Life-stage specific effects of ocean temperatures on the hatchery chum salmon

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Short running title: Causal effects for declining chum salmon

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CONFLICT OF INTEREST

The authors have declared that no conflict of interests exist.

Abstract

Pacific salmon (*Oncorhynchus* spp., Salmonidae) are exposed to environmental and anthropogenic stresses due to their wide geographic distribution and complex life history. We investigated the causal effects on return rates of Japanese chum salmon (*O. keta*, Salmonidae), focusing on the period of sharp decline since the early 2000s, using more than 40 years of fishery and hatchery release data and high-resolution sea surface temperature (SST) datasets along the Japanese coasts and SST along the Japanese chum salmon migration route. We examined the geographic distribution of chum salmon allele frequencies using published isoenzyme datasets and a single nucleotide polymorphism (SNP) dataset collected from the range, focusing on lactate dehydrogenase (LDH), growth hormone, gonadotropin-releasing hormone and mitochondrial DNA loci. The effect of SST increases or decreases varied depending on the life history stage of the chum salmon. Winter SST in overwintering areas had a positive effect on return rates, whereas summer SST in coastal areas had a negative effect. The spike in 2022 was driven by an increase in age 4 fish, and the shift in age structure towards younger age at maturity occurred in all areas, being consistent with recent studies throughout Alaska. Allele frequencies varied with geographical patterns, with those in Japan significantly different from the overall trend, and those involved in metabolism and growth were close to Alaskan populations. We hypothesise that relaxed selection in hatcheries has altered allele frequencies, resulting in better growth in the first and second winters, thereby promoting a younger age at maturity.

KEYWORDS

Anthropogenic selection, climate change, countergradient variation, growth and maturation, metabolism, younger age at maturity

1 | INTRODUCTION

Pacific salmon are widely distributed in the North Pacific and adjacent waters, and their life history is complex, with large variations in time spent in freshwater, coastal marine habitats, and the international waters (high seas) (Groot & Margolis, 1991; Quinn, 2018). Juvenile chum and pink salmon *(O. gorbuscha*, Salmonidae) spend a short time in freshwater before migrating to the ocean, while other Pacific salmon spend months to several years in freshwater, depending on their specific life history (Beamish, 2022). Salmon populations often consist of hundreds of subpopulations with diverse life history traits and local adaptations to environmental variation in spawning and rearing habitats (Hilborn et al., 2003). Their wide geographic range, long migrations for growth and reproduction, and complex life histories expose salmon populations to environmental and anthropogenic stressors at both local and North Pacific-wide scales (Cline et al., 2019).

The effects of climate change, ocean acidification, and large-scale hatchery releases on the productivity of Pacific salmon populations and body size decline have received increasing attention in recent years (Jeffrey et al., 2017; Cunningham et al., 2018; Cline et al., 2019; Losee et al., 2019; Connors et al., 2020; Ohlberger et al., 2022). Declines in body size, primarily due to a shift in age structure towards younger ages at maturity, have been found in chum, Chinook (*O. tshawytscha*, Salmonidae), coho (*O. kisutch*, Salmonidae), and sockeye (*O. nerka*, Salmonidae) salmon from large-scale analyses across Alaska and have been linked to climate change, increased inter- and intra-specific competition due to an overabundance of salmon in the high seas (Lewis et al., 2015; Oke et al., 2020; Ohlberger et al., 2023). This represents a trade-off between fish abundance and body size reduction, and the consequences for fisheries and ecosystems could be substantial (Oke et al., 2020; Ohlberger et al., 2023).

Pacific salmon abundance in the ocean is currently at an all-time high, and the most abundant species in the commercial catch is pink salmon, followed by the larger-bodied chum salmon (Myers et al., 2016; Beamish, 2022). In contrast, abundance in Japan and British Columbia, Canada, is at its lowest level on record, and the commercial chum salmon fishery was closed off the central coast of British Columbia in 2021 (Atlas et al., 2022). The abundance of salmon in the ocean is thought to be initially regulated by predation soon after the fish enter the ocean and is related to the size of the fish, the abundance and type of predators, and the density of juveniles; the second phase of mortality is a consequence of growth rate in the early ocean period and the ability of a fish to survive the first ocean winter (Beamish & Mahnken, 2001; Beamish, 2022). The effects of climate change on the winter ecology of salmon are importance for predicting coastal salmon fisheries and spawning biomass (Myers et al., 2016). Warm winter SST has been associated with improved growth, while summer SST has been associated with reduced growth of sockeye salmon in Bristol Bay, Alaska (Ohlberger et al., 2023).

Pacific salmon have the longest history of artificial propagation, beginning in the mid-1800s, and management of these species comprises the largest set of hatchery release programmes (Naish et al., 2007).

The hatchery release of chum salmon constitutes the largest marine stock enhancement and sea-ranching programme in the world (Amoroso et al., 2017; Kitada, 2018). Japan is located at the southern limit of the geographic distribution of chum salmon (Salo, 1991) and runs the world's largest hatchery release programme of chum salmon. The Japanese chum salmon hatchery release began in 1888 (Kobayashi, 1980) and has continued for 135 years (=27 generations, assuming a generation time of 5 years). Juvenile chum salmon releases from Japan have increased remarkably since the 1970s to ~2 billion per year. The number of returning chum salmon to Japan has increased dramatically since the 1970s. However, decreases in mean body weight and 'older' age at maturity occurred in 1970s-1980s, possibly due to the density-dependent effect in the high seas (Kaeriyama, 1989; Ishida et al., 1991; Hayashizaki & Ida, 1993; Morita & Fukuwaka, 2007). Despite continued hatchery releases, the number of returning chum salmon declined sharply after the early 2000s. Previous studies have reported that higher spring SSTs in the coastal zone contributed to better survival of juvenile chum salmon through improved feeding, growth and swimming ability (Saito & Nagasawa, 2009; Kuroda et al., 2020; Honda et al., 2021). Conversely, shorter inshore stays associated with warming SSTs could lead to lower juvenile survival along the Honshu Pacific coast (Kaeriyama, 2022). It is generally accepted that a warming climate may cause a decline in return rates of chum salmon. However, the underlying mechanisms leading to the decline of Japanese chum salmon remain largely unknown because few studies have used data at both the coastal and North Pacific-wide scales, from ocean entry to migration route, to infer causal effects on survival or return rates.

The number of chum salmon returning to Japan (Table S1) reached an all-time low of 19 million fish in 2021, but unexpectedly increased in 2022 (169% of the previous year in all of Japan), especially in the Hokkaido Sea of Japan (182%) and the Sea of Okhotsk (179%), while remaining very low in the Honshu Pacific (112%), the former main production area. In the Chitose River in the Sea of Japan, where Japan's oldest hatchery operates, 587,000 fish were returned in 2022, surpassing the historical record of 551,000 in 1995 (Chitose Aquarium, 2023). The sudden increase in 2022 came as a big surprise to fishers, hatchery managers, local people and biologists. This unusual phenomenon may provide us with an opportunity to understand the underlying mechanisms of chum salmon population dynamics. Several regions in the USA and Russia also showed rebounds in chum salmon catches in 2022 (Figures S1, S2). The mean body weight (BW) of Japanese chum salmon in Hokkaido and Honshu has decreased since 2000 (Yamaguchi et al., 2021; Watanabe et al., 2022). The mean BW of chum salmon returning to Japan in 2022 was 2.83 kg in Hokkaido and 2.76 kg in Honshu, which was the historical low after 1989 and 1994, respectively (Fishery Research Agency, 2023). Selection in hatcheries may cause a reduction in body size, as allele frequencies of several SNPs were significantly differentiated beyond the neutral population structure in Japanese chum salmon populations (Kitada & Kishino, 2021).

In this study, we investigate the effects of changing climate, stocking practices, predators, salmon abundance (chum and pink), and selection in hatcheries on Japanese chum salmon population dynamics, focusing on the period of sharp decline since the early 2000s. We estimated size at release and time of release for 31 million juveniles based on 58 thousand release events in 355 rivers in Hokkaido and Honshu (1998-2020). We calculated mean SSTs for the time of release based on high-resolution monthly mean SSTs in 30 coastal areas of Japan (1982-2020), and age composition based on 1,853 surveys of 1.2 million adult fish returned to Japan (1999-2019). We identified potential predators of juvenile chum salmon using catch data from Japanese fisheries covering 70 species (1980-2020). For the high seas environment, we defined the seasonal migration routes of Japanese chum salmon based on the results of the previous high seas studies (Myers et al., 2007; Urawa et al., 2018) and calculated the monthly mean SST at summer feeding and wintering grounds in the North Pacific (1982-2022). We estimated return rates for releases from 2003 to 2019 based on age composition and the number of juveniles released and adults returning. Using these data, we inferred causal factors for the decline of Japanese chum salmon through multiple regression analysis of return rates on climate, stocking practices, predation and competition at both local and North Pacific scales. Finally, we inferred the geographic distribution of chum salmon gene allele frequencies focusing on metabolism, growth, maturation, and oxygen consumption, using the published LDH allozyme data set (18,892 individuals from 147 populations), with re-examination of SNP data set (53 loci from 10,458 individuals from 114 populations) of adult chum salmon collected from the Pacific Rim.

2 | METHODS

2.1 | Data sets

We compiled data on the release and catch of Japanese chum salmon. The catch (coastal catch plus hatchery broodstock catch) and release numbers of chum salmon from 1970 to 2022 in Hokkaido were obtained from the Hokkaido Salmon Enhancement Association (HSEA, temporal translation). Those in the prefectures in Honshu were obtained from FRA. For Aomori Prefecture (in the northernmost part of Honshu), which has both Pacific and Sea of Japan coastlines, catch and release data by reporting region were obtained from the Aomori Prefectural Government (APG). They were divided into the Pacific (Pacific Coast, Tsugaru Strait and Mutsu Bay) and Sea of Japan coasts because the Tushima Current in Tsugaru Strait flows from the Sea of Japan to the Pacific Ocean (Kuroda et al., 2020), through which released juveniles recruit in the Pacific Ocean. We summarised the catch and release data of chum salmon for the seven management areas (Table S1, Figure S3): Sea of Okhotsk, Nemuro Strait, Hokkaido Eastern Pacific, Hokkaido Western Pacific, Hokkaido Sea of Japan, Honshu Pacific, and Honshu Sea of Japan (Saito & Nagasawa, 2009; Miyakoshi et al., 2013). The management areas coincided with the genetic structure of the population (Beacham et al., 2008).

Datasets on size at release and month of release from 1998 to 2020 and age composition from 1997 to 2019 in rivers in Hokkaido and Honshu were downloaded from the FRA Salmon Database (http://salmon.fra.affrc.go.jp/zousyoku/fri_salmon_dept/sdb.html) (Data S1, S2). Annual commercial catch data for all marine species in Japan from 1980 to 2020 were also downloaded from the Ministry of Agriculture, Forestry and Fisheries (MAFF, https://www.jfa.maff.go.jp/j/kikaku/toukei/). Catch (1925-2022) and release (1952-2022) data for chum and pink salmon in the North Pacific were obtained from North Pacific Anadromous Fish Commission statistics (NPAFC, https://npafc.org/statistics/).

We downloaded the global 0.25°×0.25° monthly mean SST data file from 1982 to 2022 ("sst.mnmean.nc") from the NOAA OISST high-resolution dataset (https://downloads.psl.noaa.gov/Datasets/noaa.oisst.v2/). For the Japanese coasts, we downloaded the 0.25°×0.25° daily mean SST datasets from 1982 to 2021 for 18 areas in Hokkaido (Data S3) and 12 areas in Honshu (Data S4) from the Japan Meteorological Agency (JMA). The names of the SST observation areas and the map with the JMA sources are shown in Table S2.

2.2 | Size and time at release, and age composition

The Japanese chum salmon hatchery programme recommended a release size greater than 1 g (BW) and a release time when the coastal SST ranged from 5 to 13 °C (Honda et al., 2020). Increasing body weight (BW) at release has been associated with increased return rates of chum salmon (Saito & Nagasawa, 2009), and survival of Chinook and coho salmon (James et al., 2023). We selected release events with no missing measurements of BW and fork length (FL) for Hokkaido and Honshu from the FRA salmon database (Data S1). The number of release events was 37,886 in 184 rivers in Hokkaido and it was 19,605 in 171 rivers in Honshu between 1998 and 2020. Since the number of individuals released (n_l) varied among release events ($l = 1, \dots, L$), we calculated the weighted means size at release for BW (1998-2020) as $\overline{BW} = (\sum_{l=1}^{L} BW_l\, n_l)/\sum_{l=1}^{L} n_l$, where $L = 37{,}886$, $\sum_{l=1}^{L} n_l = 21{,}332{,}093$ for Hokkaido and $L = 19{,}605$, $\sum_{l=1}^{L} n_l = 9{,}588{,}413$ for Honshu. Weighted means were also calculated for FL and Fulton's condition factor ($K = BW(g)/FL(cm)^3 \times 100$) in a similar manner.

