Effects of climate, release practices, predation, and competition on declining hatchery-enhanced chum salmon

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Short running title: Causal effects for declining chum salmon

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Abstract

Pacific salmon (*Oncorhynchus* spp.) are exposed to environmental and anthropogenic stresses due to their wide geographic distribution, long migrations, and complex life histories. Understanding how these stressors interact to affect population abundance is essential for conservation and sustainable management of salmon. We investigate the causal effects on population dynamics of hatchery-enhanced Japanese chum salmon (*O. keta*), focusing on the period of sharp decline since the early 2000s and the rebound in 2022. We used 50 years of fishery and hatchery release data and 40 years of high-resolution SST datasets in 30 coastal areas in Japan, as well as monthly mean SST data along the Japanese chum salmon migration route in the high seas. We provide initial evidence that SST at release and that in the migration route, size at release, northward expansion of a piscivorous fish, and intraspecific competition influence the abundance of Japanese chum salmon. The sudden increase in 2022 was driven by an increase in Age-4 fish. The age structure shift towards younger age at maturity was observed in all areas except the Honshu Pacific and was particularly pronounced in the Hokkaido Sea of Japan and the Sea of Okhotsk and, where winter SST in the North Pacific and the Gulf of Alaska had a positive effect on return rates. Size at release and Russian chum salmon also had a positive effect. On the other hand, SST at release and yellowtail (*Seriola quinqueradiata*), as well as summer SST in the Sea of Okhotsk had a negative effect on return rate. Our regression model predicted the return rate well, while explaining 43-75% of the variation in regional populations. Our results highlight winter SST as a driver of younger age at maturity but the trade-off between returned fish and body size.

KEYWORDS

age structure shift, chum salmon, climate change, hatcheries, predators, winter SST

1 | INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) 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 high seas (Groot & Margolis, 1991; Quinn, 2018). Chum and pink (*O. gorbuscha*) salmon fry spend a short time in freshwater before migrating to the ocean, while other Pacific salmon spend months to several years in freshwater according to 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). The wide geographic range, long migrations for growth and reproduction, and complex life histories expose salmon populations to environmental and anthropogenic stressors such as hatcheries 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 (Cunningham et al., 2018; Cline et al., 2019; Connors et al., 2020; Ohlberger et al., 2022) and body size decline of Pacific salmon populations (Lewis et al., 2015; Losee et al., 2019; Oke et al., 2020; Ohlberger et al., 2023) have received increasing attention in recent years. Understanding how these stressors interact to affect population structure and productivity is essential for effective conservation of salmon populations and continued sustainable harvest (Cline et al., 2019; Ohlberger et al., 2022).

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). On the other hand, abundance in Japan and British Columbia, Canada, is at its lowest level on record, and commercial chum salmon fisheries closed in 2021 on the central coast of British Columbia (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, and 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 salmon wintering ecology are of great importance for predicting coastal salmon fisheries and spawning biomass (Myers et al., 2016). Recently, age structure shifts to younger ages at maturity and declining body size have been found in Chinook (*O. tshawytscha*), chum, coho (*O. kisutch*) and sockeye salmon (*O. nerka*) throughout Alaska (Lewis et al., 2015; Oke et al., 2020; Ohlberger et al., 2023). The decline in salmon size attributed to a shift to younger age at maturity linked to climate change, increased inter- and intra-specific competition due to overabundance of salmon in the high seas (Lewis et al., 2015; Oke et al., 2020; Ohlberger et al., 2023), and predation by killer whales (Ohlberger et al., 2019). Warm winter SST has been linked to improved growth of sockeye salmon in the Bristol Bay, Alask, while summer SST has been linked to reduced growth (Ohlberger et al., 2023).

Pacific salmon has the longest history of artificial propagation, which started in the middle of the eighteenth century, and management of these species constitutes the world's largest set of hatchery release programs

(Naish et al., 2007). Hatchery release of chum salmon comprises the world's largest marine stock enhancement and sea-ranching program (Amoroso et al., 2017; Kitada, 2018). Japan is located at the southern limit of the geographical distribution of chum salmon (Salo, 1991), and runs the world's largest chum salmon hatchery release program. Releases of chum salmon juveniles from Japan have increased remarkably since the 1970s—to ~2 billion per year. The number of returning chum salmon to Japan increased sharply after the 1970s, with substantial economic benefits (Kitada, 2020). Despite continuous hatchery releases, the number of returning chum salmon declined sharply after the early 2000s. Previous studies have reported that higher spring sea surface temperatures (SSTs) in the coastal zone contribute to better survival of juvenile chum salmon in the Hokkaido Pacific coast through improved feeding, growth and swimming ability (Saito & Nagasawa, 2009; Kuroda et al., 2020; Honda et al., 2021). On the contrary, shorter inshore stays associated with warming climate could lead to lower survival of juveniles in the Honshu Pacific coast (Kaeriyama, 2023). It is generally accepted that a warming climate may cause a decline in chum salmon survival. 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 the ocean entry to the migration route, to infer causal effects on survival or return rates.

The number of chum salmon returning to Japan 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%). In the Chitose River in the Sea of Japan, where Japan's oldest hatchery operates, 587,000 fish were returned, surpassing the historical record of 551,000 in 1995 (https://chitose-aq.jp/). The sudden increase in 2022 was a big surprise to fishers, hatchery managers, people and biologists. This unusual phenomenon may provide us with an opportunity to understand the mechanisms of salmon population dynamics and may contribute to effective conservation of salmon populations and sustainable fisheries. Several regions in the USA and Russia also showed increases in chum salmon catches in 2022 (Figures S1, S2).

In this study, we investigate the effects of release practices, predators, changing ocean conditions, and salmon abundance (chum and pink) on Japanese chum salmon population dynamics, focusing on the period of sharp decline since the early 2000s and the sudden increase in 2022. 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 comprising 70 species (1980-2020). Based on the results of high seas studies (Myers et al., 2007; Urawa et al., 2018), we defined the seasonal migration route of Japanese chum salmon and calculated the monthly mean SST in the summer feeding and overwintering grounds in the North Pacific (1982-2022). We obtained return rates for releases from 2003 to 2019 based on age composition, and numbers

of juveniles released and adults returned. Using these data, we infer causal factors for Japanese chum salmon return rates at both local and North Pacific scales via multiple regression analysis.

