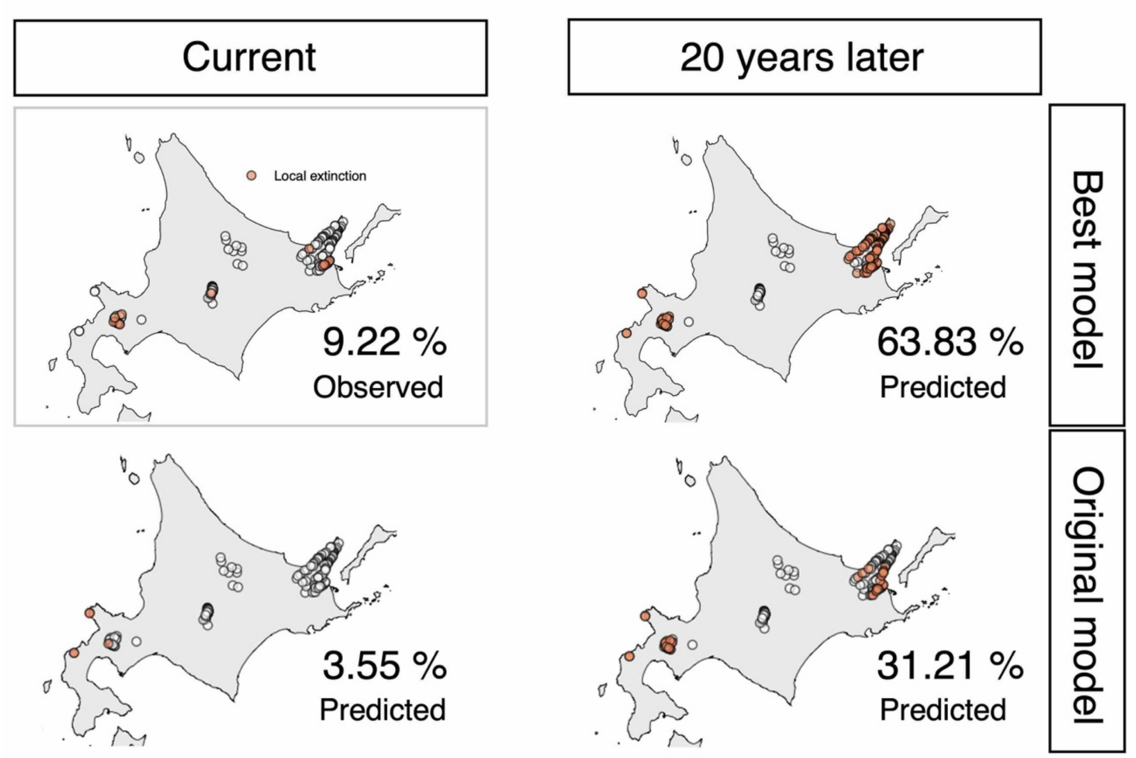

FIGURE 4-1 Current (observed, top left) and predicted (bottom left) local extinction of Dolly Varden in Hokkaido, Japan, 20 years later. The best model from this study is shown in the top right, while the original model by Nakano et al. (1996) is in the bottom right.

SUPPLEMENTARY FILES

TABLE S4-1. Results of model averaging for full models and conditional models (ΔAIC < 2). Asterisks for each variable indicate moderate to strong evidence against the null hypothesis. The top two variables with the largest effect size (estimate) are shown in bold.

Full model average

Variable	Estimate	Standard error	Adjusted standard error	Z-value	P (> | Z |)	Significance
(Intercept)	−3.02	0.97	0.98	3.07	0.0021	**
Air temp summer in 2020	−0.0025	0.11	0.12	0.022	0.98	
Air temp summer rise	−0.0094	0.12	0.12	0.08	0.94	
ERA-5 summer in 2020	−0.74	0.34	0.34	2.16	0.031	*
ERA-5 summer rise	0.11	0.28	0.28	0.40	0.69	
Observed stream water temperature	**0.96**	0.43	0.44	2.21	0.027	*
Stream depth mean	0.17	0.38	0.38	0.45	0.65	
Water velocity mean	**0.94**	0.60	0.61	1.55	0.12	
Substrate roughness	0.49	0.48	0.48	1.03	0.31	
Cover area total	0.28	0.33	0.33	0.84	0.40	

Conditional model average

Variable	Estimate	Standard error	Adjusted standard error	Z-value	P (> | Z |)	Significance
(Intercept)	−3.02	0.97	0.98	3.07	0.0021	**
Air temp summer in 2020	−0.053	0.52	0.53	0.10	0.92	
Air temp summer rise	−0.19	0.52	0.52	0.36	0.72	
ERA-5 summer in 2020	−0.73	0.34	0.34	2.16	0.031	*
ERA-5 summer rise	0.43	0.40	0.40	1.06	0.29	
Observed stream water temperature	**0.96**	0.43	0.44	2.21	0.027	*
Stream depth mean	0.66	0.48	0.49	1.35	0.18	
Water velocity mean	**1.09**	0.51	0.51	2.12	0.034	*
Substrate roughness	0.70	0.43	0.43	1.62	0.11	
Cover area total	0.47	0.31	0.31	1.53	0.13	