Juvenile chum salmon spend only a short time in freshwater before migrating to the ocean (Groot & Margolis, 1991; Quinn, 2018; Beamish, 2020). In Japan, most rivers where chum salmon are released are short (less than 50 km in Hokkaido) and released fish spend only ~10 days or less before entering the ocean (Kobayashi, 1980). Therefore, the time of release can be related to the critical period in the coastal environment (Beamish & Mahnken, 2001; Beamish, 2022). To estimate the distribution of release times in Japan, we counted the number of release events by month.

Age composition is necessary to estimate the number of fish returning from each stocking. We compiled age composition data of chum salmon returns (1997-2019) with sample size in each survey (Data S2), from which we calculated the weighted mean age composition as $\hat{p}_a = (\sum_{h=1}^{H} p_{la}\, n_h)/\sum_{h=1}^{H} n_h$, where h refers to each survey ($H = 1{,}853$), n_h is the sample size (individuals) ($\sum_{h=1}^{H} n_h = 1{,}170{,}817$) and a refers to age at return (a=2,…,8<). These calculations were made for each year by management area. We summarised the compiled data for size at release (Table S3, Figures S4-S6), month of release (Figure S7) and age composition (Table S4, Figure S8).

2.3 | Long-term SST changes across the range of Pacific salmon

Pacific salmon are distributed throughout the high seas of the North Pacific, Bering Sea, Gulf of Alaska and Sea of Okhotsk (Walker et al. 2000; Myers et al. 2007; Urawa et al., 2018). Early juvenile chum salmon have recently been found in the North American Arctic (Dunmall et al., 2022). Environmental conditions such as SST at regional spatial scales largely determine salmon survival and are better predictors of survival than large-scale climate indices such as PDO (Mueter et al., 2002). To understand the long-term changes in SST in the salmon distribution area, we created the monthly mean 1°×1° SST isoclines in the North Pacific Ocean for 1900, 2000, 2010 and 2022 using the Plot COBE Sea Surface Temperature system at the NOAA Physical Sciences Laboratory (https://psl.noaa.gov/data/gridded/data.cobe.html), based on the COBE SST dataset from the Japan Meteorological Agency (JMA). The 1°×1° monthly mean SST isoclines around Japan for 1980, 2000 and 2022 are also generated in a similar way.

2.4 | SST at release

To approximate the SST values near the estuaries that juvenile salmonids are most likely to experience after entering the ocean (Oke et al., 2020), we calculated the monthly mean SSTs from 1982 to 2020 for the 18 areas in the Hokkaido coast and the 12 areas in the Honshu coast based on the 0.25°×0.25° daily SST data from the JMA (Table S2). Based on the monthly mean SSTs of the areas, we calculated the monthly mean SSTs from 1982 to 2020 in the seven chum salmon management areas (Figure S3). The monthly mean SSTs for the Sea of Okhotsk were obtained by averaging the monthly mean SSTs in the Abashiri, Monbetsu and Soya regions. For the Nemuro region, the monthly mean SSTs of the Nemuro Strait were used. Monthly mean SSTs for the Hokkaido Eastern Pacific were calculated by averaging those over Nemuro Pacific, Kushiro, and Tokachi, and for the Hokkaido Western Pacific over Hidaka, Iiburi, Uchiura Bay, western Tsugaru Strait, and Tsugaru Strait. For the Hokkaido Sea of Japan, we averaged the monthly mean SSTs of northern and southern Rumoi, Ishikari, western Shiribeshi and Hiyama. For the Honshu Sea of Japan, monthly mean SSTs were averaged from Aomori, northern and southern Iwate, Miyagi, Fukushima and northern Ibaraki. For the Honshu Sea of Japan, monthly mean SSTs were averaged from Aomori, Akita, Yamagata, northern and southern Niigata, and Toyama Bay. Finally, the mean SSTs for the months of release (Fig. S7) were calculated by management area: Sea of Okhotsk (Apr-Jun), Nemuro (Mar-Jun), Hokkaido Eastern Pacific (Mar-Jun), Hokkaido Western Pacific (Mar-May), Hokkaido Sea of Japan (Mar-May), Honshu Pacific (Feb-May), and Honshu Sea of Japan (Feb-Apr) (Table S5).

2.5 | Japanese chum salmon migration route and SST

The seasonal migration of Japanese chum salmon was modelled based on a series of high seas studies, including genetic stock identification (Myers et al., 2007; Urawa et al., 2018). According to these studies, juvenile chum salmon (age 0) are distributed in the Sea of Okhotsk until autumn (Aug-Nov) and migrate to a narrow area in the western North Pacific (hereafter North Pacific) to overwinter. After the first overwintering period, age 1 chum salmon migrated to the Bering Sea to feed until the following summer. Immature salmon began migrating to the Gulf of Alaska in late autumn for the second overwintering period (age 2). The following year, they return to the Bering Sea and again migrate to the Gulf of Alaska to overwinter (age 3). The migration between the Bering Sea and the Gulf of Alaska is repeated until they return to Japan through the Bering Sea.

Juvenile chum salmon born in rivers along the Pacific coast of Japan migrate to the Sea of Okhotsk (Honda et al., 2017). Juvenile chum salmon from all regions of Japan are found in the Sea of Okhotsk, and there is a significant positive correlation between the abundance of juvenile Japanese chum salmon and adult returns to Japan (Urawa & Bugaev, 2021). Juvenile chum salmon were abundant in coastal areas of the Sea of Okhotsk from May to June when SST were between 8 and 13°C, while they disappeared from coastal waters after late June when SST exceeded 13°C (Nagata et al., 2007). Based on these results, we assumed that juvenile chum salmon released in all areas would migrate to the Sea of Okhotsk and disperse offshore in July.

Based on information obtained from field surveys (Urawa et al., 2018; Urawa et al., 2022), we defined the locations of four main areas of Japanese chum salmon migration: 1. Sea of Okhotsk Japan Coast (45.2°N-46.5°N, 142.5°E-148.5°E), 2. North Pacific Ocean (NPO, 42°N-45°N, 158°E-165°E), 3. Bering Sea (53°N-58°N, 175°E-170°W), 4. Gulf of Alaska (48°N-56°N, 140°W-150°W). Using the NOAA OISST 0.25°×0.25° data "sst.mnmean.nc", we calculated the monthly mean SSTs from 1982 to 2022 for the migration areas using the `fldmean` function in the `cdo-2.1.1` package (Climate Data Operators, https://code.mpimet.mpg.de/projects/cdo) (Data S5). We described the areas and migration routes on the map using the `sf` package in R. Trends in the monthly mean summer and winter SSTs (Table S6) were tested using the `MannKendall` function in R.

2.6 | Catch of marine species in Japan

Predation immediately after fish enter the ocean is considered a major cause of salmon mortality, depending on fish size, juvenile density, and predator abundance and species (Beamish, 2022). To identify potential predators of juvenile chum salmon, we summarised commercial catches of all marine species landed in Japan with no missing data from 1980 to 2020. Marine mammals were excluded because they are subject to strict catch limits. This resulted in catch data for 56 out of 70 species, including 39 fish, six crustaceans, five shellfish, four animals and two algae (Table S7). To characterise temporal changes in catch, we performed principal components analysis (PCA) on the catch data for the 56 marine species using the `prcomp` function in R. Changes in chum salmon catch and species with increasing catch in the chum salmon range were plotted on the map.

2.7 | Return rates

Return rate has been widely used as a general measure of the effectiveness of enhancement of marine stocks, including salmonids (Kitada, 2018, 2020). It has been used as a measure of relative survival for chum salmon (Kaeriyama, 1999; Saito & Nagasawa, 2009), Chinook and coho salmon (James et al., 2023). It is generally accepted that most chum salmon in Japan are hatchery-reared fish (Hiroi, 1998; Kaeriyama, 1999; Kaeriyama & Edpalina, 2004; Kobayashi, 1980; reviewed by Iida et al., 2018). We assumed that all returning chum salmon were hatchery-released. Return rates were estimated for each management area. The total number of fish returning from releases in year *t* (Y_t, coastal commercial catch plus river catch for hatchery broodstock) from releases in year t is estimated as

$$\hat{Y}_t = \sum_{a=A_{min}}^{A_{max}} y_{t+a-1}\, \hat{p}_{a,t+a-1} = \sum_{a=A_{min}}^{A_{max}} \hat{Y}_{a,t}$$

where y_{t+a-1} is the observed number of fish returned in year $t+a-1$ from juveniles released in year t, and$\hat{p}_a$ is the estimated proportion of age *a* fish among the fish returned in year $t+a-1$,The return rate of juveniles released in year *t* was estimated by $\hat{R}_t = \hat{Y}_t / X_t$, where X_t is the number of hatchery-reared juveniles released in year *t* (known). The age-specific return rate was estimated as $\hat{R}_{a,t} = \hat{Y}_{a,t} / X_t$. We summed the number of fish returned from ages 2 to 5 ($A_{min} = 2$, $A_{max} = 5$) because the main ages of return were ages 4 and 5, and there were very few returns older than Age 6 (Table S4).

We estimated the age composition from Data S2 (1997-2019), but it was not available for 2020-2023, which was estimated as a moving average of the previous three years. The number of fish returning in 2023 was currently unknown (September 2023) and we estimated it as an average of those in 2021 and 2022 to predict only the number of age 5 fish returning in 2023 from the 2019 release. Based on the age composition, we calculated the number of returning fish (ages 2-5) for each release year, from which we estimated return rates and age-specific return rates from 2003 to 2019. We summarised the return rates by management area used for the regression analysis (Table S8).

The distances between return rates in the management areas were measured by $1 - r_{jk}$ and visualised by a neighbour-joining (NJ) tree in the R package `ape`, where r_{jk} is the correlation coefficient between pairs of return rates. We visualised the relationship between geographical distance and return rates by management area. Great circle geographical distances between hatcheries and the central coast of the Sea of Okhotsk (off Monbetsu, 44.5°N, 143.5°E) were calculated using the distm function in the R package `geosphere`, assuming 6 waypoints representing reasonable migration paths from the hatcheries to off Monbetsu: Fukaura (40.6°N, 139.9°E) and Wakkanai (45.5°N, 141.6°E) on the Sea of Japan coast, and Shimokita (41.4°N, 141.5°E), Erimo (41.9°N, 143.2°E), Nemuro (43.4°N, 145.8°E), and Shiretoko (44.3°N, 145.3°E) on the Pacific coast. We used 254 of the 262 hatchery locations identified in our previous study (Kitada, 2020), excluding 8 hatcheries whose locations could not be identified.

2.8 | Regression analysis of return rates

Our model describes the relationship between return rates across all ages ($\hat{R}_t$) and explanatory variables such as SSTs, size at release and catch of potential predators and competitors (See next section for details). We transformed the return rate to the log scale for model fitting in a multiple linear regression:

$$\log(\hat{R}_t) = \log \beta_0 + \sum_{i=1}^{s} \beta_i z_i + \varepsilon_t$$

where β_0 is the intercept, the explanatory variables are denoted by $\boldsymbol{z}$. The egression coefficients were denoted by $\boldsymbol{\beta}$ and $\varepsilon_t \sim N(0, \sigma^2)$ is the error which was assumed to be normally distributed.

We performed a regression analysis by areas that had a similar trend in return rates based on the NJ tree, using a model selection using AICc (Sugiura, 1978), which is a small sample correction of the Akaike Information Criterion (AIC, Akaike, 1973). We used the results of the best model rather than model averaging, which may not be reliable in the presence of multicollinearity between explanatory variables (Cade, 2015). The use of an unstandardised measure is usually preferred to a standardised measure if the units of measurement are useful as effect sizes at a practical level (Wilkinson, 1999). We therefore used the regression coefficient for unstandardised explanatory variables as the effect size: $\exp(\hat{\beta}_i)$ for coefficient i, visualised using the `forestplot` function in R.