2 | METHODS

2.1 | Data sets

We compiled release and catch data of Japanese chum salmon. The numbers of catch (coastal catch plus hatchery propagation catch) and release of chum salmon from 1970 to 2022 in Hokkaido were obtained from the Hokkaido Salmon Enhancement Association (HSEA, temporal translation). Those in prefectures in Honshu were obtained from the Fisheries Research and Education Agency (FRA). For Aomori Prefecture (in the northernmost part of Honshu), which has both Pacific and Sea of Japan coastlines, we obtained catch and release data by reporting region 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). We summarized chum salmon catch and release data 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 genetic population structure (Beacham et al., 2008).

Datasets of release size and time at release of Japanese chum salmon 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 from 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 0.25°×0.25° global monthly mean SST data file from 1982 to 2022 ("sst.mnmean.nc") from the NOAA OISST high-resolution data set (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 and 12 areas in Honshu from Japan Meteorological Agency (JMA) (Data S3, S4). The names of the SST observation areas and the map with JMA sources are shown in Table S2.

2.2 | Size and time at release, and age composition

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). The Japanese chum salmon hatchery program recommended size at release greater than 1 g (BW) and time of release when coastal SST ranged from 5 to 13 °C (Honda et al., 2020). 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. Because the number of released individuals (n_l) varied across release events ($l = 1, \ldots, L$), we calculated the weighted means of 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.

Chum and pink salmon fry spend only a short time in freshwater before migration 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. To estimate the distribution of the time of release in Japan, we counted the number of release events by months.

Age composition is necessary for estimating the number of fish returned from each release. We compiled age composition data of chum salmon return (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 performed for each year by management area. We summarized 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 | SSTs in the North Pacific and Japanese coasts

Pacific salmon are distributed throughout the international waters 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). Near shore SST along the coastline of Alaska was closely associated with Pacific salmon productivity (Oke et al., 2020). To understand the long-term changes in SST in the salmon distribution range, we created the monthly mean SST isoclines of the 1°×1° 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 monthly mean SST isoclines of the 1°×1° around Japan for 1980, 2000 and 2022 are also generated in a similar manner.

To approximate SST values close to the river mouths which juvenile salmonids are most likely to experience after ocean entry (Oke et al., 2020), we calculated the monthly mean SSTs from 1982 to 2020 for the 18 areas in the coast of Hokkaido and the 12 areas in the coast Honshu 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 Pacific, the monthly mean SSTs of Aomori, northern and southern Iwate, Miyagi, Fukushima, and northern Ibaraki were averaged. For the Honshu Sea of Japan, the monthly mean SSTs of Aomori, Akita, Yamagata, northern and southern Niigata, and Toyama Bay were averaged. Finally, we calculated mean SSTs for the months of release 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, Figure S7).

2.4 | Japanese chum salmon migration route and SSTs

The seasonal migration of Japanese chum salmon was modeled based on a series of high-seas studies, including genetic stock identification (Myers et al., 2007; Urawa et al., 2018). According to the studies, juvenile chum salmon (Age 0) are distributed in the Sea of Okhotsk until fall (Aug-Nov) and migrate to a narrow area in the western North Pacific (hereafter, North Pacific) for wintering. 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 fall for the second overwintering period (Age 2). The following year, they return to the Bering Sea and again migrate to the Gulf of Alaska for wintering (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 on the Pacific coast of Japan migrate to the Sea of Okhotsk (Honda et al., 2017). In the Sea of Okhotsk, juvenile chum salmon from all areas of Japan are found 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). From 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 set the 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 (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.

2.5 | 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 summarized 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 characterize the temporal changes in the catches, we performed a principal components analysis (PCA) on the catch data of 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.

2.6 | Causal effects on chum salmon return rates

The return rate has been widely used as a common measure of the effectiveness of marine stock enhancement, including salmonids (Kitada, 2018). It has been used as a measure of the relative survival of chum salmon (Kaeriyama, 1999; Saito & Nagasawa, 2009), Chinook and coho salmon (James et al., 2023). It is generally accepted that hatcheries are responsible for most of the chum salmon in Japan and that there are no wild chum salmon (Hiroi, 1998; Kaeriyama, 1999; Kaeriyama & Edpalina, 2004; Kobayashi, 1980; reviewed by Iida et al., 2018). We assumed that all returning chum salmon were hatchery reared and used the return rate as the objective variable. Return rates were calculated by management area. The total number of fish returned (Y_t, coastal commercial catch plus river catch for hatchery broodstock) from releases in year t is obtained as

$$Y_t = \sum_{a=2}^{5} y_{t+a-1}\,\hat{p}_{a,t+a-1} = \sum_{a=2}^{5} Y_{a,t}$$

where y_{t+a-1} is the total 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 $t+a-1$. We summed the number of fish returned from Ages 2 to 5 ($a = 2, \ldots, 5$) because the main ages of return were Age 4 and 5, and there were very few returns older than Age 6 (Table S4). Return rate of juveniles released in year *t* was estimated by $R_t = Y_t / X_t$, where X_t is the number of hatchery-reared juveniles released in year *t*. The age-

specific return rate was calculated as $R_{a,t} = Y_{a,t}/X_t$.

Great circle geographic distances between the hatcheries and the central coast of the Sea of Okhotsk (off Monbetsu) were calculated using the distm function in the R package `geosphere`, assuming 5 waypoints representing reasonable migration paths from the hatcheries to the central coast of the Sea of Okhotsk (off Monbetsu). The calculation was done by year of release and management area. The distances between return rates in the management areas were measured by $1 - r_{jk}$ and visualized by a neighbor-joining (NJ) tree in the R package `ape`, where r_{jk} is the correlation coefficient between pairs of return rates.