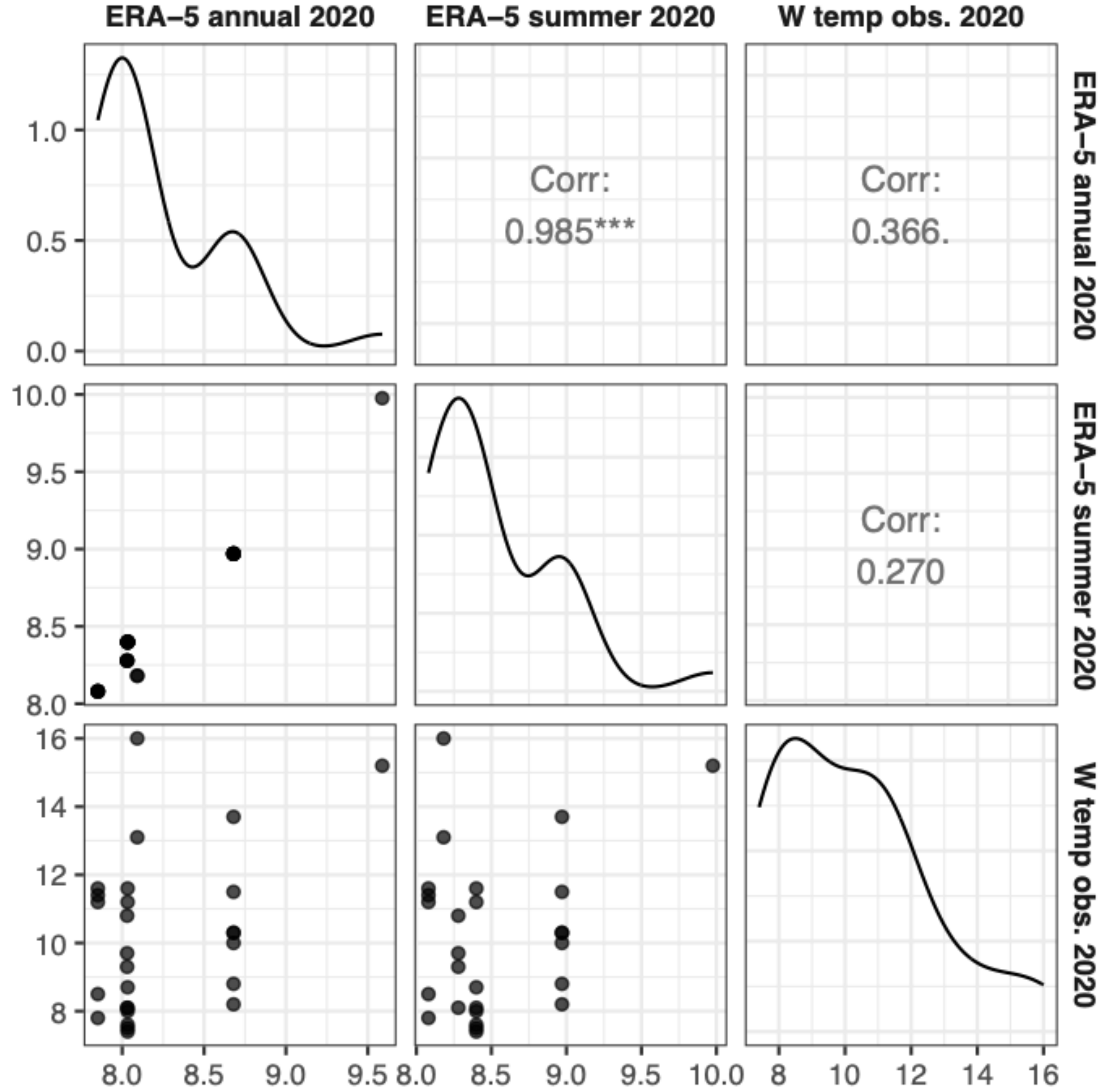

FIGURE S4-1 Correlation matrix between mean annual groundwater temperature predicted by ERA-5 in 2020, summer groundwater temperature predicted by ERA-5 in 2020, and observed stream water temperature (W temp obs.). The Pearson's correlation coefficient and its significance are shown in the upper right of all the figures. The asterisks indicate the significance of the paths: . $0.05 \leq p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

APPENDIX

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Causal relationships among local water temperature, Dolly Varden, and white-spotted charr: A test using long-term time series data

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Abstract

In the context of climate change, while many studies to predict species abundance focus on the relationship between macroclimate and species distribution, the role of local environments or microclimates remains largely unexplored. Identifying the factors that affect species abundance at the local scale is challenging because local environments are difficult to isolate spatially and are also influenced by macroclimate. Moreover, although species abundance is often predicted based on environmental correlations, the underlying causal relationships remain poorly understood. Therefore, verifying the impact of climate change with long-term data is crucial. In this study, I applied convergent cross mapping (CCM) to 18 years of census data from 22 streams to estimate the causal relationships between Dolly Varden, water temperature, and white-spotted charr. These streams, which have either spring-fed or non-spring-fed sources, exhibit random spatial variation in water temperature. My results indicated that a higher proportion of non-spring-fed water increased the likelihood of detecting a positive causal relationship between early summer water temperature and the abundance of white-spotted charr. In contrast, no causality was detected between water temperature and Dolly Varden. These findings suggest that local environments, such as spring-feds, may obscure the effects of water temperature on species abundance. Such long-term data are essential for understanding these microclimatic effects and accurately evaluating the impacts of climate change.

INTRODUCTION

Species distributions and abundances are changing dramatically due to climate change (Kelly & Goulden, 2008; Trisos et al., 2020). Consequently, there is growing interest in projecting future species distributions and abundances within the context of climate change, especially in terms of species conservation (e.g., Porfirio et al., 2014; Casazza et al., 2021). Many of these studies focus on correlations with macroclimate (Stanton et al., 2012). Interactions across different spatial scales of climate also influence species' habitat associations and the formation of species diversity (Pateman et al., 2016; König et al., 2024). However, the analysis of microclimate associations—believed to have a significant influence on many species distributions—remains at the frontier of research (Zellweger et al., 2022). For example, focusing on microclimates may improve the accuracy of predicting the impacts of climate change on organisms (Maclean & Early, 2023). On the other hand, the variation in microclimates can provide refugia, offering protection from broader climatic changes (Rull, 2009; Stark et al., 2022). Therefore, species distribution predictions may vary significantly depending on the spatial resolution of species distributions, environmental predictors, and the proportion of microclimates in the study area (Lembrechts & Lenoir, 2020).

The current fundamental challenge in predicting species abundance under climate change lies in making dynamic predictions from correlations based on static data (Essl et al., 2024). In fact, using such data to predict distribution changes has shown poor ability to predict actual distributional shifts (Santini et al., 2021; Piirainen et al., 2023). Since correlation and causation are distinct concepts (Shipley, 2016; Arif & MacNeil, 2022), it has been suggested that causality should be integrated into distributional predictions (Arif & MacNeil, 2023; Da Re et al., 2024; but see Kearney et al., 2010).

Achieving this requires validation with long-term time series datasets (e.g., Kim et al., 2022).

Another challenge in predicting changes in species distribution and abundance is spatial autocorrelation (Crase et al., 2014; Guélat & Kéry, 2018). Spatial autocorrelation refers to the correlation of environmental variables at spatially proximate points (Legendre, 1993). Furthermore, given the influence of climatic factors across spatial scales on species distributions, it is crucial to consider spatial autocorrelation at multiple scales (Václavík et al., 2012). When focusing on microclimates, it is essential to consider the influence of macroclimates and the challenges in identifying them (e.g., discovery methods outlined by Maclean et al., 2021; the importance of specific micro-mechanisms: Potter et al., 2013), which may result in overlooking the influence of nearby microclimates. Thus, there is a risk of overlooking the influence of adjacent microclimates. Verification methods that consider microclimates assume that microclimates can be unambiguously identified, and designs that minimize spatial autocorrelation with other factors are preferable.

Here I used the data on two congeneric fish species, Dolly Varden (*Salvelinus curilus*) and white-spotted charr (*S. leucomaenis*) from 22 tributaries (local populations) of Sorachi River system in Hokkaido, Japan, sampled at the same period each year over an 18-year period. This data was combined with local water temperature (microclimate) to determine the causal relationships and direction of influence between the species and temperature, using the convergent cross mapping (CCM) and multivariate S-map methods (details are provided in the following "METHODS"). Dolly Varden, a cold-water species, and white-spotted charr, a warmer-water species, are the dominant species in this system. Experiments confirmed the competitive dominance of white-spotted charr in warmer areas (Taniguchi & Nakano, 2000; Watz et al., 2019). In the context of global warming, distribution models predict a direct impact of increased water temperature on the cold-water species, Dolly Varden, and an indirect negative impact through intensified competition with white-spotted charr (Nakano et al., 1996).

This system is well suited for examining the causal relationships between local water temperature (i.e., microclimate) and both species. The sampled tributaries are small, measuring 100 m in length and 1–3 m in width, and their origins may or may not be volcanic springs (Koizumi & Maekawa, 2004; Ishiyama et al., 2023). They flow into the mainstem, and the spatial arrangement of the spring water is more or less randomly arranged by the geology (Ishiyama et al., 2023). The spring fed water maintains a low temperature (ca. 6–8°C), so it is cooler than the non-spring fed tributaries in the summer. When this is captured in reverse-scape, it appears as a mosaic of various water temperatures (see chapter 2; Uemura et al., under review). Moreover, because the physical environment, aside from stream temperature, is relatively uniform, this system eliminates concerns about spatial autocorrelation of other local environmental factors when assessing the effects of water temperature (Uemura et al., under review). Additionally, because each sampling site is small enough for the water temperature to remain constant with minimal variation, the water temperature in each tributary can be considered as a separate microhabitat. Moreover, the timing of the formation of these water temperatures remains consistent from year to year.