We used 14 explanatory variables (s=14), and the hypothesised mechanisms were summarised in Table 1. We selected the most parsimonious model (hereafter, best model) from 2^{14} (=16,384) models with the minimum AICc value using the `dredge` function in the `MuMIn` package in R. In our model, size at release and SST at release were the area-specific, while July SST in the Sea of Okhotsk was common to all management areas because juvenile chum salmon from all regional populations in Japan are distributed in the Sea of Okhotsk in summer (Urawa et al., 2018). Yellowtail (*Seriola quinqueradiata*, Carangidae) has been identified as a potential predator of juvenile chum salmon (see Section 3.5 for details). Winter SSTs in the North Pacific and Gulf of Alaska were used to infer effects during the first and second overwintering at ages 1 and 2, while summer SSTs in the Bering Sea were used to infer effects during feeding of age 1 fish (Myers et al., 2007; Urawa et al., 2018). The stomach contents of chum and pink salmon were similar in the Bering Sea, Gulf of Alaska and Western Subarctic Gyre (Davis et al., 1998; Kaeriyama et al., 2004; Qin & Kaeriyama, 2016; Daly et al., 2019), and the catches of Russian, US and Canadian chum and pink salmon (Figures S9, S10) were used as explanatory variables to infer intra and interspecific competition for food. The age composition of Japanese chum salmon showed that Age 4 fish were dominant (Table S4, Figure S8), so the catches of Russian, US and Canadian chum salmon in year t+3 were used as explanatory variables to measure intraspecific competition with Japanese chum salmon released in year t, as they return in year t+3 as Age 4 fish. They were assumed to spend 3 years in the shared environment of the North Pacific and adjacent waters. Pink salmon have a fixed life span of 2 years (Groot & Margolis, 1991; Quinn, 2018), and Russian, US and Canadian catches in year t+1 were used as explanatory variables to measure interspecific competition with Japanese chum salmon released in year t. They were assumed to spend 1 year in the shared environment. We have summarised the explanatory variables specific to each management area (Table S9) and common to all management areas (Table S10).

2.9 | Gene frequencies for metabolism, growth, and maturation

First, we focused on LDH-A$_4$ and LDH-B$_4$ as isoenzyme markers (Markert & Møller, 1959) that are potentially useful for understanding physiological thermal adaptation and evolution in fish (Merritt, 1972; Place & Powers, 1979; Powers et al., 1991; Fields & Somero, 1998; Somero, 2004; Somero, 2010; Somero, 2022). The LDH-A$_4$ isozyme is commonly found in vertebrate skeletal muscle and the LDH-B$_4$ isozyme is predominantly found in the heart (Powers et al., 1991; Somero, 2004). The metabolism of white muscle (skeletal muscle) is predominantly anaerobic and expresses the LDH-A$_4$ locus, whereas red muscle (heart) has significant aerobic metabolism and expresses almost exclusively the LDH-B$_4$ locus (Powers et al., 1991). The LDH-A$_4$ locus mainly involved in the conversion of pyruvate to lactate (i.e., anaerobic glycolysis), whereas the LDH-B$_4$ locus mainly converts lactate to pyruvate (i.e., gluconeogenesis and aerobic metabolism) (Somero, 2004, 2010; Powers et al., 1991). The lactate is resynthesized to glycogen in the liver and used as an energy source, while pyruvate produce adenosine triphosphate (ATP) for new energy, which are critical fuel metabolites during exercise (Liang et al., 2016).

Second, we re-examined the geographic distribution of chum salmon SNP allele frequencies (Seeb et al., 2011), focusing on growth hormone (GHII3129), gonadotropin-releasing hormone (GnRH373), and the combined mitochondrial DNA3 (mtDNA3) locus of chum salmon SNPs. Growth hormone (GH) is an important regulator of somatic growth in salmonids (Björnsson, 1997). Gonadotropin-releasing hormone (GnRH) regulates reproduction in vertebrates including salmonids (Khakoo et al., 1994). mtDNA plays a key role in aerobic ATP production and contributes to the ability of endurance exercise (reviewed by Stefàno et al., 2019). The mtDNA control region has functions in Dntp metabolism (Nicholls & Minczuk, 2014) and oxygen consumption (Kong et al., 2020).

We organised the allele frequencies of the LDH-A1 (LDH-A$_4$) and LDH-B2 (LDH-B$_4$) locus in chum salmon in the Pacific Rim (Supplementary Methods). To avoid the problems associated with standardization of electrophoretic bands obtained in different laboratories, we only used data generated using the same protocol (Aebersold et al., 1987) and followed the American Fisheries Society genetic nomenclature (Shaklee et al., 1990). These were collected in Japan (Sato & Urawa, 2015), Japan and the northern Russia (Winans et al., 1994), Sakhalin (Salmenkova et al., 2008) and the Russian Far East (Ivankova & Efremov, 2009). For populations in Alaska, the Alaska Peninsula, Southeast Alaska, British Columbia and Washington, allele frequencies were summarised from Seeb et al. (1995). As done in Seeb et al. (1999), we confirmed that the equal allele frequencies of LDH-A1 *100 (LDH-A_4^a) were obtained in the same rivers in Japan and Russia. All Japanese samples were caught at weirs in hatchery-reared rivers and hatcheries and were therefore hatchery-reared fish and/or wild-born hatchery progeny. In contrast, the northern Russian samples were collected from natural streams; these fish were assumed to be wild, as most Russian chum salmon are naturally maintained (Winans et al., 1994). The North American samples included 3 hatchery samples out of 42 (Seeb et al., 1995). The Russian samples from Sakhalin and the Russian Far East included 12 and 6 samples of hatchery fish out of 19 and 14 samples, respectively. We used the most common alleles, LDH-A1*100, and LDH-B2*100 in our analysis of allele frequencies. We obtained allele frequencies in 147 chum salmon populations collected throughout the range in 1986-2005 (n = 18,892) (Data S6).

For the nuclear SNPs (Seeb et al., 2011), we converted the original genotype data to Genepop format (Rousset, 2008) and loaded the data using the read.GENEPOP function in the R package `FinePop2`. We used minor alleles that had a mean allele frequency across populations of less than 0.5 (Kitada & Kishino, 2021). We summarised the SNP allele frequencies of GHII3129, GnRH373, and mtDNA3 in 114 chum salmon populations collected throughout the range in 1989-2006 (n = 10,458) (Data S7). The mtDNA3 locus had five alleles, and the major allele (second one) was used for the analysis. The sample from South Korea (n = 96) was excluded from the analysis, due to our focus on Japanese chum.

We recorded the approximate longitude and latitude of the sampling locations based on the names of the rivers and/or areas and the maps of the original studies using Google Map (Data S6 and S7). We plotted the locations on the map using the `sf` package in R. Sampling points were visualized by a color gradient of allele frequencies.

3 | RESULTS

3.1 | Long-term SST changes across the range of Pacific salmon

The mean SST isoclines show that SSTs are generally lower on the Asian side than on the American side (Figure 1, Figures S11-S13). Until 2010 (during 110 years) the increase in SST was relatively slow in all seasons, while after 2010 a rapid increase in summer was observed. Summer SST (June-August) increased in the Bering Sea, the Sea of Okhotsk, the western, central and eastern North Pacific, and the Gulf of Alaska, while spring (April-May), autumn (October-November) and winter (January) SST were stable throughout the Pacific salmon range until 2010, with relatively slow increases over the past decade. Around Japan, SST increased gradually but continuously in May, June and July (Figure S14). The Pacific side of Japan has denser SST contours than the Sea of Japan side. Higher SSTs were observed along the Sea of Japan coast than in the Honshu Pacific for the same latitude.

3.2 | Japanese chum salmon migration route and SST

The map shows the migration route of Japanese chum salmon until their return, and the box plot shows the changes in SST along the seasonal migration of Japanese chum salmon (Figure 2). In the Sea of Okhotsk, the SST (mean ± standard deviation) in July was very high (12.3 ± 1.2°C). In the North Pacific, SST remained relatively high even in December (8.0 ± 0.9°C), but decreased significantly by 2.0°C in January (6.0 ± 0.7°C,

$t = 10.9, p = 0.0000$, Welch t-test). SSTs were lower but stable in February (5.0 ± 0.6°C), March (4.7 ± 0.5°C), and April (5.0 ± 0.5°C), and increased in May (6.2 ± 0.6°C) to the same level as in January. In the Bering Sea, the SST remained low in June (5.7 ± 0.6°C). It increased in July (8.0 ± 0.7°C) and was the highest in August (9.7 ± 0.8°C) and remained high in September (9.3 ± 0.8°C). It decreased significantly in October (7.4 ± 0.6°C) and November (5.4 ± 0.5°C). In the Gulf of Alaska, SSTs were 1.5°C higher in December (6.9 ± 0.8°C) than in November in the Bering Sea, and then decreased significantly in January (6.0 ± 0.7°C, $t = 5.2,\ p = 0.0000$). SSTs were lower but stable in February (5.6 ± 0.7°C), March (5.4 ± 0.7°C), and April (5.7 ± 0.6°C), and increased in May (6.9 ± 0.8°C) to a similar level in December.

Interestingly, the mean January SST was just the same in both wintering areas. However, the February-April mean SST was significantly lower than the January SST in the North Pacific ($t = 8.3,\ p = 0.0000$) and in the Gulf of Alaska ($t = 3.3,\ p = 0.0012$), and was significantly lower in the North Pacific (4.9 ± 0.5°C, $t = -5.3,\ p = 0.0000$) than in the Gulf of Alaska (5.5 ± 0.6°C). January SST and February-April mean SST were positively correlated in the North Pacific ($r = 0.78, t = 7.9, p = 0.0000$) and Gulf of Alaska ($r = 0.91, t = 13.6, p = 0.0000$), but the linear relationship was weaker in the North Pacific (Figure S15). From the characteristics of winter SSTs between and within wintering areas, we chose both the January SST and the February-April mean SST as explanatory variables, leaving the choice of which to use to model selection. For the summer SST, the Sea of Okhotsk July SST and the Bering Sea August-September mean SST were used as explanatory variables (Table 1).

July SST in the Sea of Okhotsk showed an increasing trend (Mann-Kendall trend test, $\tau = 0.38, p = 0.0005$), and the recent increase was remarkable (Figure 3). August-September SST in the Bering Sea increased $\tau = 0.43, p = 0.0001$), but decreased with variability after a strong increase in 2013. Winter SST trends in the North Pacific were insignificant for both January ($\tau = 0.21, p = 0.0506$) and February-April ($\tau = 0.21, p = 0.0562$). In the Gulf of Alaska, winter SST trends were also insignificant both for January ($\tau = -0.06, p = 0.5821$) and February-April ($\tau = -0.03, p = 0.7875$).

3.3 | Chum salmon enhancement and SST at release

From 1970 to 2021, a total of 86,357 million juvenile fish were released and 2,266 million fish (2.6%) were returned (Figure 4). As the number of fish released increased, the total number of fish returned increased significantly until 1996, when the historical maximum of 88 million fish was reached. Despite the relatively stable trend in the number of fish released, the number of fish returned has continued to decline since 2004 and will reach the four-decade minimum of 19 million in 2021. In particular, the number of fish returned increased in 2022, especially in the Sea of Okhotsk and the Hokkaido Sea of Japan. The trend across Japan was synchronised in the two main production areas, Nemuro Strait and Honshu Pacific, as shown by the dashed lines. Hokkaido Eastern Pacific and Hokkaido Western Pacific showed a similar trend after the mid-2000s. In contrast, the other major production area, the Sea of Okhotsk, showed a unique trend where the number of fish returned increased with large fluctuations, reaching the historical maximum in 2013, with a large decrease until 2019, but recovering significantly in 2022. The Hokkaido Sea of Japan also had a unique trend, but showed a similar significant increase in 2022. It is worth noting that the recovery in 2022 was observed in all areas, although the recovery in 2022 was highly variable.

SST at release (Figure 4) increased in the Sea of Okhotsk (5.5 ± 0.4°C, $\tau = 0.37, p = 0.001$), Nemuro (3.9± 0.6°C, $\tau = 0.36, p = 0.001$), the Hokkaido Sea of Japan (7.5 ± 0.4°C, $\tau = 0.35, p = 0.002$), and the Honshu Sea of Japan (9.9 ± 0.5°C, $\tau = 0.28, p = 0.016$), while the trends were insignificant in the Hokkaido Eastern Pacific (4.4 ± 0.4°C, $\tau = 0.06, p = 0.611$) and the Hokkaido Western Pacific (6.2 ± 0.6°C, $\tau = 0.06, p = 0.578$), and the Honshu Pacific (10.1 ± 0.8°C, $\tau = -0.09, p = 0.421$).