We performed regression analysis by area that had a similar trend of return rates based on the NJ tree. Our model describes the relationship between return rates across all ages (R_t) and the explanatory variables such as SSTs, size at release, and abundance (catch) of possible predators and competitors, whose hypothesized mechanisms were summarized in Table 1. We transformed the return rate to the log scale for model fitting in a multiple linear regression:

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

where β_0 is the intercept, the explanatory variables are denoted by $\boldsymbol{z}$. We used 14 explanatory variables (s=14). 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. In the 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). Winter SSTs in the North Pacific and Gulf of Alaska were used to infer effects during overwintering of Age 1 and Age 2 fish, 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 Gyle (Davis et al., 1998; Qin & Kaeriyama, 2016; Daly et al., 2019), and catches of Russian, US and Canadian chum and pink salmon (Figures S9, S10) were used as explanatory variables to infer intra and interspecific competition of food. The age composition of Japanese chum salmon showed that Age 4 fish were dominant (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 lifespan of 2 years (Groot & Margolis, 1991; Quinn, 2018), and Russian, US and Canadian catches in t+1 year 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 summarized the objective variables (return rates) and explanatory variables by management area (Tables S8-S10). Age composition (1997-2019) was used to estimate the number of fish returned by age, while 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 only predict 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 performed a model selection using AICc (Sugiura, 1978), which is a small sample correction of Akaike Information Criterion (AIC, Akaike, 1973). We selected the most parsimonious model (hereafter, best model) from 2^{14} (=16,384) models that had the minimum AICc value using the `dredge` function in the `MuMIn` package in R. We used the results of the best model rather than model averaging, which may not be reliable when there is multicollinearity among explanatory variables (Cade, 2015). The use of an unstandardized measure is usually preferred to a standardized measure if the units of measurement are useful as effect sizes on a practical level (Wilkinson, 1999). We used the regression coefficient for unstandardized explanatory variables as the effect size: $\exp(\hat{\beta}_i)$ for coefficient *i*, visualized using the `forestplot` function in R.

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 (110 years), the increase in SST was relatively slow in all seasons., while after 2010 a rapid increase was observed in summer. Summer SSTs (June-August) increased in the Bering Sea, the Sea of Okhotsk, the western, central, and the eastern North Pacific, and the Gulf of Alaska, while spring (April-May), fall (October-November), and winter (January) SSTs were stable throughout the Pacific salmon range until 2010, increases over the past decade have been relatively slow. 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 have been observed in 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 (Figure 2) shows the migration route of Japanese chum salmon until they return, and the box plot shows changes in SST along the seasonal migration of Japanese chum salmon. In the Sea of Okhotsk, 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 similar level in January. In the Bering Sea, 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), but significantly decreased in October (7.4 ± 0.6°C) and November (5.4 ± 0.5°C). In the Gulf of Alaska, the SST was 1.5°C higher in December

(6.9 ± 0.8°C) than the Bering Sea November SST, 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 the similar level in December.

The mean January SST was just the same in both wintering areas. However, the February to 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 ($t = 3.3,\ p = 0.0012$). February-April mean SST 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 the winter SSTs between and within the wintering areas, we chose both the January SST and the February-April mean SST as explanatory variables, and which one would be chosen was left 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.

July SST in the Sea of Okhotsk had 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 sharp increase in 2013. Winter SST trends in the North Pacific were both 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 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 were returned (Figure 4). Along with the increased number of fish released, the total number of fish returned had increased significantly by 1996, when the catch reached the historical maximum of 88 million fish. Despite the relatively stable trend in the number of fish released, the number of fish returned has continued to decline since 2004, reaching the four-decade minimum of 19 million in 2021. Notably, the returned fish increased in 2022. The trend across Japan was synchronized in the two main production areas, Nemuro Strait and Honshu Pacific as indicated by the broken lines. The Hokkaido Eastern and the Hokkaido Western Pacific showed a similar trend after the mid-2000s. On the contrary, in another major production area, the Sea of Okhotsk, there was 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, which 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 great variation in the 2022 recovery.

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

3.4 | Return rate and size at release by management area

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

Higher return rates were obtained in the management areas whose geographic distances were nearer to the central Sea of Okhotsk (Figure 6a,b). The weighted mean size at release (Figure 6c) was greater than the recommended threshold (BW > 1g) in all management areas. Weighted mean size 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 four geographic areas: Sea of Okhotsk, Hokkaido Sea of Japan, Honshu Sea of Japan, and Hokkaido and Honshu Pacific (combined 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, and catches of yellowtail were summed over the four areas. The number of chum salmon returned and released 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 PCA (Figure 7a) identified differences between 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 changes in commercial catches of 56 marine species in Japan after 2000 were characterized mainly by the four species, which increased in recent decades: yellowtail, Japanese Spanish mackerel (*Scomberomorus niphonius*), Japanese scallop (*Mizuhopecten yessoensis*) and round herring (*Etrumeus micropus*) (Figure S16). Among these, yellowtail and 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 in landings of yellowtail to 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 the results, we defined yellowtail as a possible predator of chum salmon juveniles.

3.6 | Causal effects on chum salmon return rates

Model selection of 2^{14} (=16,384) models was performed using AICc for each geographic area. Table 2 summarizes the best models from the regression analysis. The 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 size 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 positive effect of winter SST (Feb.-Apr.) in the North Pacific, and the negative effects of summer SST (Jul.) in the Sea of Okhotsk. The size at release also had a negative impact 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 size 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 of the observed return rates in the four areas well (Figure 8), and all observed values were within the 95% prediction intervals.

The effect size for each regression coefficient (Figure 9) was measured by $\exp(\hat{\beta}_i)$, which represents the rate of change per unit. In particular, winter SST in the North Pacific and the Gulf of Alaska had a positive effect in 3 areas. A 1°C 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°C 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, size 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, size at release had a negative effect, reducing the return rate by 34%. Russian chum salmon abundance had a positive effect on Sea of Okhotsk chum salmon, but it was small, increasing the return rate by 3% per million chum salmon caught.