I investigated how the causal relationships among three variables change when tributaries with different sensitivities to local water temperature (distinct microclimates) are randomly combined and their proportions varied. Based on the static results from previous studies conducted in the same system (Uemura et al., under review), I predicted that: (1) the local water temperature has a positive effect on white-spotted charr and a negative effect on Dolly Varden, (2) there is a negative effect from white-spotted charr on Dolly Varden. Moreover, because spring-fed water is less sensitive to temperature, I predicted that a higher proportion of spring water would reduce the likelihood of detecting such causal effects.

METHODS

Study system

This study was conducted in 22 tributaries of the Sorachi River, which drains into the mainstem of the Sorachi River in the central part of Hokkaido, Japan (Table SA-1). These tributaries are classified as either spring-fed (derived from volcanic springs) or non-spring-fed (Koizumi & Maekawa, 2004; Ishiyama et al., 2023). The tributaries exhibit variability in water temperature, ranging from low variability with consistently low temperatures to high variability with high temperatures in summer (Uemura et al., under review). In this system, the tributaries are distributed in a mosaic-like pattern, and the spatial autocorrelation of water temperature (e.g., higher elevations correspond to lower temperatures) is relatively low (see chapter 2). The two dominant species in these tributaries are Dolly Varden and white-spotted charr, with very few other competitive species present (Koizumi, I., unpublished data). Dolly Varden spawn in the tributaries, where their young also grow. In contrast, white-spotted charr predominantly spawn in the mainstem, with some fry entering tributaries during early summer (Yamada et al., 2023; Koizumi, I., unpublished data). Therefore, early summer tributaries provide a suitable habitat for investigating the effects of physical environmental factors on both species, as well as the interactions between the two species.

Fish abundance and imputed missing values

Field surveys were conducted annually, 18 times during a one-week period in late June, from 2007 to 2024 (Figure SA-1). Survey transects were established in each tributary, and both species were sampled in the same manner each year using the two-pass removal method (three-pass before 2007). The abundance data were estimated by multiplying the abundance recorded in the first pass by the number of individuals observed in the second pass. To estimate population density using the removal method (2-pass removal method, model M(b), program CAPTURE; https://www.mbr-pwrc.usgs.gov/software/capture.html; Zippin, 1958), a hand net (approximately 2 mm mesh) was used in conjunction with a backpack electrofishing unit (model 12-B, Smith-Root Corporation, Vancouver, WA, USA). To minimize negative effects on individuals and other aquatic organisms, the electrofishing unit was set to direct current (DC) with voltage modulated between 200–300 V, based on the electrical conductivity of each site (Snyder, 2003). Adequate time was allowed between passes to allow for recovery of individuals not captured in the first pass. Fork length and body weight of each individual were measured to the nearest 1.0 mm and 0.1 g, respectively, after administering an anesthetic (approximately 0.5 mL per 1.0 L of water; FA100, DS Pharma Animal Health, Osaka, Japan). Age cohorts (> 0 and > 1 years) were determined based on field observations and fork length distribution (cf. Koizumi et al., 2008). Each species was visually identified. All individuals were confirmed to have recovered from anesthesia before being released at the point of capture. All field surveys involving freshwater fish, including charr, at the study site were conducted with special permission from the Hokkaido government.

Of the data, the Dolly Varden age-0 abundance data and the white-spotted charr abundance data were used in the following analysis. I also caught freshwater sculpin (*Cottus nozawae*), Sakhalin taimen (*Parahucho perryi*), stone loach (*Barbatula oreas*), and brook lamprey (*Lethenteron* sp.), but they were excluded from the following statistical analyses in this chapter. Some years had missing data, which were imputed using the kalman smoothing with *na_kalman* function from the *inputeTS* package version

3.3 in R (Moritz, 2022). All population data were *Z*-transformed (mean = 0, variance = 1) and used in all subsequent statistical analyses.

Stream temperature measurement and prediction

Local water temperature measurements in all tributaries were recorded continuously during the field period in 2009 to 2013 with an automatic-temperature logger (logged hourly; HOBO UA-001, UA-002, U20L, Onset Computer Corporation, Bourne, MA, USA; Table SA-1). I then constructed a generalized additive model for each river to predict water temperature based on data from the nearest meteorological station (Figure SA-2; Japan Meteorological Agency; available from https://www.data.jma.go.jp/obd/stats/etrn/). This allowed us to determine the sensitivity of water temperature to environmental factors for each river (cf. Valentine et al., 2024). The tributary-specific sensitivity value was considered fixed for each river and multiplied by the mean water temperature in late June of each year for that river to obtain the mean annual air temperature in June for each of 2007 to 2024 (Figure SA-3). To calculate the sensitivity, the generalized additive model, in which the target variable was the measured water temperature, the explanatory variable was the measured air temperature. The family was "gamma" (link function = "log"), was performed using the *gam* function of the R package *mgcv* version 1.9.1 (Wood & Pya, 2016). Then I classified the predicted water temperatures into two clusters, spring-fed type (low sensitivity by air temperature) and non-spring-fed type (high sensitivity by air temperature), using a Gaussian mixture model and the coefficient of variation (CV) of the water temperature. This analysis was conducted using the functions *mclustBIC* and *densityMclust* of the package *mclust* version 6.1.1 (Scrucca et al., 2023) of R version 4.4.1 (R Core Team, 2024).

Statistical analyses

All analyses were performed using R version 4.4.1 (R Core Team, 2024). Statistical significance in all analyses is indicated by *p* values, and corresponding evidence strength is reported following Blad (1986) and Muff et al. (2022).

Convergent cross mapping

Convergent cross mapping (CCM, hereafter) is a method used to test causality between two time series by examining whether the historical state of one time series can predict the future state of another. The method relies on the concept of convergent cross mapping, which involves embedding each time series in a high-dimensional space. If the time series are causally related, the embedded state of one series should map to the state of the other series. In this analysis, the optimal embedding dimension (E) was determined for each species pair by maximizing the cross-correlation between the time series. This process was repeated for multiple species pairs to determine the direction and strength of causal relationships.

To investigate the dynamic interactions between species, I applied the CCM method using the *multispatialCCM* package version 1.3 in R (Clark et al., 2015). This package provides causal inference with the same reliability as normal CCM, despite relatively short time series data, by covering them with multi-point replication. First, I determined the optimal embedding dimension (E) for each time series using the *SSR_pred_boot* function, which calculates the sum of squared residuals for different values of E. This is a crucial step for selecting an appropriate E, which ensures that the CCM method can accurately capture the underlying dynamical relationships between the species. I tested embedding dimensions from 2 to 16 and stored the results in matrices because the maximum value of time series points for this data was 18. The optimal embedding dimension for each species pair was identified by selecting the *E* that maximized the cross-correlation (rho) between the series. The *SSR_check_signal* function then verified that the system was not completely random and that the noise was not too large. The core of the CCM analysis was performed using the *CCM_boot function*, which implements bootstrapping to assess the significance of causal interactions between pairs of species. For each pair (e.g., Accm and Bccm, representing species A and B), I conducted 1,000 iterations of CCM to estimate the causal relationship. I then used the *ccmtest* function to test the significance of the causal direction (e.g., whether species A causes species B or vice versa). I repeated the above process for all relevant species pairs. For each species pair, *p* values were calculated to test the null hypothesis of no causal relationship. These *p* values were interpreted to assess whether changes in one species' abundance could be causally related to the abundance of another species. For these analyses, I used one set of 11 spring-fed streams, one set of 11 non-spring-fed streams, and 10 randomly selected sets of 11 streams to avoid bias toward any particular stream type, from the total of 22 streams in the dataset to test whether the percentage of spring-feds affects the power to detect causality.