3.4 | Return rate and weight at release

Return rates had common local peaks for the 2004, 2006, 2012 and 2015 releases (Figure 5). The return rate for ages 2-5 was highest in the Sea of Okhotsk (6.5 ± 2.2%). The recent increase was synchronised in the Hokkaido Sea of Japan (1.2 ± 0.6%). Age-specific return rates revealed that the increase in return rates for the 2019 release in the Sea of Okhotsk and the Hokkaido Sea of Japan was driven by an increase in those at age 4, while the return rate at age 5 decreased slightly. Conversely, return rates remained low in other areas, with a slight increase in the 2019 release: Nemuro (3.3 ± 2.0%), Hokkaido Eastern (1.7 ± 1.4%) and Hokkaido Western Pacific (2.0 ± 1.0%), Honshu Pacific (1.1 ± 0.7%) and Hoshu Sea of Japan (0.6 ± 0.2%). The younger ages at maturity was also observed in these areas, although the increases were relatively small.

Higher return rates were obtained in the management areas that were geographically closer to the central Sea of Okhotsk (Figure 6a,b). The weighted mean size at release (Figure 6c) was above the recommended threshold (BW > 1g) in all management areas. The mean weight at release was maintained over the two decades in the Hokkaido Western Pacific (1.3 ± 0.03g, $\tau = 0.01, p = 0.967$), while decreasing trends were found in other areas: the Sea of Okhotsk (1.2 ± 0.06g, $\tau = -0.43, p = 0.019$), Nemuro Strait (1.2 ± 0.09g, $\tau = -0.50, p = 0.006$), Hokkaido Sea of Japan (1.1 ± 0.05g, $\tau = -0.43, p = 0.019$), Honshu Pacific (1.3 ± 0.16g, $\tau = -0.65, p = 0.000$) and Honshu Sea of Japan (1.0 ± 0.20g, $\tau = -0.50, p = 0.006$). In the Hokkaido Eastern Pacific, it was relatively high, but the trend was insignificant with large variations (1.5 ± 0.13g, $\tau = -0.15, p = 0.434$).

The NJ tree (Figure 6d), which measures pairwise differences in return rates between management areas, showed that the Hokkaido Sea of Japan, Sea of Okhotsk and Honshu Sea of Japan were distinct, while the Nemuro Strait, Hokkaido Eastern Pacific and Hokkaido Western Pacific and Honshu Pacific had a similar trend in return rates and were very close to each other. In subsequent analyses, we used the 4 geographical areas: Sea of Okhotsk, Hokkaido Sea of Japan, Honshu Sea of Japan, and Hokkaido and Honshu Pacific (combining the Nemuro Strait, Hokkaido Eastern Pacific, and Hokkaido Western Pacific and Honshu Pacific).

For the Hokkaido and Honshu Pacific area, simple averages were calculated for SST and weighted size at release over the four areas. The number of returned and released chum salmon was also summed over the areas and the return rate was calculated.

3.5 | A possible marine predator of juvenile chum salmon

The biplot of the PCA (Figure 7a) identified differences in the magnitude of catches as a primary component (PC1, 51% variance), while the second component (PC2, 17% variance) corresponded to the trends in catches in 1980-1998 and 1999-2020. The PCA confirmed that the changes in commercial catches of 56 marine species in Japan after 2000 were mainly 15ertilized15ed by the 4 species that increased in recent decades: yellowtail, Japanese Spanish mackerel (*Scomberomorus niphonius*, Scombridae), Japanese scallop (*Mizuhopecten yessoensis*, Pectinidae) and round herring (*Etrumeus micropus*, Dussumieriidae) (Figure S16). Among these, yellowtail and Japanese Spanish mackerel are strong piscivores. The map of changes in catches of chum salmon and the two piscivores by prefecture (Figure 7b) shows the northward shift of yellowtail landings into the chum salmon distribution areas, Honshu North Pacific, Hokkaido Pacific, Hokkaido Sea of Japan and the Sea of Okhotsk. In fact, there were significant increases in these areas (Figure S17). On the other hand, the increase in catches of Japanese Spanish mackerel remained in the Eastern Japan area, with slight increases in the Honshu North Pacific. Based on these results, we defined yellowtail as a possible predator of juvenile chum salmon, and catches of yellowtail were also summed over the areas.

3.6 | Causal effects on chum salmon return rates

Table 2 summarises the best models from the regression analysis. 75% of the variation in return rates from the Sea of Okhotsk was explained by the positive effects of winter SST (Jan) in the Gulf of Alaska and Russian chum salmon, and the negative effect of yellowtail. In the Hokkaido and Honshu Pacific, the positive effect of weight at release explained 43% of the variation in return rates. In the Hokkaido Sea of Japan, 49% of the variation in return rates was explained by the largest positive effect of winter SST (Feb-Apr) in the North Pacific and the negative effect of summer SST (July) in the Sea of Okhotsk. Weight at release also had a negative effect on the return rate. The 69% of the variation in return rates from the Honshu Sea of Japan was explained by the positive effects of weight at release and winter SST (Jan) in the Gulf of Alaska, and the negative effect of SST at release.

The correlation between predicted and observed return rates were high in the Sea of Okhotsk ($r = 0.89, t = 7.73, p = 0.0000$) and Honshu Sea of Japan ($r = 0.86, t = 6.63, p = 0.0000$), while moderate in Hokkaido and Honshu Pacific with a wider 95% prediction interval ($r = 0.68, t = 3.61, p = 0.0026$) and Hokkaido Sea of Japan ($r = 0.77, t = 4.6, p = 0.0003$) (Figure S18). Our regression models predicted the trends in the observed return rates in the 4 areas well (Figure 8), and all observed values were within the 95% prediction intervals.

The effect size for each regression coefficient (Figure 9), measured by $\exp(\hat{\beta}_i)$, represents the rate of change per unit. Winter SST in the North Pacific and the Gulf of Alaska had a positive effect in 3 areas. A 1℃ increase in winter SST in the Gulf of Alaska increased the return rate by 36% in the Sea of Okhotsk, and 25% in the Honshu Sea of Japan. In particular, the positive effect of winter SST was greatest in the Hokkaido Sea of Japan, where a 1℃ increase in the North Pacific increased the return rate by 98%. In contrast, summer SST in the Sea of Okhotsk reduced the return rate for the Hokkaido Sea of Japan by 30%. In the Honshu Sea of Japan, SST at release had a significant negative effect, reducing the return rate by 41%. Yellowtail also had a negative effect in the Sea of Okhotsk, reducing the return rate by 18%. On the other hand, weight at release had a positive effect in 2 areas, and the effect was much greater in the Hokkaido and Honshu Pacific, where a 0.1g increase in size at release increased the return rate by 82%, than in the Honshu Sea of Japan, where the increase was 10%. In the Hokkaido Sea of Japan, weight at release had a negative effect, reducing the return rate by 34%. The abundance of chum salmon in Russia had a positive effect on chum salmon in the Sea of Okhotsk, but it was small, increasing the return rate by 3% per million chum salmon caught.

3.7| Geographical patterns of allele frequencies

LDH-A1*100 allele frequencies (Figure 10) were distributed along a north-to-south gradient. A significant latitudinal gradient was observed in the Russian and American samples, while the allele frequencies in Etorofu Island (Figure S3) and Japan were distributed outside the geographic gradient and were similar to those in the northernmost western Alaska and Yukon River populations. LDH-A1*100 allele frequencies were higher in warmer areas and lower in colder environments. On the other hand, the frequency of LDH-B2*100 allele was 1.0 or close to 1.0 for all samples (Figure S19).

Except for Japan, GHII3129 SNP allele frequencies (Figure 10) also showed a latitudinal gradient from north to south. In contrast, GnRH373 allele frequencies (Figure S20) were at relatively similar levels across the Pacific, but those of Japan were the highest among the populations. The allele of mtDNA3 (Figure S20) was fixed at close to 1.0 in American and Russian populations, whereas the allele frequencies were significantly lower in Japanese populations.

4 | DISCUSSION

We provide initial evidence that the sudden increase in the number of returning chum salmon in 2022 is due to an increase in age 4 fish, leading to higher return rates for the 2019 release. This shift in age composition towards younger age at maturity is observed in all areas, particularly pronounced in the Hokkaido Sea of Japan and the Sea of Okhotsk. Our results are consistent with evidence of body size decline primarily resulting from younger age at maturity from large-scale analyses throughout Alaska (Lewis et al., 2015; Oke et al., 2020; Ohlberger et al., 2023). North Pacific February-April SST during the first overwintering period had the largest positive effect on return rates, and Gulf of Alaska January SST during the second overwintering period also had a positive effect on return rates. In coastal areas, summer SST, SST at release and a northward expansion of piscivorous fish had a negative effect. Our regression analysis did not infer causal effects of younger age at maturity (age-specific return rates) on the environmental variables but did infer causal effects of total return rates. LDH-A1*100 (LDH-A_4^a) and GHII3129 allele frequencies in Japan were outside the latitudinal gradient and close to those in western Alaska and the Yukon, while the allele frequencies of the GnRH373 and mtDNA3 SNPs were significantly higher and lower than other populations. In contrast, LDH-B2*100 allele frequencies are fixed at or near 1.0 in all populations.

On Etorofu Island, near Shiretoko Peninsula, Hokkaido, LDH-A1*100 allele frequencies (Figure 10) were at the similar level to those in Japan. Japan started salmon hatcheries on Etorofu Island in the 1890s and operated 10 hatcheries before World War II (Yagisawa, 1970). Between 1920 and 1944, the Etorofu hatchery, the most representative, produced 654 million fertilised eggs from 495 thousand parent chum salmon and released 602 million fries. Currently, Russia operates the largest chum salmon hatchery programme on this island, with 14 salmon hatcheries producing 240-250 million juveniles per year, and almost all chum salmon returning to the island are hatchery fish (Klovach et al., 2021). Japanese salmon seed production methods and facilities have been inherited in the island. The LDH-A1*100 allele frequencies obtained from hatchery and wild chum salmon may be due to intensive hatchery releases in the smaller population.

In Japanese hatcheries, fertilised eggs are generally kept in incubators for about 2 months until hatching, and hatched larvae are reared in indoor rearing ponds for about 2 months until emergence, both in a very dark environment with calm water flow (Salmon and Freshwater Research Institute, 2023). Metabolic activity in Atlantic salmon (*Salmo salar*, Salmonidae) was significantly higher in daylight than in darkness, and the daily oxygen consumption was correlated with sunrise and day length (Maxime et al., 1989). The blind, cave-dwelling form of the Mexican tetra (*Astyanax mexicanus*, Characidae), which lives in complete darkness, consumes far less oxygen than the surface morph, and uses ~27% less energy per day (reviewed by Boggs & Gross, 2021). The evidence suggests that the rearing environment from eggs to emergence (calm water flow in the dark in indoor ponds for about 4 months) may reduce metabolic activity and oxygen consumption in hatchery fish, leading to selection at the LDH-A1*100 and mtDNA3 loci. Hatchery steelhead (*O. mykiss*, Salmonidae) grow significantly faster in hatcheries (Blouin et al., 2021). Hatchery reared chum salmon are fed daily formulated diets and must grow with reduced metabolic activity where growth hormone may have a significant effect, potentially altering GHII3129 allele frequencies. Efforts to increase the early-run population since the early 1980s have induced changes in run timing distribution and the late-run populations have almost disappeared in Hokkaido, the main production area (Miyakoshi et al., 2013). The strong selection of early-run salmon could result in GnRH373 allele frequencies above Pacific Rim levels. On the contrary, LDH-B2*100, which is associated with cardiac activity (Powers et al., 1991; Somero, 2004), may be conservative even under anthropogenic selection (Figure S19). The deviation of Japanese chum salmon allele frequencies in LDH-A1*100, GHII3129, GnRH373 and mtDNA3 (Figures 10, S20) from the geographic pattern could occur during hatchery rearing by relaxing natural selection (Heath et al., 2003; Araki et al., 2008). Although LDH and SNP allele frequencies were estimated from old samples collected in 1986-2006, allele frequencies are expected to be similar or more influenced as hatchery releases continue at similar levels (Figure 4).