4 | DISCUSSION

We present preliminary evidence that the abundance of chum salmon returning to Japan is influenced by regional climate, release practices, global climate and intraspecific competition. Furthermore, we show that the increase in the number of chum salmon returned in 2022 is due to a rise in Age 4 fish, leading to higher return rates for the 2019 release. This shift toward younger age at maturity is observed in all areas except the Honshu Pacific and is particularly pronounced in the Hokkaido Sea of Japan and the Sea of Okhotsk. North Pacific February-April SST during the first overwintering period had the greatest positive effect on return rate, and Gulf of Alaska January SST during the second overwintering period also had a positive effect on return rates. Size at release typically had a beneficial impact on return rate. Russian chum salmon also had a positive effect. On the other hand, SST at release, July SST in the Sea of Okhotsk, and the rapid northward expansion of yellowtail negatively affected the return rates. Our regression model predicted return rates well, while explaining 43-75% of the variation in regional populations.

Our regression model assumed that all Japanese chum salmon are hatchery-reared and that there are no wild fish. Field studies provide evidence that natural reproduction of chum salmon occurred 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 throughout the northern Honshu Sea coast of Japan (Iida et al., 2018; Iida et al., 2021). Escapement of returned fish has not been a common practice in Hokkaido, although all weirs for broodstock collection in the enhanced rivers of the Kitami region, Sea of Okhotsk, have been redesigned to allow passage of fish for spawning (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 impede upstream migration of chum salmon (Iida et al., 2018). Rivers in Japan are relatively short, and hatchery fish are released in most large rivers (Miyakoshi et al, 2013), while naturally spawning chum salmon populations persist in many small (short) rivers in Hokkaido (Kitada, 2014). The very high gene flow between populations facilitates the genetic admixture of hatchery-born fish and wild-born hatchery descendants in the entire Japan population (Kitada & Kishino, 2021). The relative reproductive success (RRS) of hatchery-reared salmon has been about

50% of that of wild-origin fish when they spawn in the wild (Araki et al., 2007; Christie et al., 2014; Shedd et al., 2022), with significant variation (Kitada et al., 2011). Survival of hatchery-born chum salmon from emergence to release was very high at 97 ± 1% (Nogawa & Yagisawa, 2011), while 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).

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 S19). 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 of predators is a seabird, the rhinoceros auklet (*Cerorhinca monocerata*), which preys on juvenile chum salmon from late June to mid-July on the Pacific coast of Hokkaido, with an estimated consumption of 317 tons (31.7 million juveniles if we assume 10g 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 Chitose River, Hokkaido Sea of 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 scooped up in a net in rivers in Etrofu Island, where Japan operated salmon hatcheries (Yagisawa, 1970). The Chitose River has the oldest salmon hatchery in Japan, beginning in the 1888 (Kobayashi, 1980) and continuing for over 135 years (=27 generations assuming 5 years of generation time). A significant reduction in the mtDNA allele frequency in the current Japanese chum salmon might be caused by intended and unintended selection in hatcheries and reduce the efficiency of aerobic exercise ability and endurance, energy metabolism, and oxygen consumption (Kitada & Kishino, 2021). The effect of predation by piscivorous fish can be significant when many slow swimming juveniles are released at the same time.

The positive effect of size at release was the greatest in the Hokkaido and Honshu Pacific, where a 0.1 g increase in size at release increased the return rate by 82% (Figure 9). In the Sanriku coast, Honshu Pacific, Iino et al. (2022) found that chum salmon juveniles reared at low food levels allocate less than half of their energy to growth at high temperatures compared to juveniles reared at high food levels. Long-distance migration from the Honshu Pacific coast to the Sea of Okhotsk (Figure 6) could have a negative effect on the growth and survival of juveniles. In the Honshu Sea of Japan, the effect of size at release was smaller; a 0.1 g increase in size at release increased the return rate by 10%, while a 1°C increase in SST at release reduced the return rate by 41%. The positive effect of size at release might be reduced by the effect of increasing SST. Unexpectedly, in the Hokkaido Sea of Japan, the effect of size at release was negative; a 0.1 g increase in size at release decreased the return rate by 34%, suggesting that the current size at release (1.04 ± 0.03 g, average for 2016-2020) is sufficient in this region.

February-April SST in the North Pacific, where juvenile chum salmon spend their first winter, has the largest positive effect, with a 1°C increase increasing return rates by 98% in the Hokkaido Sea of Japan. A 1°C increase in January SST in the Gulf of Alaska, where chum salmon spend their second (and subsequent) winters, increases return rates by 36% in the Sea of Okhotsk and by 25% in the Honshu Sea of Japan. Our results highlight that the sudden increase in the number of returning fish in 2022 is driven by an increase in the number of Age 4 fish (Figures 4, 5). The shift in age structure towards younger age at maturity was particularly pronounced in the Hokkaido Sea of Japan and the Sea of Okhotsk, which had started in 2011 and 2017. The geographic distribution of chum salmon SNP allele frequencies (Figure 10) of the growth hormone2 (GHII3129) and GnRH (gonadotropin-releasing hormone) (Seeb et al., 2011) showed the uniqueness of Japanese chum salmon populations (Kitada & Kishino, 2021). Growth hormone (GH) is an important regulator of somatic growth in salmonids (Björnsson, 1997). GnRH regulates reproduction in vertebrates including salmonids (Khakoo et al., 1994). These results suggest that the warm winter SSTs in the overwintering grounds facilitated the growth of hatchery-born Japanese chum salmon and resulted in younger age at maturity. The apparent increase in survival is due to returning one year earlier. This represents a trade-off between the number of returning fish and body size, and the consequences for fisheries and ecosystems can be crucial (Oke et al., 2020; Ohlberger et al., 2023). The average weight of Japanese chum salmon has decreased since 2000 in Hokkaido and Honshu (Yamaguchi et al., 2021; Watanabe et al., 2022).