Multivariate S-map for estimating causal direction

The Multivariate S-map method extends the original S-map technique by allowing for the simultaneous modeling of multiple variables within a system. This is particularly useful in ecological studies where interactions among several species or environmental factors need to be understood. By embedding each time series in a high-dimensional space and using neighboring data points as predictors, the method can account for complex nonlinear relationships between variables (Deyle et al., 2016; Ushio et al., 2018; Miki et al., 2024).

To explore the dynamic interactions between stream temperature and both species abundances, I employed the multivariate S-map method, which is an extension of the S-map technique designed to capture interactions among multiple variables in a nonlinear and embedded manner. This method is well-suited for modeling causal relationships in ecological systems where time series data are available, and it can identify both direct and indirect influences among multiple variables.

Key to the S-map method is the estimation of E, which determines the number of past states used to predict future states. The theta parameter controls the degree of smoothing applied to the predictions. A higher theta value leads to smoother predictions, while a lower theta value may capture more variability in the data. Optimal values of E and theta were determined through a series of trials that maximized the prediction accuracy, measured by the rho between the predicted and observed values. The S-map method uses a state-space approach, where each time series is embedded in a high-dimensional phase space. The technique predicts one variable based on the past states of itself and others in the system. The optimal embedding dimension, E, and the smoothing parameter, theta, are key parameters that influence the model's accuracy.

Specifically, the time series data were then prepared by selecting the optimal embedding dimensions for each pairwise interaction, which were previously identified from the CCM analysis. Using the *PredictNonlinear* function from the R package *rEDM* version 1.15.4 (Park et al., 2024), I estimated the optimal theta value, which controls the smoothness of the model's predictions. I performed multivariate S-map modeling for each of the following interactions:

Stream temperature → Dolly Varden abundance

Stream temperature → White-spotted charr abundance

White-spotted charr abundance → Dolly Varden abundance

Dolly Varden abundance → White-spotted charr abundance

Each interaction was modeled using the *SMap* function, where the optimal theta and embedding dimensions were determined. The coefficients of the model (i.e., the sensitivity of one variable to the other) were then extracted, with particular attention to the mean, standard deviation, and median values of the coefficients across all time points. These values were used to assess the strength and consistency of the interactions.

RESULTS

Contrary to the prediction, multispatial CCM detected no causal relationship between water temperature and Dolly Varden abundance (*p* = 0.25; Figure A-1a). Water temperature had a positive causality to white-spotted charr abundance (*p* = 0.016; Figure A-2b), consistent to the initial prediction. On the other hand, no causal relationship was detected between Dolly Varden and white-spotted charr abundance (*p* for causality of Dolly Varden to white-spotted charr = 0.35, *p* for causality of white-spotted charr to Dolly Varden = 0.43; Figure A-1c).

As predicted, multispatial CCM detected a significant causal relationship between local water temperature and the effect on white-spotted charr only in the dataset with a lower proportion of spring-fed water (i.e., non-spring feds). Additionally, as the proportion of spring-fed water increased, no significant causal relationship was detected (Figure A-2). Furthermore, the direction of causality from local water temperature to white-spotted charr, as estimated by the mean value of the coefficient using the multivariate S-map method, was positive (Figure A-3a). Contrary to expectations, no causal relationship was detected between water temperature and Dolly Varden, nor between the two species (Figure A-3c). Moreover, the direction of causality from water temperature to Dolly Varden was negative (Figure A-3b).

DISCUSSION

Long-term monitoring of multiple species and locations, as well as detailed measurements of local water temperature, revealed a positive causal relationship between water temperature and the abundance of white-spotted charr (Figures A-1b, 2b). This indicates a positive causal relationship between local water temperature and white-spotted charr especially in non-spring-fed areas. During this period, mean temperatures rise, and the days are longest between summer and spring, affecting non-spring-fed water (Figures SA-2, 3), which is sensitive to air temperature, to also increase. White-spotted charr born in the mainstem of this river system also temporarily enter the tributaries regardless of the temperature (Koizumi, I., unpublished data). It is known that higher temperatures increase the swimming endurance of white-spotted charr (Yamada et al., 2020). Additionally, the inflow of cold water generally reduces the swimming ability of fish (Lyon et al., 2008), which could further promote the invasion of white-spotted charr into non-spring-fed areas with little temperature difference from the mainstem.

The negative causal direction from water temperature to Dolly Varden may also support the underlying mechanism of this process. In this study, I did not detect a causal relationship, contrary to my expectations, but the direction of the relationship was consistently negative (Figure A-4). According to my previous static study, there was a strong negative correlation between Dolly Varden density and water temperature in summer (see chapter 2; Uemura et al., under review). Furthermore, this relationship was consistent during seasons with high temperatures other than summer (Yamada et al., 2023). My past field experiment results suggest that under limited resources in a tributary, Dolly Varden density may act as a cost (i.e., exploitative competition) for white-spotted charr invasion and growth (Uemura et al., under review). Moreover, when considering that no causal relationship was detected between the abundances of the two species, it is possible that white-spotted charr were not displaced by Dolly Varden, but rather that water temperature negatively affected Dolly Varden abundance, allowing white-spotted charr to replace them.

There are several reasons why I have been unable to detect multiple causal relationships in this study, regardless of the proportion of spring-fed water. In this water system, Dolly Varden have established metapopulations, and there is interaction between local populations (tributaries), where populations from other tributaries become established in vacant patches (Koizumi et al., 2006b). This suggests the possibility of recovery even after local extinction (e.g., due to rising water temperatures) and may have obscured the causal relationship between the two. Additionally, there is an asymmetric competitive relationship between the two species in summer, which causes habitat segregation in this water temperature mosaic scape (Hubbell et al., 2020; Skoglund et al., 2024; Uemura et al., under review). Moreover, in summer, when food resources are limited, the foraging behaviors of both species is plastic, and their diets are divided (Nakano et al., 1999). These seasonal and species-specific factors may act as a mechanism for the local coexistence of the two species and may also contribute to the difficulty of detecting interspecific interactions. However, when I examine the regional air temperature data from the observatory in this water system, I can see that it is rising (Figure SA-4). If temperature sensitivity spreads not only to non-spring-fed areas but also to spring-fed areas (Benz et al., 2024), the water temperature mosaic in the system may decrease in summer, making the situation more favorable for the invasion of white-spotted charr (Taniguchi & Nakano, 2000; Watz et al., 2019).

The important aspect of these results is that, although I did not observe a linear relationship in which either species increased or decreased (i.e., a non-linear relationship), I detected a positive causal relationship between water temperature and white-spotted charr abundance. In fact, my results and previous studies also showed a correlation between Dolly Varden and water temperature based on static data (Yamada et al., 2023; Uemura et al., under review), but no causal relationship was found in the long-term data. This highlights the possibility that, when attempting to unravel the mechanisms of population fluctuations, failing to consider microclimate and long-term processes (rather than static correlations) may lead to incorrect conclusions (Strayer et al., 2006; Morita, 2018). This also applies to distribution models analyzing climate change, as most ESMs predict changes in species distribution (i.e., variability) based on static environmental data and the corresponding static species distribution and abundance (i.e., inconsistency between input and output; Essl et al., 2024). In fact, in European forest ecosystems, the response speed of plant communities to micro- and meso-climates varied and was closely related to microclimate (Zellweger et al., 2020). In other words, when predicting the dynamic distribution of organisms, it is effective to use long-term data to clarify the time lag and degree of agreement between the spatio-temporal response of species abundance dynamics and predictors such as climate, and to incorporate this information into the models (Essl et al., 2024).