The LDH-A1*100 and GHII3129 allele frequencies show countergradient variation (CnGV) (Conover, 1995). CnGV is a negative covariance between genotypic and environmental effects on phenotype (Cov $(G,E) < 0$) and occurs when the genotypic influence on the phenotype counteracts the environmental influence, so that phenotypic variation between environments is minimised (Conover, 1995; Albecker et al., 2022). CnGV has been reported for several traits in several species (Conover, 1995), including Atlantic salmon for growth and digestion (Nicieza et al., 1994) and maturation (Åsheim et al., 2023). CnGV of growth rate is one of the most common examples (Wikipedia, 2023). Adaptation to cold environments often requires an increase in growth rate to compensate for the slowdown in growth and metabolism that occurs at lower temperatures (Åsheim et al., 2023). In other words, during the short growing season, northern fish must grow much faster than southern fish (Conover, 1990). CnGV adjusts metabolism and growth in the latitudinal cline, minimising variation in salmon body size. Salmon are highly migratory and populations from different countries spend several years in the high seas with similar water temperatures. CnGV in metabolism (LDH-A1*100) and growth (GHII3129) could therefore be generated during their early life stages in freshwater and coastal waters.

LDH-A1*100 (LDH-$\mathrm{A}_4^{\mathrm{a}}$) and GHII3129 allele frequencies outside the latitudinal gradient and close to those in western Alaska and the Yukon (Figure 10) suggest that Japanese chum salmon may have similar metabolic and growth characteristics to Alaskan chum salmon, where younger age at maturity has been found in large-scale analyses (Lewis et al., 2015; Oke et al., 2020; Ohlberger et al., 2023). LDH-A_4 is cold-adapted (Fields & Somero, 1998). In a common environment experiment in the temperate freshwater fish, the fathead minnow (*Pimephales promelas*, Cyprinidae) (Supplementary Methods), Merritt (1972) was found that the homozygote of the northern allele LDH-$\mathrm{A}_4^{\mathrm{bb}}$ had significantly higher Michaelis constant of pyruvate, K_m^{PYR} (lower substrate affinities=lower catalytic efficiency) than the homozygote of the southern allele LDH-$\mathrm{A}_4^{\mathrm{aa}}$ and the heterozygote LDH-$\mathrm{A}_4^{\mathrm{ab}}$ at 25°C and above. The result shows that individuals homozygous for the northern allele LDH-$\mathrm{A}_4^{\mathrm{bb}}$ require more energy (food) to grow at warmer temperatures. Although we could not find an experimental study in salmonids to assess genotype effects on catalytic efficiency, Merritt's result suggests that contemporary Japanese chum salmon, which may have similar metabolic efficiency to Alaskan chum salmon, should have lower catalytic efficiency and consume more energy at warmer temperatures along the Japanese coast. The release of Japanese chum salmon is equivalent to the release of Alaskan chum salmon in a southern environment. This results in a common environmental experiment for growth and metabolism with higher water temperatures in terms of LDH-A1 and GHII3129 loci. As a result, contemporary Japanese chum salmon grow faster but are less metabolically efficient than native Japanese populations with original allele frequencies adapted to the Japanese environment (now unobserved). In the Sanriku Coast, Honshu Pacific, Iino et al. (2022) found that juvenile chum salmon reared under low food availability (1% body weight) allocated less than half of their energy to growth at high temperatures (14°C) compared to juveniles reared under high food availability (4% body weight). The similar LDH-A1*100 and GHII3129 allele frequencies to Alaskan chum salmon may require much food to grow at high temperatures. The long distance migration from the Pacific coast of Honshu to the Sea of Okhotsk (Figure 6b) may also have a negative effect on juvenile growth and survival. This may explain the negative effect of SST at release and summer SST along the coast of the Sea of Okhotsk.

In a warmer climate, the body size of adult salmon will decrease, mainly due to a younger age at maturity (Jonsson, 2023). Younger maturing salmon grow much faster than older maturing salmon (Ricker, 1981). Growth history of salmon was more strongly associated with the probability of maturation than age or age-specific body size, and the most recent growth condition was the most important factor in determining whether a fish matured in the following breeding season (Morita & Fukuwaka, 2006). The growth history of Japanese chum salmon at early life stages with increased growth rate may result in better growth and younger age at maturity during warm winter SST in the wintering grounds, as seen in Alaskan sockeye salmon (Ohlberger et al., 2023). In the North Pacific and Gulf of Alaska, mean January SST was the same at 6.0 ± 0.7°C, and mean February SST was slightly lower at 5.6 ± 0.7°C in the Gulf of Alaska (Figures 2,3). The optimum temperature for chum salmon growth has been estimated to be 8-12°C (Kaeriyama, 1986; Urawa et al., 2019; Kaeriyama, 2022). Warm winter SST in the wintering grounds (Figure 3) may result in better growth of Japanese chum salmon, which have similar metabolic and growth characteristics to Alaska salmon, when food is abundant. The effect of food abundance remains unknown and is left for future study.

In the Sea of Okhotsk, yellowtail reduced the return rate by 18% (Figure 9). Young yellowtail and mahi-mahi (*Coryphaena hippurus*) were found in chum salmon landings in the Sea of Okhotsk in September 2012 (Figure S21). Since 2014, yellowtail have been caught along the coast of the Sea of Okhotsk in May-June (Hoshino & Fujioka, 2021), coinciding with the release period. Another candidate predator is a seabird, the rhinoceros auklet (*Cerorhinca monocerata*), which preys on juvenile chum salmon off the Pacific coast of Hokkaido from late June to mid-July, with an estimated consumption of 317 tonnes (31.7 million juveniles, assuming 10 g BW per fish) in 2014 (Okado et al., 2020). In freshwater, brown trout (*Salmo trutta*) collected near the hatchery and ~10 km downstream predated 49-481 chum salmon juveniles in the Chitose River, Hokkaido Sea, Japan (Honda et al., 2023). Piscivorous salmonids chase schools of juvenile fish, and small juvenile chum salmon are easily predated due to their slow swimming speed to escape predators (Hasegawa et al., 2021). Before 1945, wild-born chum salmon fry were too agile to be netted in the rivers of Etrofu Island, where Japan operated salmon hatcheries (Yagisawa, 1970). A significant reduction in mtDNA3 SNP allele frequency in Japanese chum salmon (Figure S20) could reduce the efficiency of aerobic fitness and swimming endurance, energy metabolism and oxygen consumption (Kitada & Kishino, 2021). The similar LDH-A1*100 allele frequencies to Alaskan chum salmon may reduce burst swimming speed in warming SST along Japanese coasts, as LDH-A is predominantly found in skeletal (white) muscle (Powers et al., 1991;

Somero, 2004). The effect of predation by piscivorous fish can be significant when many slow swimming juveniles are released at the same time. Predation by large marine animals, such as killer whales (Ohlberger et al., 2019), may also occur in the high seas.

The positive effect of weight at release was greatest in the Hokkaido and Honshu Pacific, where a 0.1 g increase in weight at release increased the return rate by 82% (Figure 9). In the Honshu Sea of Japan, the effect of weight at release was smaller; a 0.1 g increase in weight at release increased the return rate by 10%, while a 1℃ increase in SST at release reduced the return rate by 41%. The positive effect of weight at release could be reduced by the effect of increasing SST. Unexpectedly, the effect of weight at release was negative in the Hokkaido Sea of Japan, where a 0.1 g increase in weight at release reduced the return rate by 34%, suggesting that the current weight at release (1.04 ± 0.03 g, average 2016-2020) is sufficient in this region.

Our regression analysis assumed that all chum salmon returning to Japan are hatchery-reared. On the other hand, field studies provide evidence that natural reproduction of chum salmon occurs in 31%-38% of 238 non-enhanced rivers in Hokkaido (Miyakoshi et al., 2012), and in 94% of 47 hatchery-enhanced rivers and 75% of 47 non-enhanced rivers along the northern Honshu Sea coast of Japan (Iida et al., 2018; Iida et al., 2021). Escapement of returned fish is not a common practice in Hokkaido, although all broodstock collection weirs have been redesigned to allow passage of fish for natural spawning in the Kitami region, Sea of Okhotsk since 2005 (Kitada, 2014). In the Honshu Sea of Japan, about half of the streams from which hatchery broodstock are collected use small nets or hooks that do not interfere with the upstream migration of chum salmon (Iida et al., 2018). Hatchery fish are stocked in most large rivers (Miyakoshi et al., 2013), while naturally spawning chum salmon populations persist in many small (short) rivers in Hokkaido, the main production area (Kitada, 2014). The very high gene flow between populations allows genetic admixture of hatchery-born fish and wild-born hatchery progeny throughout the Japanese populations (Kitada & Kishino, 2021). The relative reproductive success (RRS) of hatchery-reared salmon is approximately 50% of that of wild-origin fish spawning in the wild (Araki et al., 2007; Christie et al., 2014; Shedd et al., 2022), with considerable variation (Kitada et al., 2011). Moreover, reduced RRS can be carried over to the next generation (Araki et al., 2009). Egg-to-size-at-release survival of wild-born fish in natural streams should be very low. Although the magnitude of recruitment from natural reproduction was unknown, it may not be substantial compared to the number of juveniles released (1-1.5 billion juveniles throughout Japan).

Using the world's largest hatchery release programme, we show how salmon populations are exposed to environmental and anthropogenic stressors at both local and North Pacific-wide scales. The geographic pattern of gene allele frequencies suggests that Japanese chum salmon have similar metabolic and growth characteristics to Alaskan chum salmon, with unique features of maturation, aerobic endurance, energy metabolism and oxygen consumption. We hypothesise that intentional and unintentional hatchery selection on Japanese chum salmon have relaxed natural selection and altered allele frequencies, reducing survival in coastal Japan, while improving growth in the first and second winters in warming climate, thereby promoting a younger age at maturity. The apparent increase in return rates of Japanese chum salmon is due to their returning one year earlier. This is a trade-off between fish abundance and body size decline. However, the underlying mechanisms for the decline in body size and younger age at maturity are largely unknown and remain the subject of future research. Although more research is clearly needed to fully understand the underlying mechanisms of Japanese chum salmon population dynamics, our findings provide a new insight into salmon conservation and hatchery release.

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DATA AVAILABILITY STATEMENT

The data generated or analysed in this study are fully described in the published article and its Supplementary Information including Supplementary Figures S1-S21. Supplementary Tables S1-S10, Supplementary Data S1-S7 and the analysis scripts and data are available at https://doi.org/10.5281/zenodo.8394732.

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TABLE 1 Explanatory variables included in the regression model and hypothesised mechanism.

Explanatory variables	Spatial scale	Age	Time scale	Unit	Mechanism
Size at release in year *t* (BW)	Japan coasts	Age 0	After release	0.1g	Larger juveniles survive better than smaller ones.
Size at release in year *t* (Condition factor)	Japan coasts	Age 0	After release		Juveniles with higher condition factors survive better than those with lower factors.
Catch of yellowtail in year *t*	Japan coasts	Age 0	After release	100 tons	Yellowtail feed on juvenile chum salmon during their extended northward migration.
Mean SST at release in year *t*	Japan coast	Age 0	After release	℃	SSTs at and after release affect survival of juvenile chum salmon.
Summer SST in the Sea of Okhotsk in year *t*	Off the Sea of Okhotsk	Age 0	Jul.	℃	SSTs affect survival of juvenile chum salmon after leaving the Sea of Okhotsk coast.
Winter SST in the North Pacific in year *t*+1 when Age 1 fish over winter	Western north Pacific	Age 1	Jan. and/or Feb.-Apr.	℃	During the first overwintering, SSTs affect the survival of young chum salmon.
Summer SST in the Bering Sea in year *t*+1 when Age 1 fish feed	Bering Sea	Age 1	Aug.	℃	During the feeding migration, SSTs affect the survival of young chum salmon.
Winter SST in the Gulf of Alaska in year *t*+2 when Age 2 fish over winter	Gulf of Alaska	Age 2	Jan. and/or Feb.-Apr.	℃	During the second overwintering, SSTs affect the survival of chum salmon.
Russian chum salmon catch in year *t*+3 (relative recruitment in year *t*)	Sea of Okhotsk and North Pacific	Age 0 - Age 4	3 years and months	million fish	Intraspecific competition in the Sea of Okhotsk and the North Pacific until return.
USA and Canadian chum salmon catch in year *t*+3	North Pacific	Age 1 - Age 4	2 years and months	million fish	Intraspecific competition in the North Pacific until return.
Russian pink salmon catch in year *t*+1	Sea of Okhotsk and North Pacific	Age 0 - Age 2	1 year and months	million fish	Interspecific competition in the Sea of Okhotsk and the North Pacific.
USA and Canadian pink salmon catch in year *t*+1	North Pacific	Age 1 - Age 2	1 year	million fish	Interspecific competition in the North Pacific.