Our results highlight that warm winter SSTs in the overwintering grounds may cause the younger age at maturity, leading to the increase in the number of chum salmon returned in 2022. This phenomenon may be related to intended and unintended selection for growth and artificial fertilization in hatcheries. Using the world's largest hatchery release program, we show how salmon populations are exposed to environmental and anthropogenic stressors at both local and North Pacific-wide scales.

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CONFLICT OF INTEREST

The authors have declared that no conflict of interests exist.

AUTHOR CONTRIBUTIONS

S.K. and H.K. conceived and designed the study. S.K. curated the data, implemented the scripts for this study,

analyzed the data, interpreted the results, and wrote the manuscript. H.K. validated the statistical analysis, interpreted the results, and reviewed the manuscript. All authors approved the final version of the manuscript.

DATA AVAILABILITY STATEMENT

Data generated or analyzed during this study are provided in full within the published article and its supplementary information, including Supplementary Figures S1–S19. Supplementary Tables S1-S10, Supplementary Data S1-S5, and the scripts for the analysis are available at https://doi.org/10.5281/zenodo.8353790.

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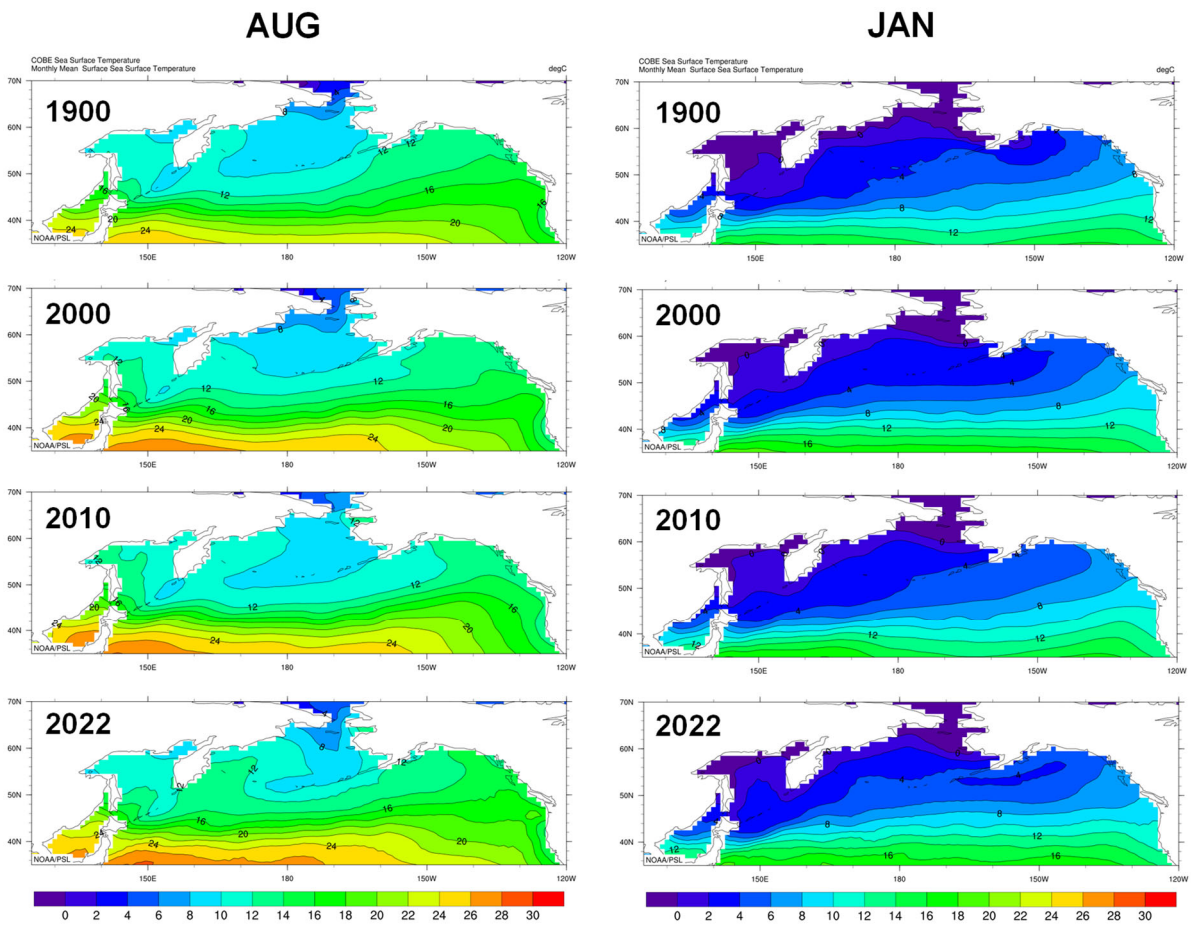

FIGURE 1 Long-term changes in the summer and winter SST isocline in the North Pacific. Plotted from Plot: COBE Sea Surface Temperature, NOAA Physical Sciences Laboratory. Changes in April, May, June, August, October and November SSTs are shown in Figures S11-13.