When microclimates provide refugia, it is important to identify their extent, not only in the context of climate change but also for species conservation (e.g., in setting up conservation areas: Ashcroft et al., 2012). However, in nature, microsites with similar microclimates can be located adjacent to each other, and thus they can influence one another and exhibit spatial autocorrelation. Therefore, identifying microclimates and defining their range is challenging, and locating them, even in the case of small-scale patches, can be difficult (Rull, 2009). On the other hand, I clarified the unit of microclimate by focusing on small tributaries (groundwater-derived and non-groundwater-derived) with different temperature sensitivities that are isolated from each other. In fact, small tributaries and their vicinity have been identified as potential micro-refuges for fish in river ecosystems (e.g., Wang et al., 2020). The concept of using tributaries as units of microclimate will be particularly useful for prediction and evaluation in river ecosystems that form fractal habitats. Furthermore, I demonstrated that the proportion of microclimates in a landscape affects the detection of causal relationships with species dynamics. In the future, considering causal relationships between climate, including microclimate, and populations will make predictions of species distribution and their application under climate change more realistic (Getz et al., 2018; Da Re et al., 2024).

FIGURES

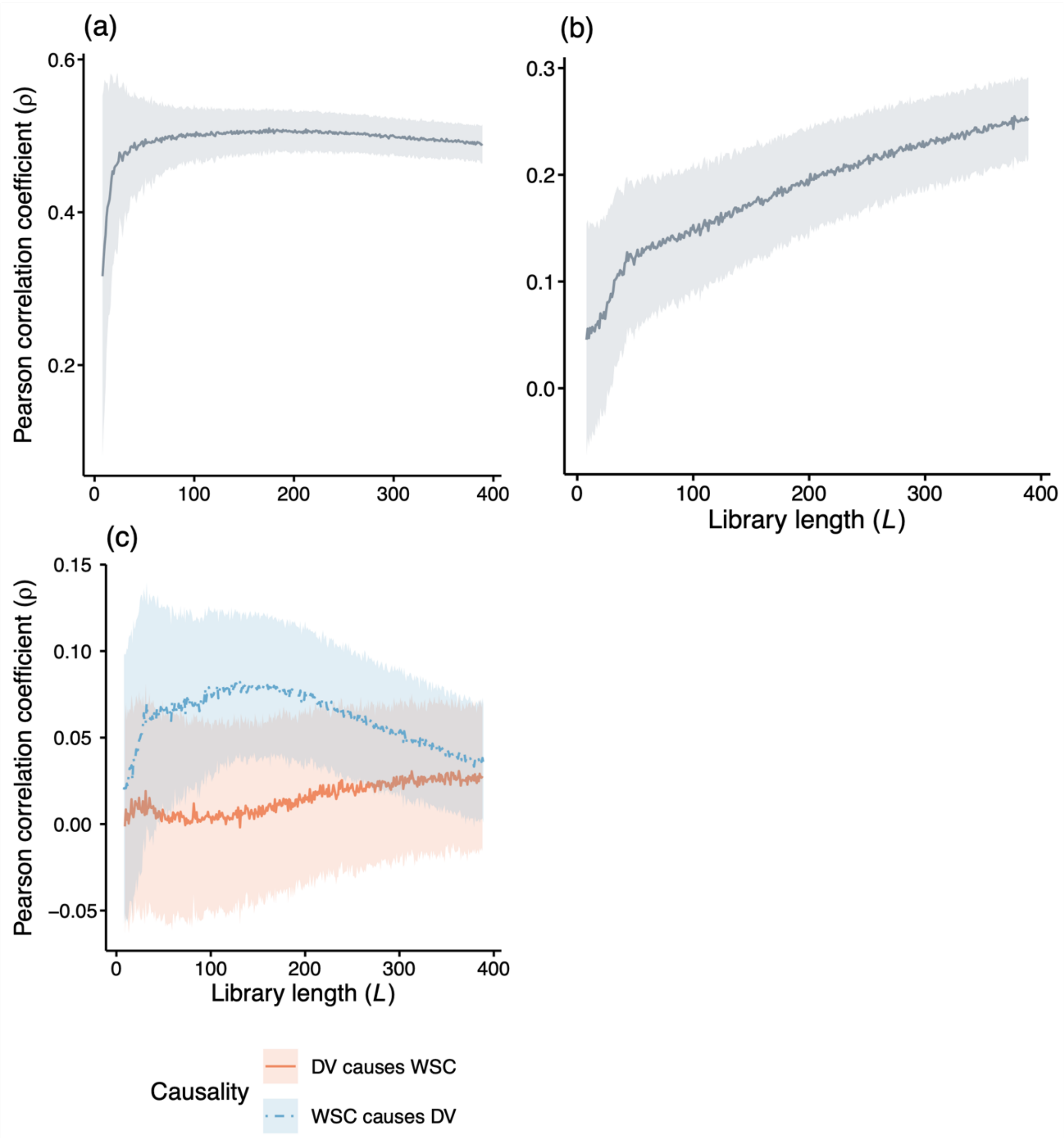

FIGURE A-1 Results of a multispatial CCM. Causal relationship (a) from water temperature to Dolly Varden abundance ($p = 0.25$). (b) From water temperature to white-spotted charr abundance ($p = 0.016$). (c) Between Dolly Varden and white-spotted charr abundance (neither was significant). Causal relationships are indicated when the Pearson correlation coefficient (ρ) increases significantly with library length, *L*.