All data including the response variable (return rate from release in year *t*), are available in the Supplementary Tables and Supplementary Data.

TABLE 2 Summary of the best fit models with minimum AICc values out of 2^{14} (=16,384) models for each geographical area.

Area	Explanatory variable	Estimate	SE	*t*-value	Pr (>|*t*|)	Adjusted R^2	*p*-value
Sea of Okhotsk	(Intercept)	-4.937	0.672	-7.34	**0.000**	0.75	**0.000**
	Gulf of Alaska winter SST [†]	0.304	0.095	3.21	**0.007**		
	Russian chum salmon	0.030	0.008	3.57	**0.003**		
	Yellowtail	-0.202	0.033	-6.14	**0.000**		
Hokkaido and Honshu Pacific	(Intercept)	-12.267	2.220	-5.53	**0.000**	0.43	**0.003**
	Size at release	0.601	0.166	3.61	**0.003**		
Hokkaido Sea of Japan	(Intercept)	1.182	2.499	0.47	0.644	0.49	**0.008**
	Size at release	-0.419	0.186	-2.25	**0.043**		
	North Pacific winter SST [‡]	0.682	0.213	3.20	**0.007**		
	Sea of Okhotsk summer SST [§]	-0.360	0.110	-3.28	**0.006**		
Honshu Sea of Japan	(Intercept)	-2.257	1.375	-1.64	0.125	0.69	**0.000**
	Size at release	0.096	0.037	2.59	**0.023**		
	Gulf of Alaska winter SST [†]	0.223	0.081	2.76	**0.016**		
	SST at release	-0.529	0.105	-5.05	**0.000**		

Bold indicates significance. [†] Jan., [‡] Feb.-Apr. (mean), [§] Jul.

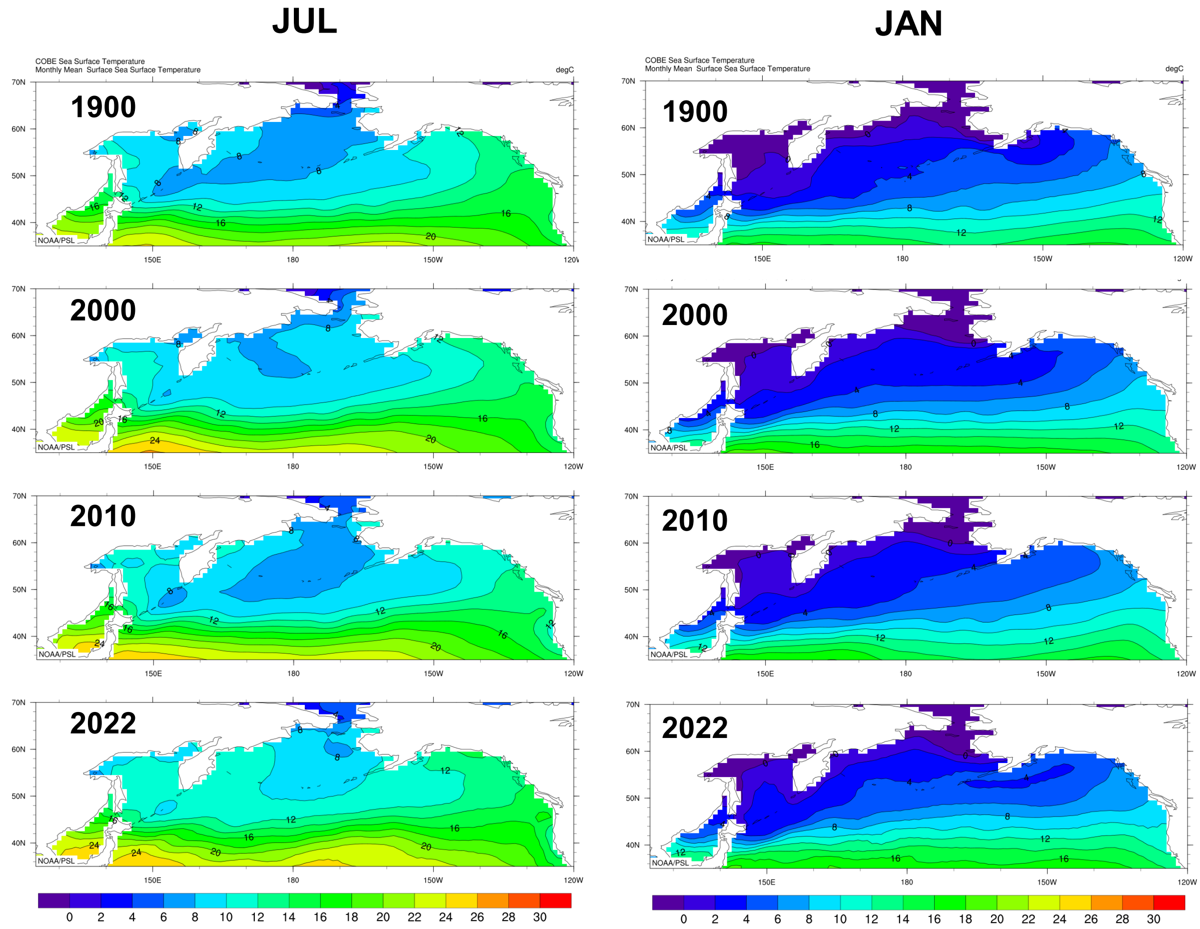


FIGURE 1 Long-term changes in the summer and winter SST isocline in the North Pacific. Plotted from Plot: COBE Sea Surface Temperature, NOAA Physical Sciences Laboratory. Changes in April, May, June, August, October and November SSTs are shown in Figures S11-13.

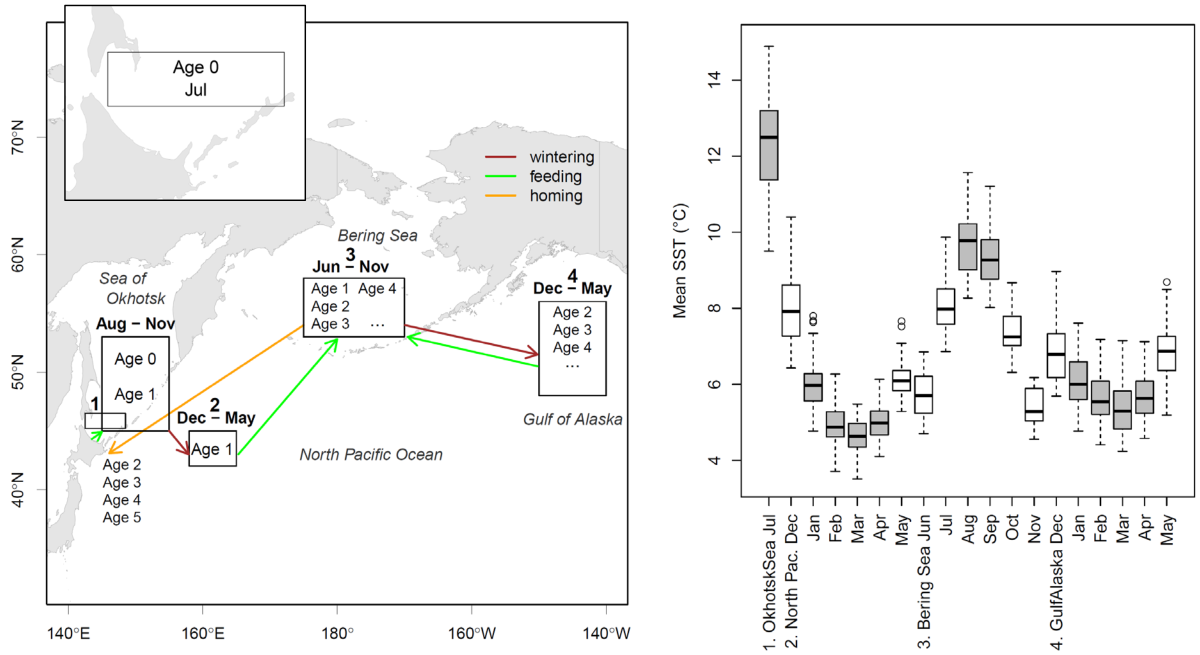


FIGURE 2 Migration routes of Japanese chum salmon and critical SSTs. Map shows migration routes estimated from the long-term field surveys, redrawn from Urawa et al. (2018). Box plots show the change in mean summer and winter SSTs of feeding and wintering areas, calculated from the NOAA 1/4° daily OISST climate record. The gray boxes show the summer and winter SSTs included in the explanatory variables.

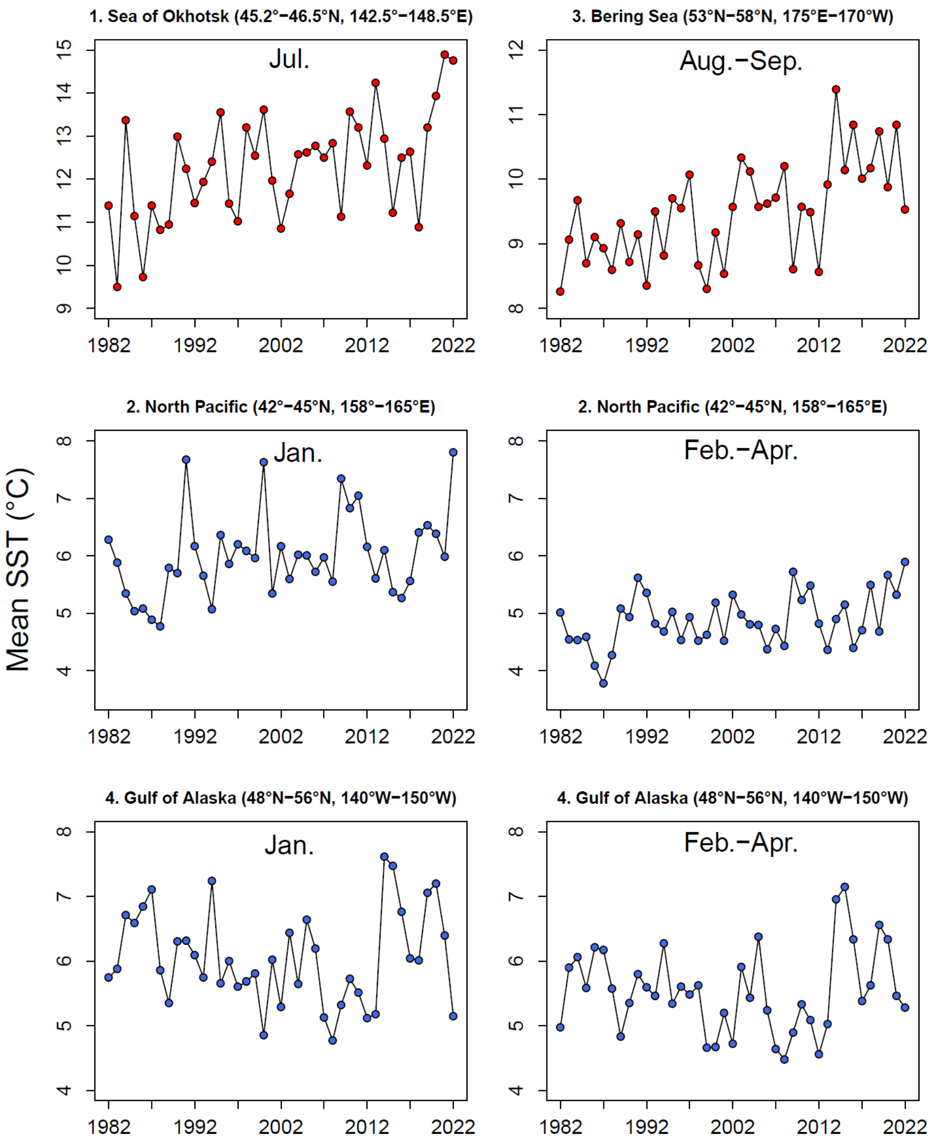


FIGURE 3 Summer and winter mean SSTs in the Japanese chum salmon migration route in Figure 2. SSTs are calculated from the NOAA 1/4° daily OISST climate record.