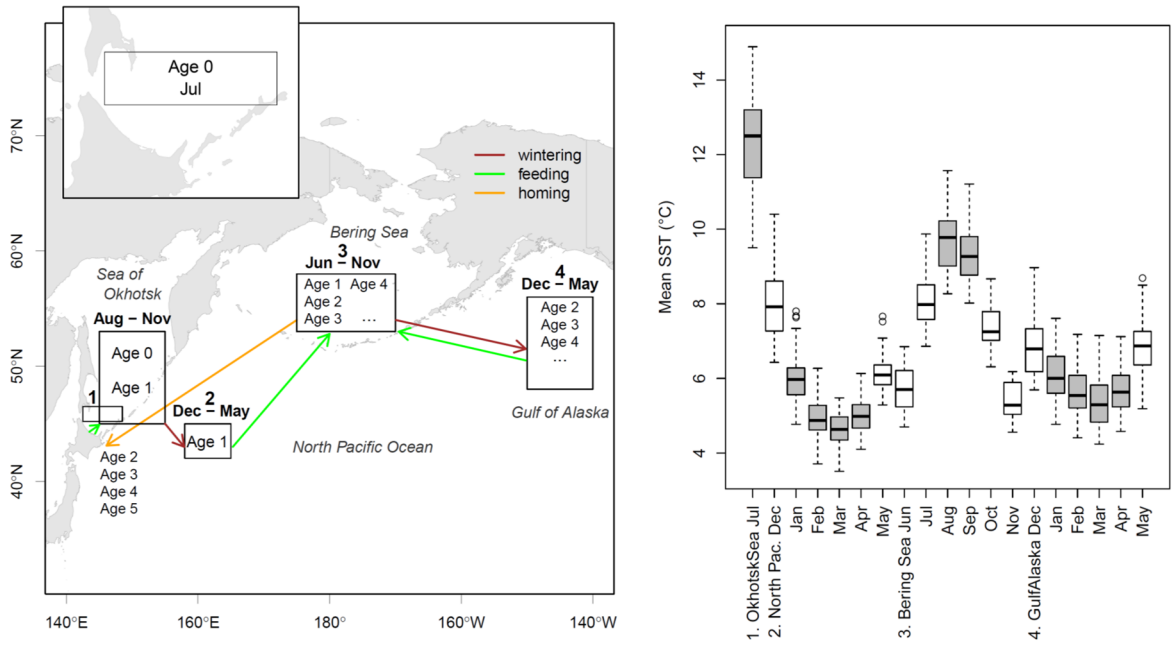

FIGURE 2 Migration routes of Japanese chum salmon and critical SSTs. Map shows migration routes estimated from the long-term field surveys, redrawn from Urawa et al. (2018). Box plots show the change in mean summer and winter SSTs of feeding and wintering areas, calculated from the NOAA 1/4° daily OISST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

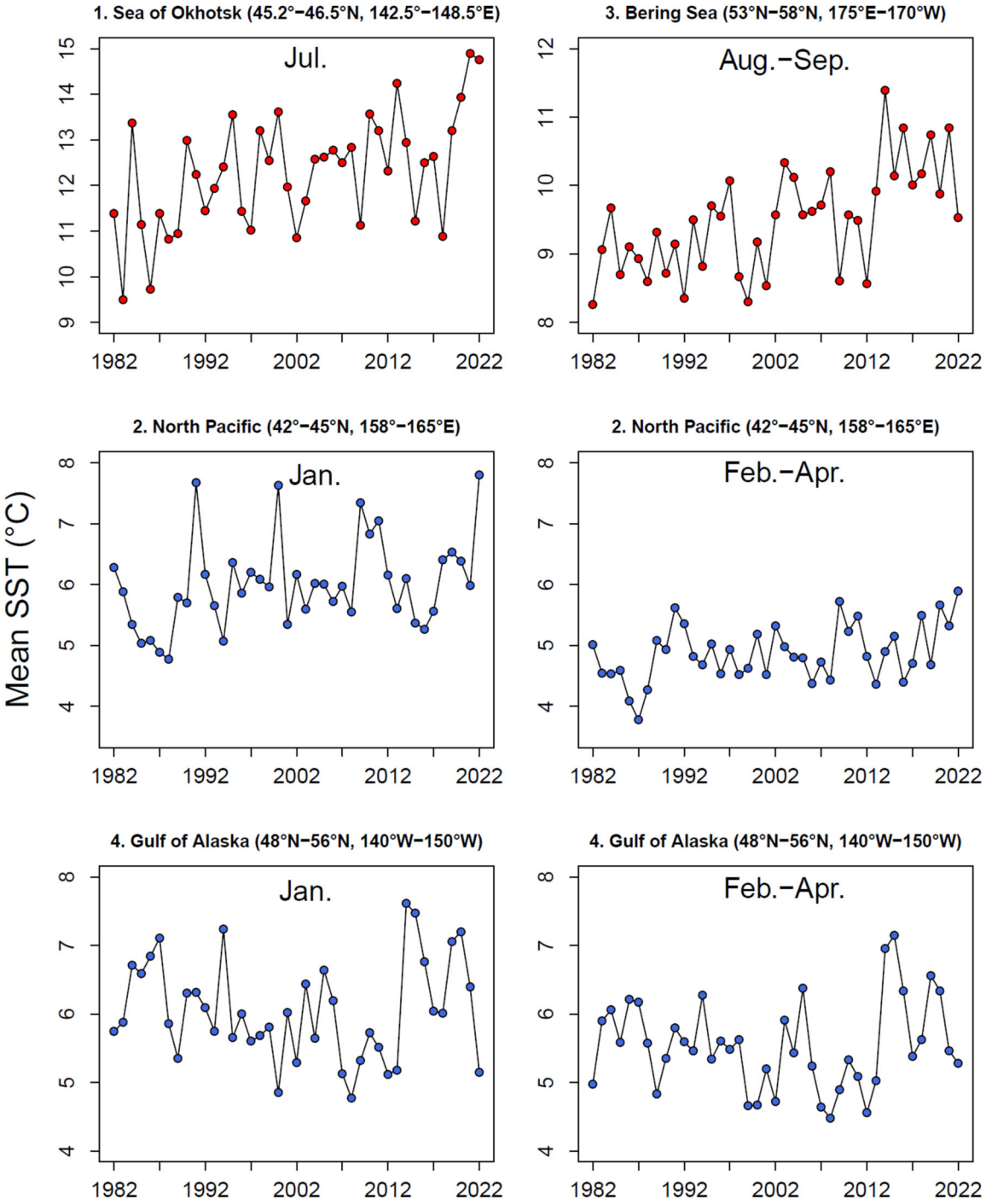

FIGURE 3 Summer and winter mean SSTs in the Japanese chum salmon migration route in Figure 2. SSTs are calculated from the NOAA 1/4° daily OISST climate record.