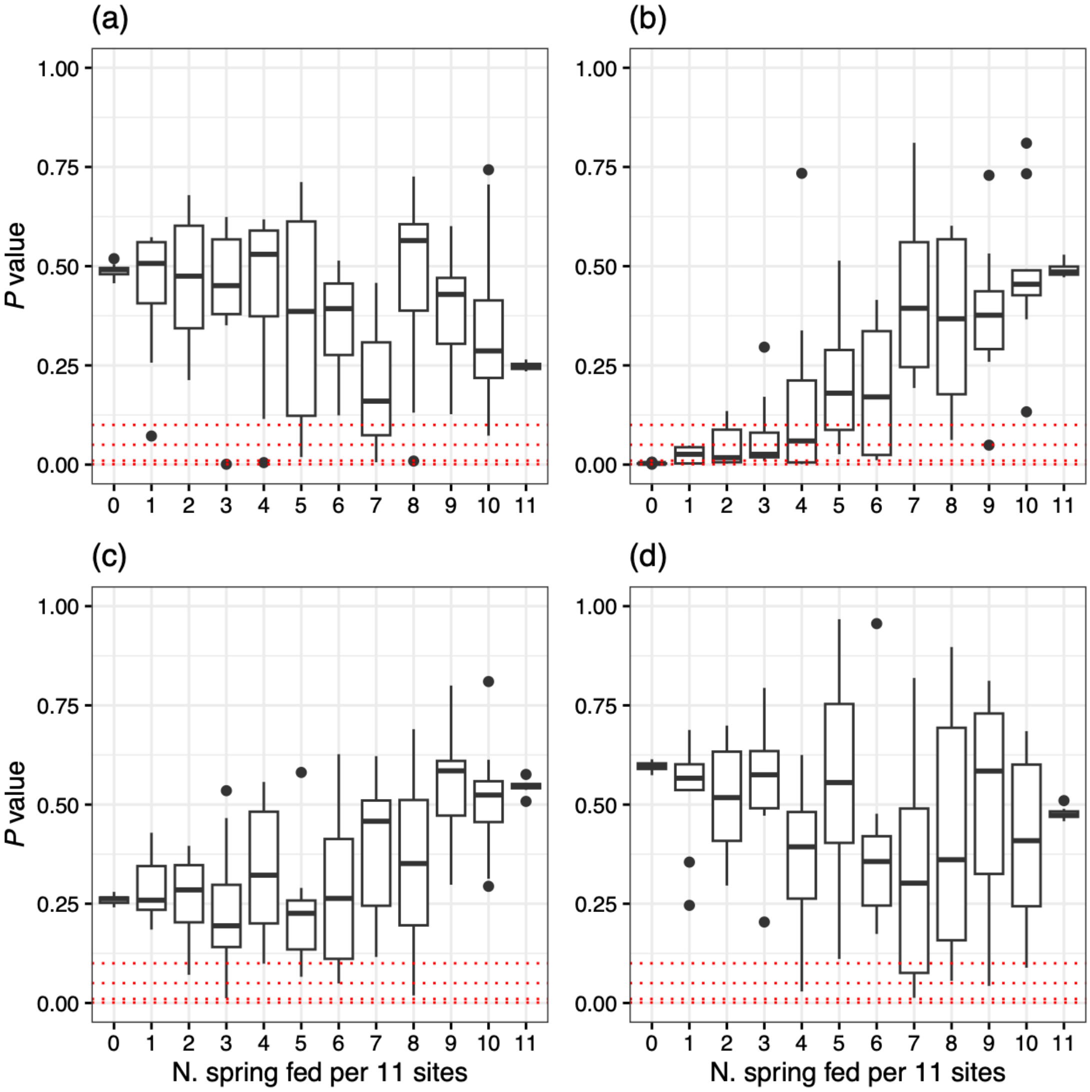

FIGURE A-2 Changes in the *p* value of the causal relationship as the proportion of spring-fed tributaries changes. (a) Causal relationship from water temperature to Dolly Varden abundance. (b) Causal relationship from water temperature to white-spotted charr abundance. (c) Causal relationship from Dolly Varden to white-spotted charr abundance. (d) Causal relationship from white-spotted charr to Dolly Varden abundance. The red dotted lines in all figures represent the significance thresholds ($p = 0.00$, 0.001, 0.01, and 0.05).

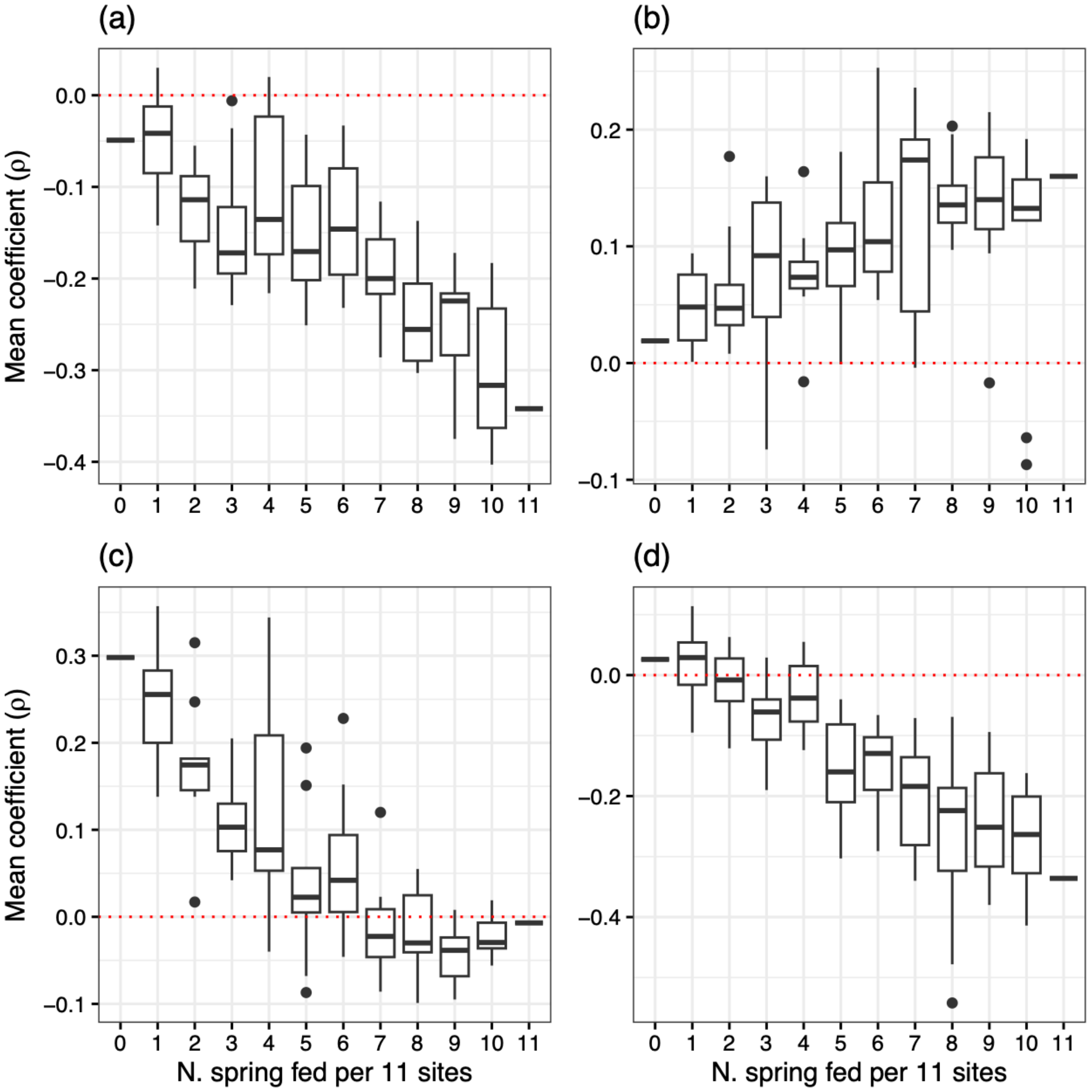

FIGURE A-3 Changes in the mean multivariate S-map coefficient as the proportion of spring-fed tributaries changes. (a) Causal relationship from water temperature to Dolly Varden abundance. (b) Causal relationship from water temperature to white-spotted charr abundance. (c) Causal relationship from Dolly Varden to white-spotted charr abundance. (d) Causal relationship from white-spotted charr to Dolly Varden abundance. The red dotted lines in the all figure represent the mean multivariate S-map coefficient is zero.

SUPPLEMENTARY FILES

TABLE SA-1. The Site ID, GPS coordinates, elevation, start and end times of water temperature measurement, and the start and end times of water temperature data used for analysis for each tributary.