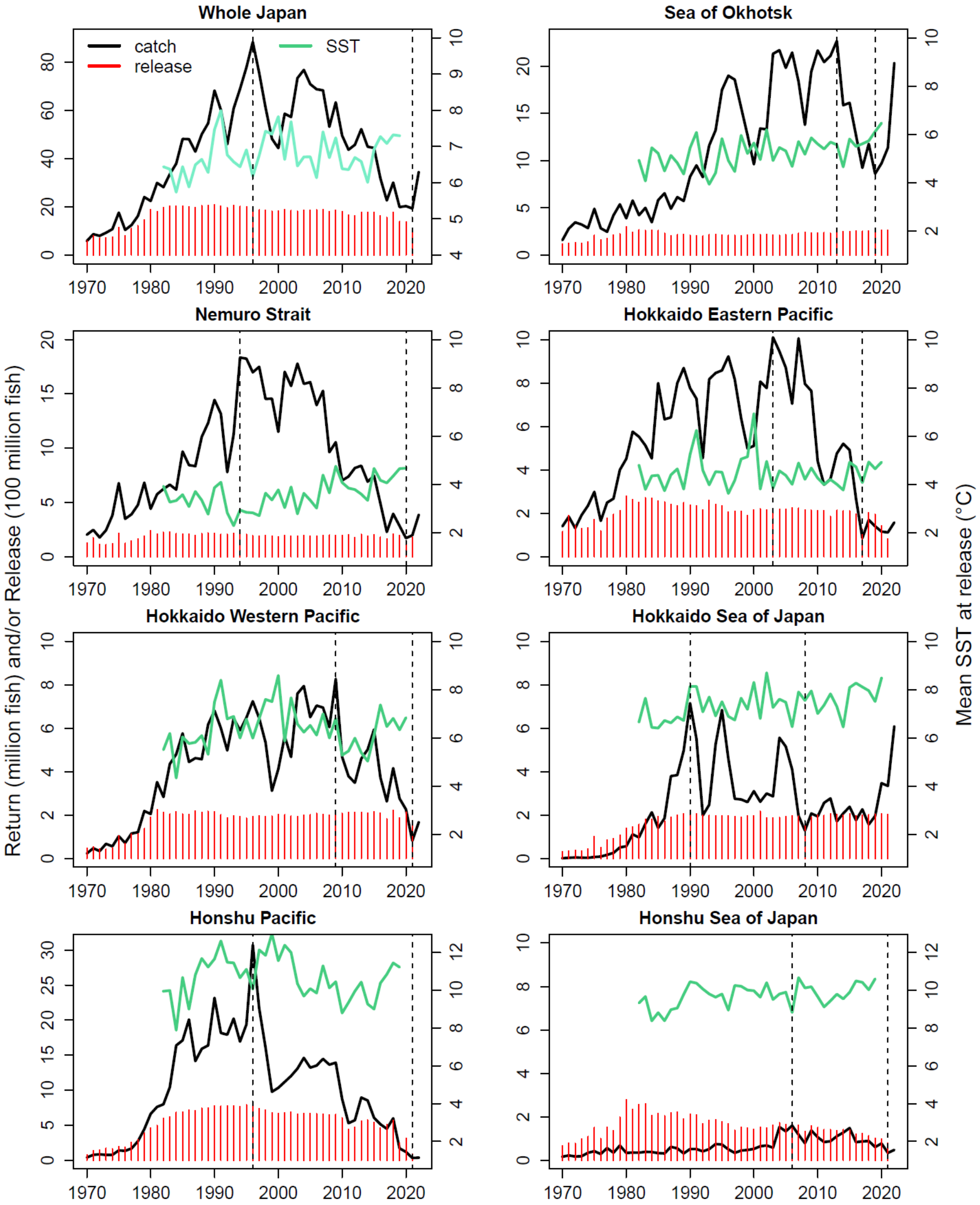
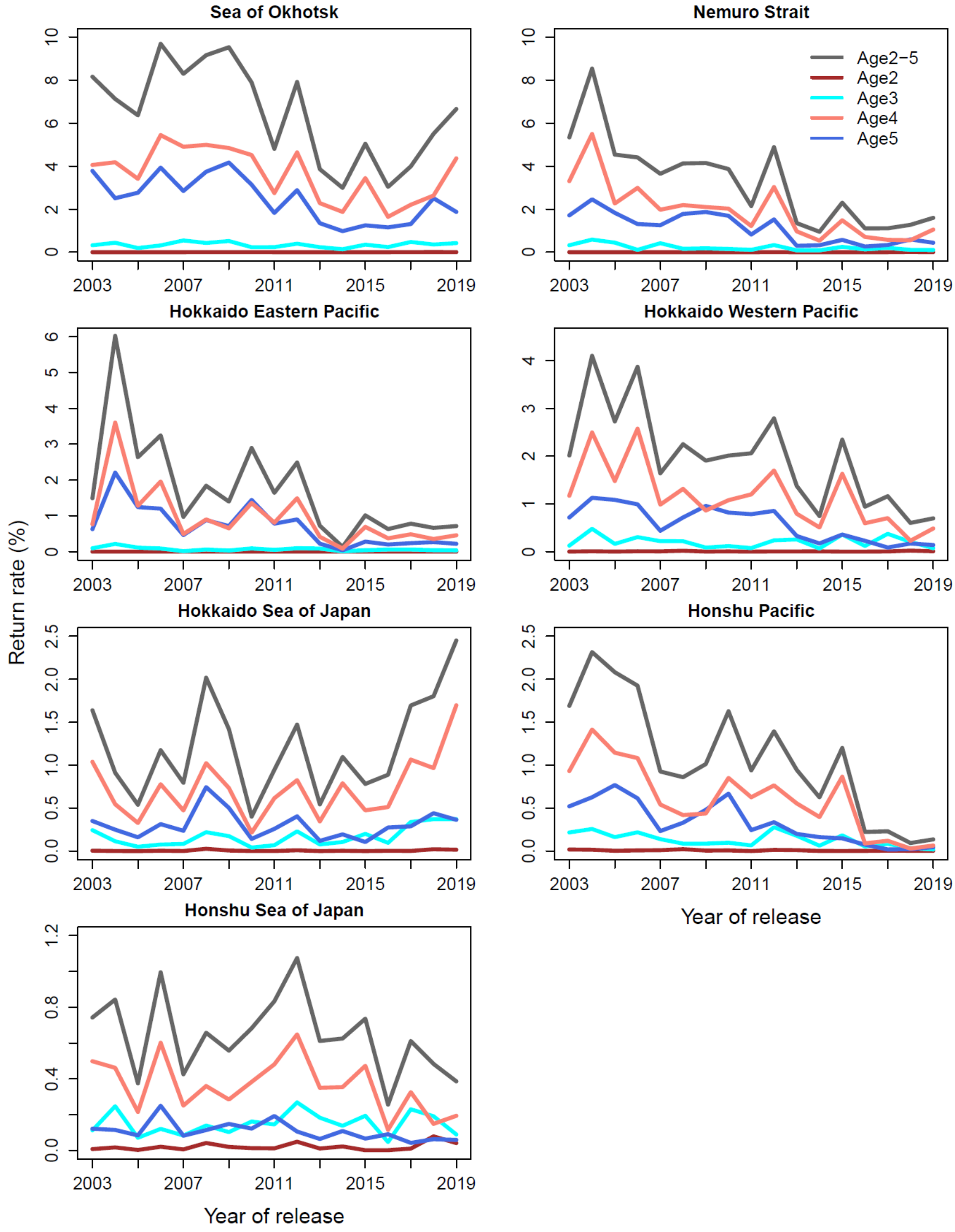


FIGURE 4 Number of chum salmon released and returned in Japan and SST at release. The dashed lines show the historical maximum and the minimum after the maximum. Mean SSTs for the release months are calculated from the 0.25°×0.25° daily mean SST datasets from the JMA (see Methods).



1083

1084 **FIGURE 5** Age-specific return rate of chum salmon by management area.

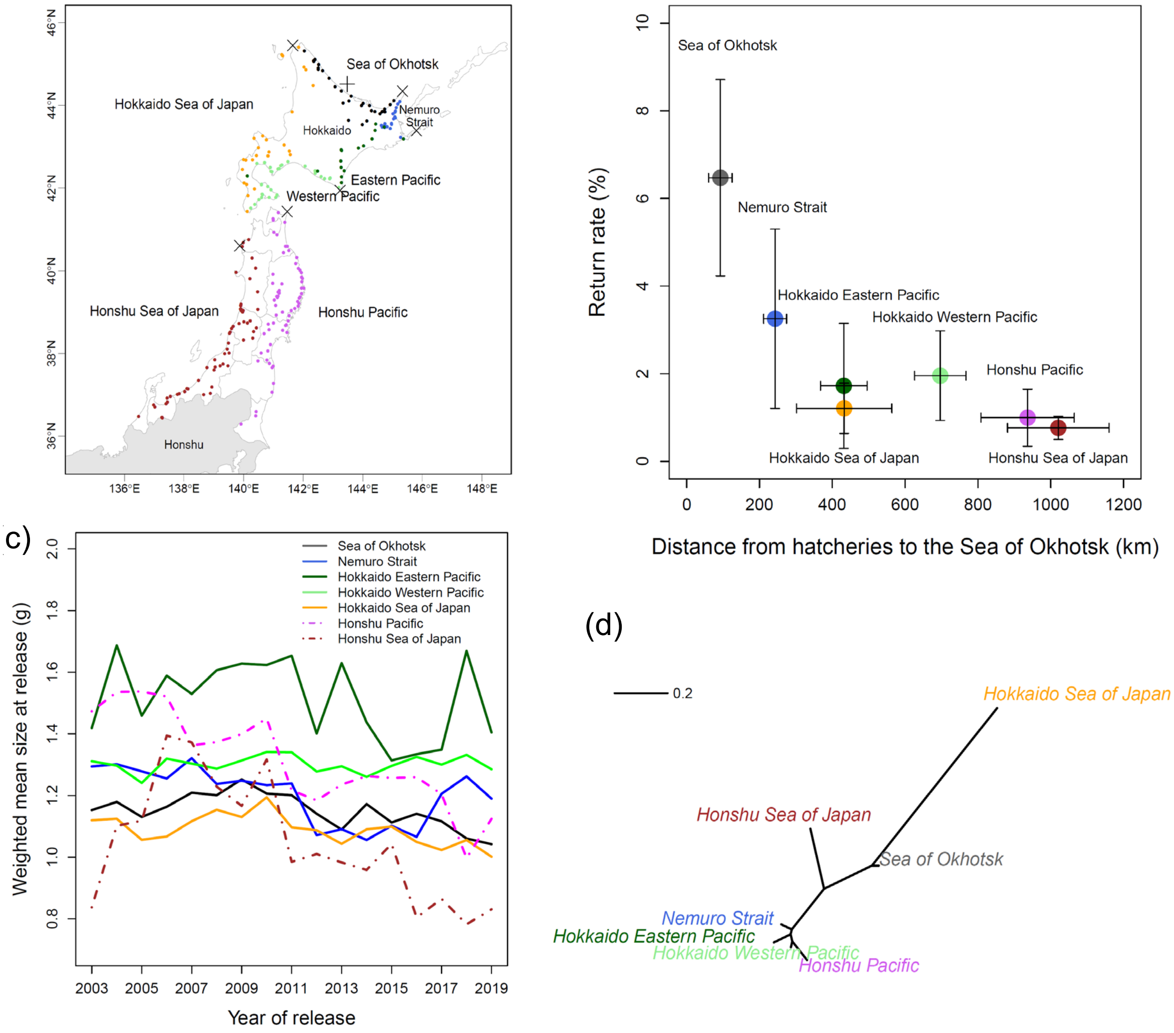


FIGURE 6 Chum salmon return rate and size at release by management area. (a) Map shows salmon hatcheries in the seven management areas in different colors and waypoints (×) to off Monbetsu, Sea of Okhotsk (+). (b) Geographic distance from hatcheries to off Monbetsu vs. return rate (Ages 2-5). (c) Mean size at release weighted by number of juveniles released. (d) Neighbor-joining tree showing pairwise differences of return rates between management areas.