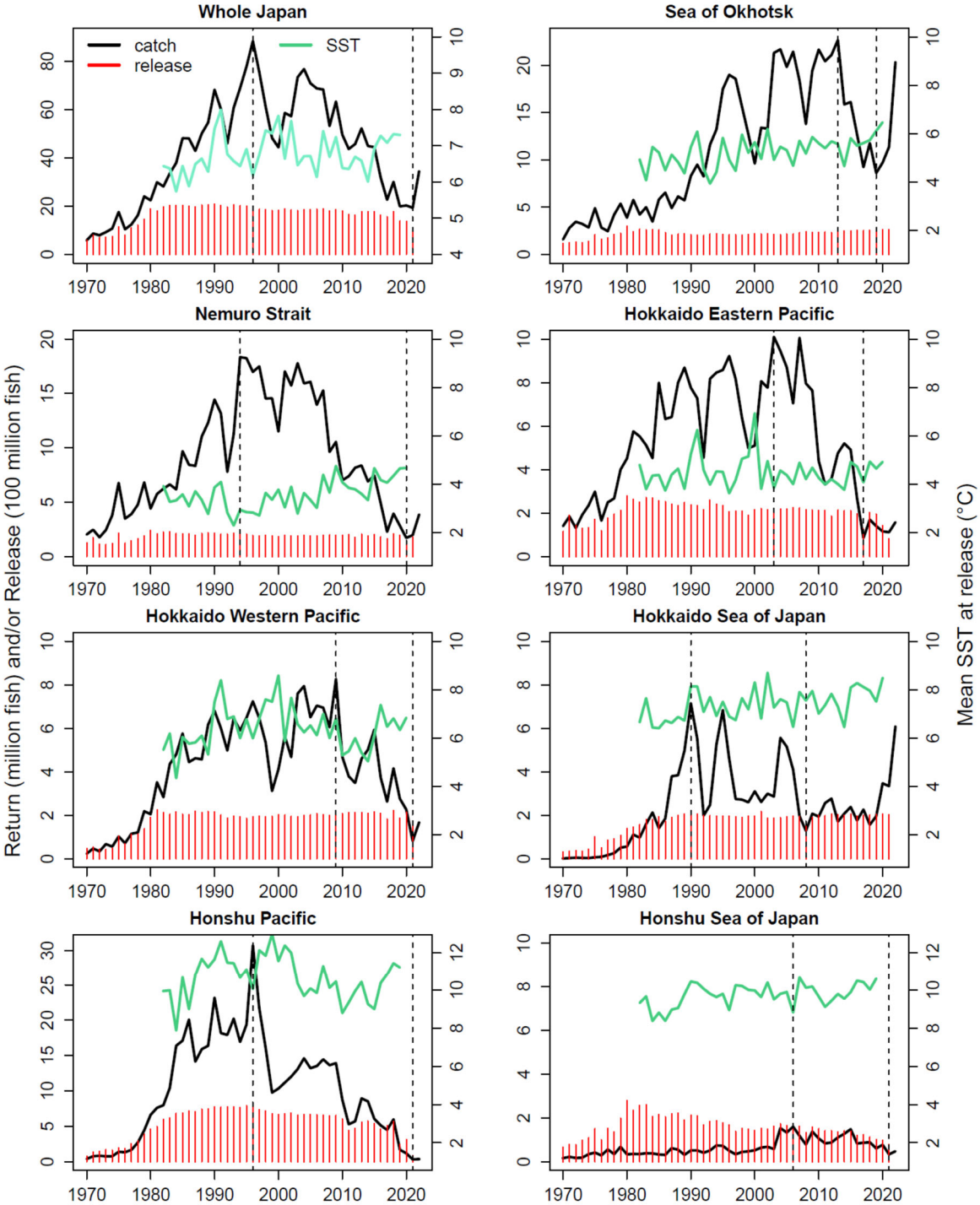

FIGURE 4 Number of chum salmon released and returned in Japan and SST at release. The dashed lines show the historical maximum and the minimum after the maximum. Mean SSTs for the release months are calculated from the 0.25°×0.25° daily mean SST datasets from the JMA (see Methods).