SiteID	GPS (latitude)	GPS (longitude)	Elevation (m)	Start time of water temperature measurement	End time of water temperature measurement	Start time of water temperature used for analysis	End time of water temperature used for analysis
T4	43.318946	142.70974	700	2012-06-26 13:00	2013-06-16 15:00	2013-06-01 00:00	2013-06-14 23:00
T6	43.313968	142.714763	685	2008-11-01 09:00	2009-06-13 10:00	2009-05-30 11:00	2009-06-13 10:00
T10	43.285883	142.729633	617	2012-05-26 14:00	2012-08-16 06:00	2012-06-01 00:00	2012-06-14 23:00
KS	43.294736	142.703262	650	2012-05-26 15:00	2012-08-16 14:00	2012-06-01 00:00	2012-06-14 23:00
T11	43.294989	142.703583	657	2012-05-26 15:00	2012-08-16 14:00	2012-06-01 00:00	2012-06-14 23:00
T13	43.281657	142.721286	614	2012-05-26 14:00	2012-08-16 05:00	2012-06-01 00:00	2012-06-14 23:00
KU	43.279028	142.72882	599	2012-05-26 13:00	2012-08-16 09:00	2012-06-01 00:00	2012-06-14 23:00
SI	43.276356	142.732013	592	2012-05-26 13:00	2012-08-16 10:00	2012-06-01 00:00	2012-06-14 23:00
T20	43.263249	142.731855	574	2012-05-26 13:00	2012-08-16 07:00	2012-06-01 00:00	2012-06-14 23:00
TA	43.253064	142.726521	560	2012-05-26 19:00	2012-08-16 18:00	2012-06-01 00:00	2012-06-14 23:00
TS	43.251257	142.726666	557	2012-05-26 19:00	2012-08-16 18:00	2012-06-01 00:00	2012-06-14 23:00
T38	43.221362	142.704592	519	2012-05-26 18:00	2012-08-16 17:00	2012-06-01 00:00	2012-06-14 23:00
SZ	43.25469	142.700472	607	2012-05-26 18:00	2012-08-16 16:00	2012-06-01 00:00	2012-06-14 23:00
T49	43.199843	142.68882	489	2012-05-26 19:00	2012-08-16 18:00	2012-06-01 00:00	2012-06-14 23:00
T50	43.195712	142.689614	487	2012-10-20 17:00	2013-06-19 07:00	2013-06-01 00:00	2013-06-14 23:00
T50.5	43.190978	142.686459	476	2012-10-20 17:00	2013-06-19 09:00	2013-06-01 00:00	2013-06-14 23:00
T51	43.192209	142.683801	479	2012-06-27 17:00	2013-06-15 13:00	2013-06-01 00:00	2013-06-14 23:00
T54	43.172641	142.678296	452	2012-05-26 19:00	2012-08-16 18:00	2012-06-01 00:00	2012-06-14 23:00
T59.5	43.146673	142.675407	434	2012-05-26 20:00	2012-08-16 19:00	2012-06-01 00:00	2012-06-14 23:00
T61	43.145989	142.674326	435	2012-10-20 19:00	2013-06-19 17:00	2013-06-01 00:00	2013-06-14 23:00
TO	43.060413	142.716789	556	2012-06-11 04:00	2012-09-23 23:00	2012-06-11 04:00	2012-06-25 03:00
IK	43.212483	142.672697	586	2012-06-11 04:00	2012-09-23 23:00	2012-06-11 04:00	2012-06-25 03:00

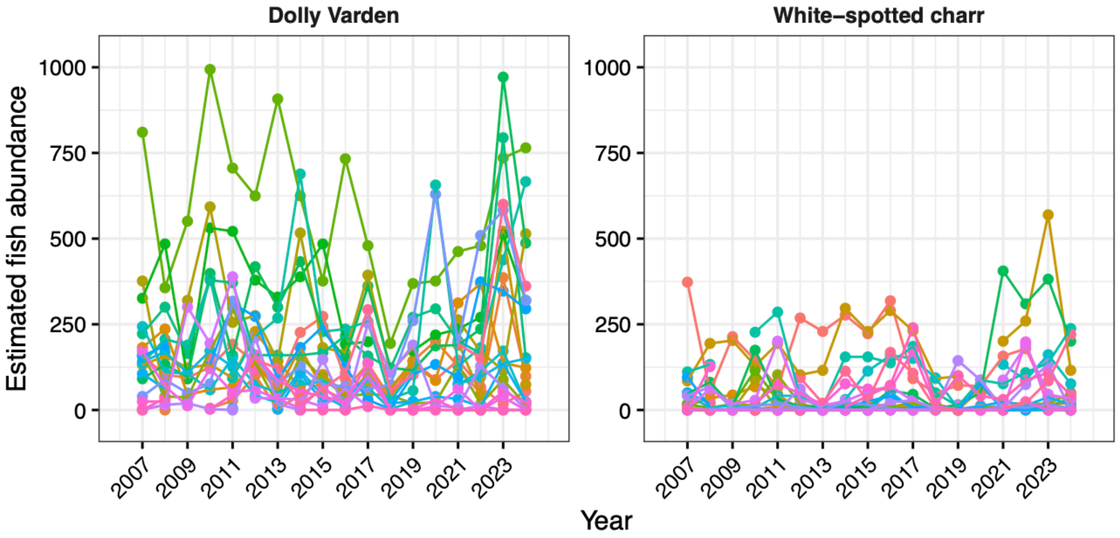

FIGURE SA-1 Dynamics of the abundance of both species based on 18 years of censuses in the Sorachi River system. Colors represent different tributaries, with tributaries that are the same connected by lines.