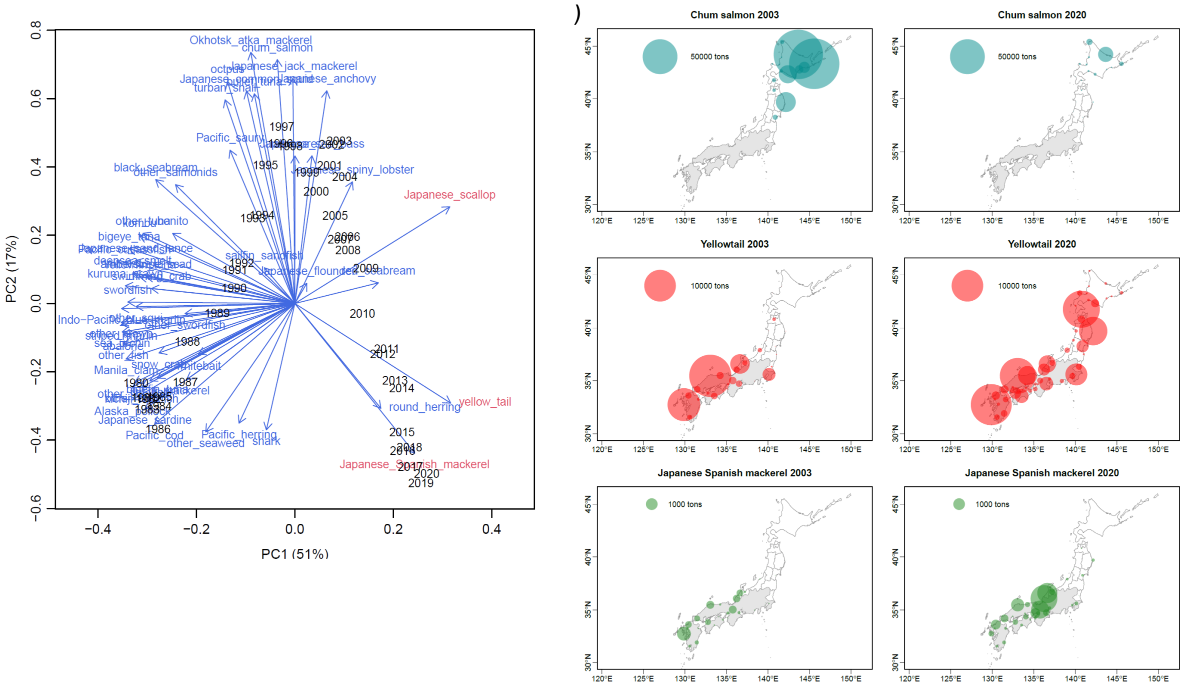


FIGURE 7 Changes in commercial catches of 56 marine species in Japan over four decades (1980-2020). (a) A biplot of the principal component analysis (PCA) based on the catch statistics. (b) Two decadal shifts in the commercial catch of chum salmon and two piscivores; yellowtail and Japanese Spanish mackerel.

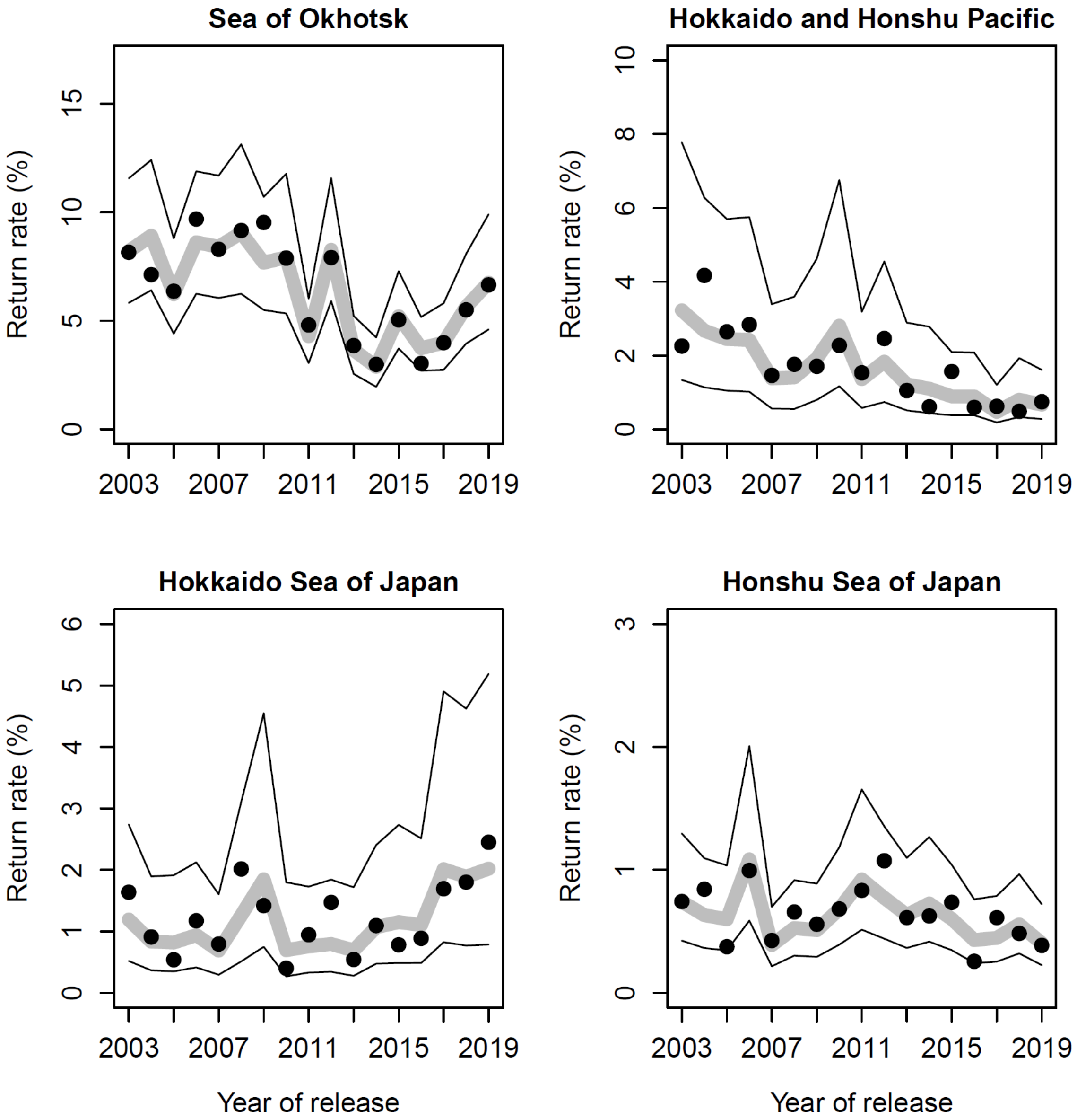


FIGURE 8 Predicted (gray line) and observed return rates (black dots) from Age 2 to Age 5 for the four geographic areas. The 95% prediction intervals are shown as black lines.

Explanatory variable	**Effect size (95%CI)**	**Unit**
Sea of Okhotsk		
a1. Gulf of Alaska Jan. SST	1.36 (1.13−1.63)	1°C
a2. Russian chum salmon	1.03 (1.01−1.05)	million fish
a3. Yellowtail	0.82 (0.77−0.87)	100 tons
Hokkaido and Honshu Pacific		
b1. Size at release	1.82 (1.32−2.53)	0.1 g
Hokkaido Sea of Japan		
c1. Size at release	0.66 (0.46−0.95)	0.1 g
c2. North Pacific Feb.−Apr. SST	1.98 (1.30−3.00)	1°C
c3. Sea of Okhotsk Jul. SST	0.70 (0.56−0.86)	1°C
Honshu Sea of Japan		
d1. Size at release	1.10 (1.02−1.18)	0.1 g
d2. Gulf of Alaska Jan. SST	1.25 (1.07−1.47)	1°C
d3. SST at release	0.59 (0.48−0.72)	1°C

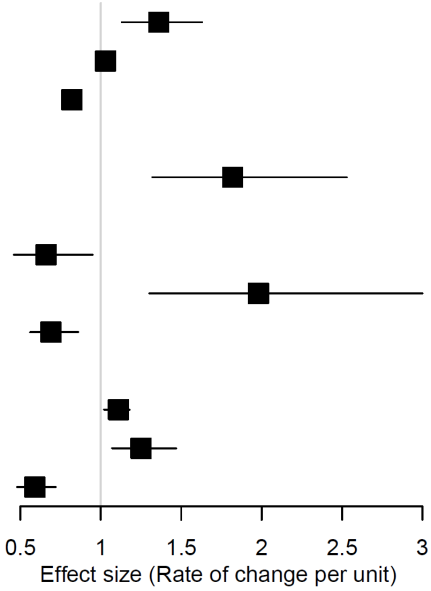


FIGURE 9 Effect size of the significant explanatory variables of the best models. The effect size indicates the rate of change per unit, calculated as the exponential of the regression coefficient.

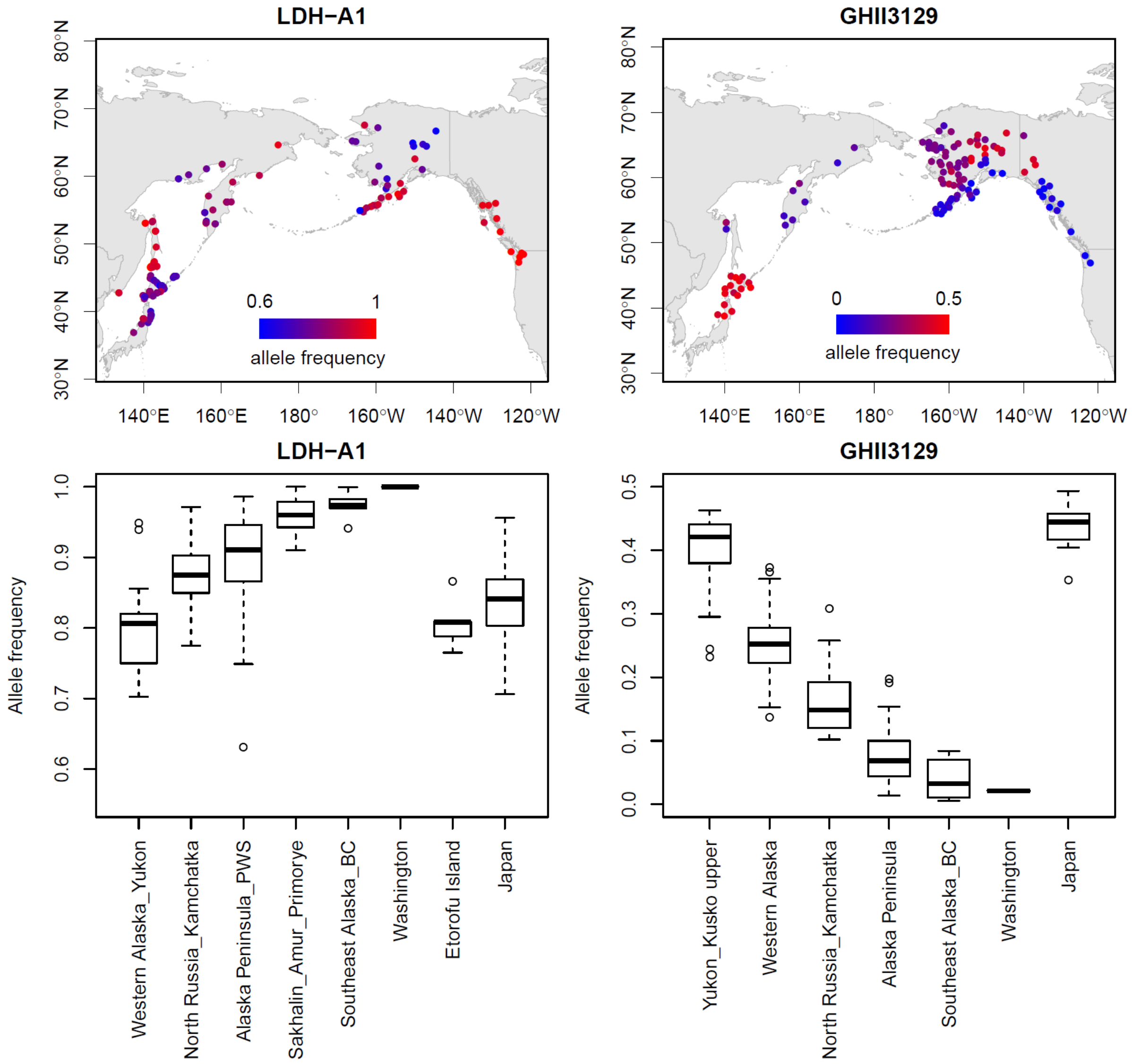


FIGURE 10 Geographic distributions of LDH-A1 and growth hormone 2 SNP (GHII3129) allele frequencies. LDH-A1 from 147 populations (*n* = 18,892) and SNPs from 114 populations (*n* = 10,458). The dots on the maps show sampling locations and allele frequencies with a continuous color gradient from blue to red for the lowest and highest allele frequencies.