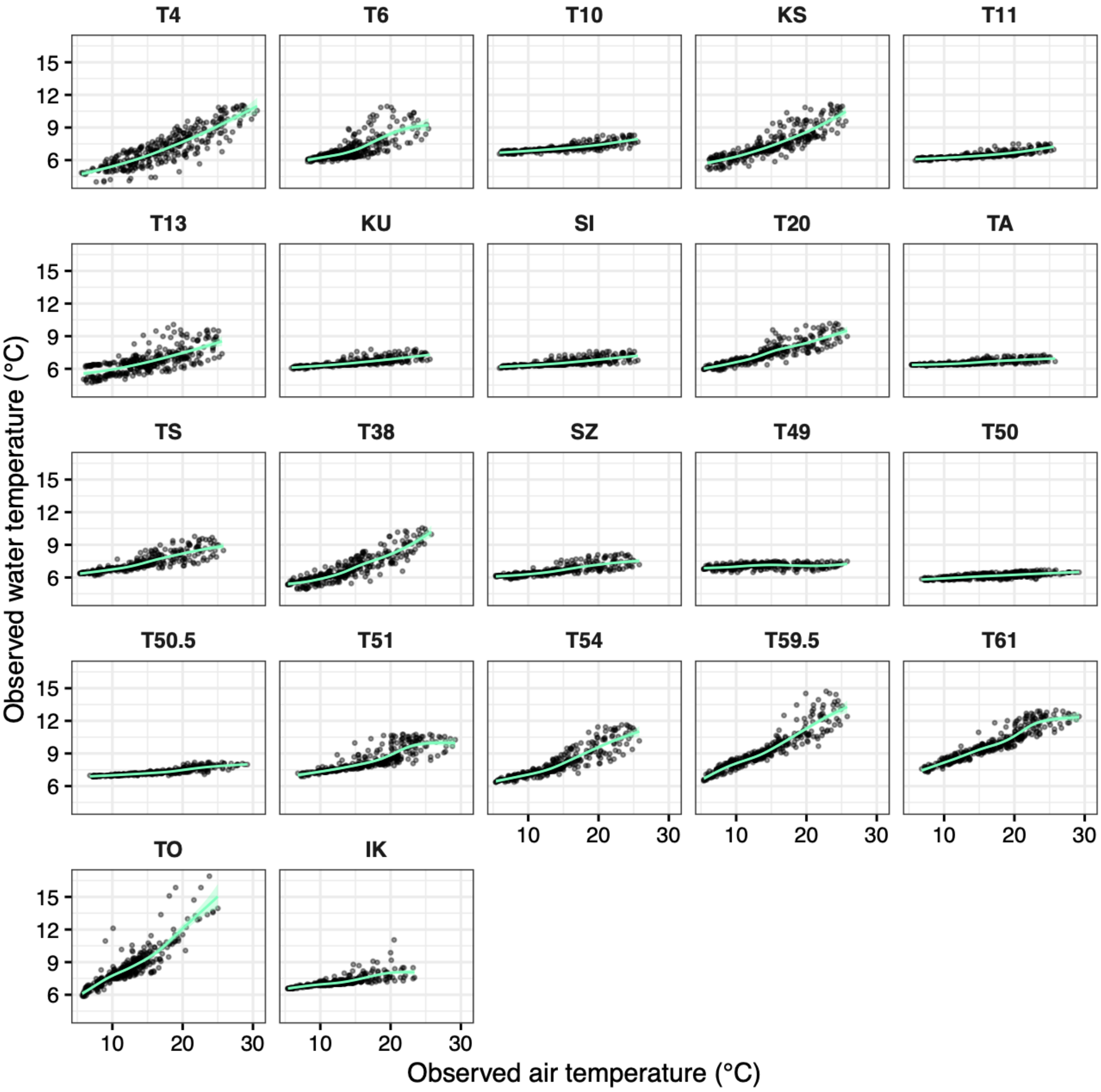

FIGURE SA-2 The relationship between water temperature and air temperature in the Sorachi River system, as measured by HOBO's loggers in snapshots between 2009 and 2013. For each tributary, the mean of the predicted values (light green solid line) and the 95% confidence interval (lighter green ribbon) obtained from the generalized additive model ("Gamma" family, "log" link function), with water temperature as the dependent variable and air temperature as the explanatory variable, are shown.

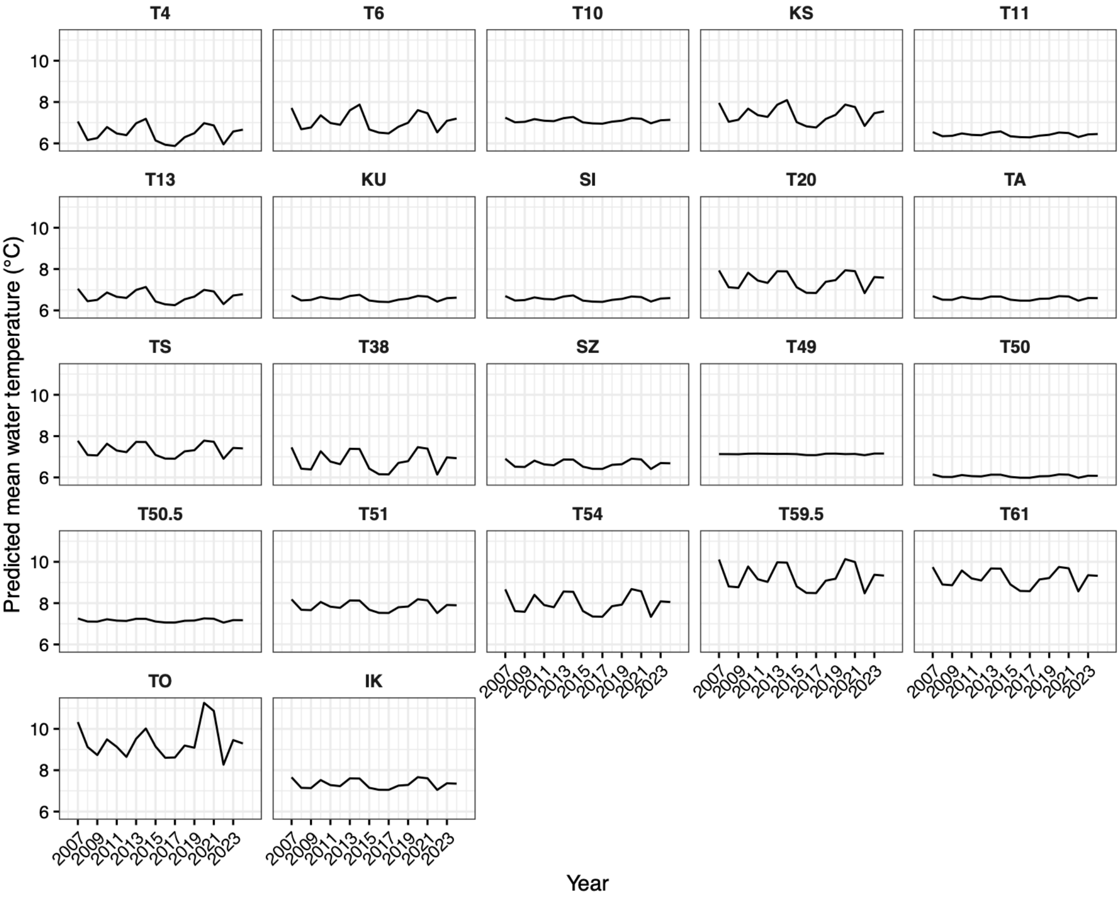

FIGURE SA-3 Mean temperatures in mid-June for each tributary and year, as predicted by the generalized additive model (see "METHODS").

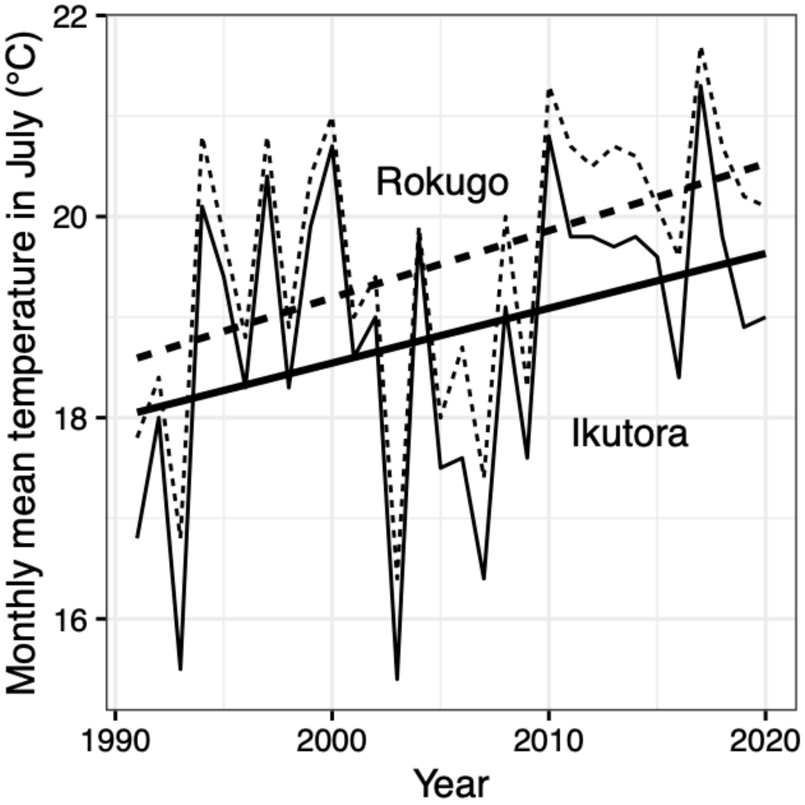

FIGURE SA-4 Changes in the mean July air temperature over the past 30 years at two temperature observation stations near the Sorachi River system. The solid line shows the results for Ikutora station, and the dashed line shows the results for Rokugo station. No time autocorrelation was detected for Ikutora (DW = 2.076, $p = 0.50$, Durbin-Watson test with the *dwtest* function in the *lmtest* package, version 0.9-40 in R). When a linear regression was performed with temperature as the dependent variable and year as the explanatory variable, the trend for year was 0.054°C ($p = 0.083$). No time autocorrelation was detected in Rokugo (DW = 2.093, $p = 0.43$, Durbin-Watson test with the same procedure), and when linear regression was performed in the same way, the annual trend was 0.067°C ($p = 0.017$).

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