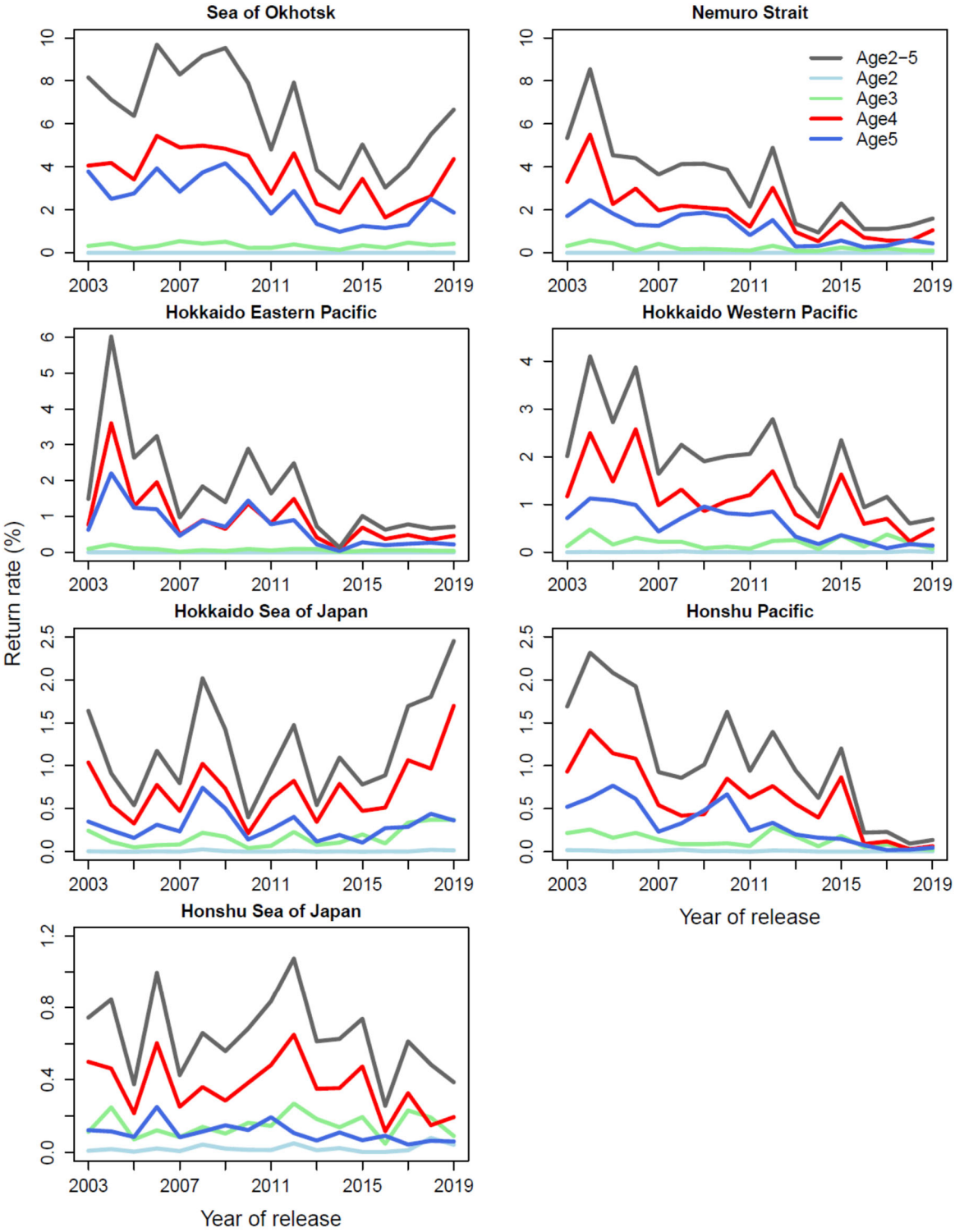

FIGURE 5 Age-specific return rate of chum salmon by management area.

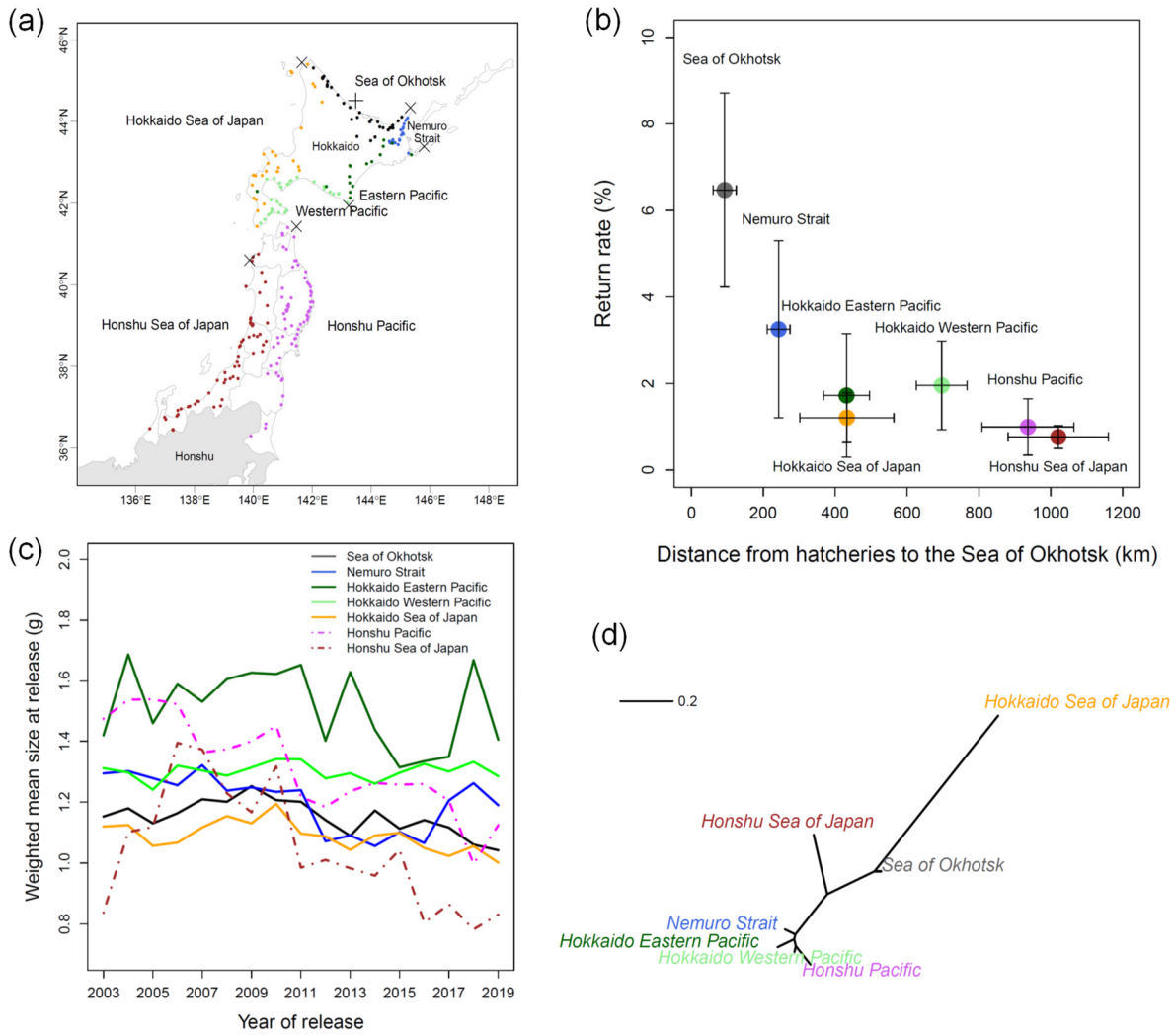

FIGURE 6 Chum salmon return rate and size at release by management area. (a) Map shows salmon hatcheries in the seven management areas in different colors and waypoints (×) to off Monbetsu, Sea of Okhotsk (+). (b) Geographic distance from hatcheries to off Monbetsu vs. return rate (Ages 2-5). (c) Mean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

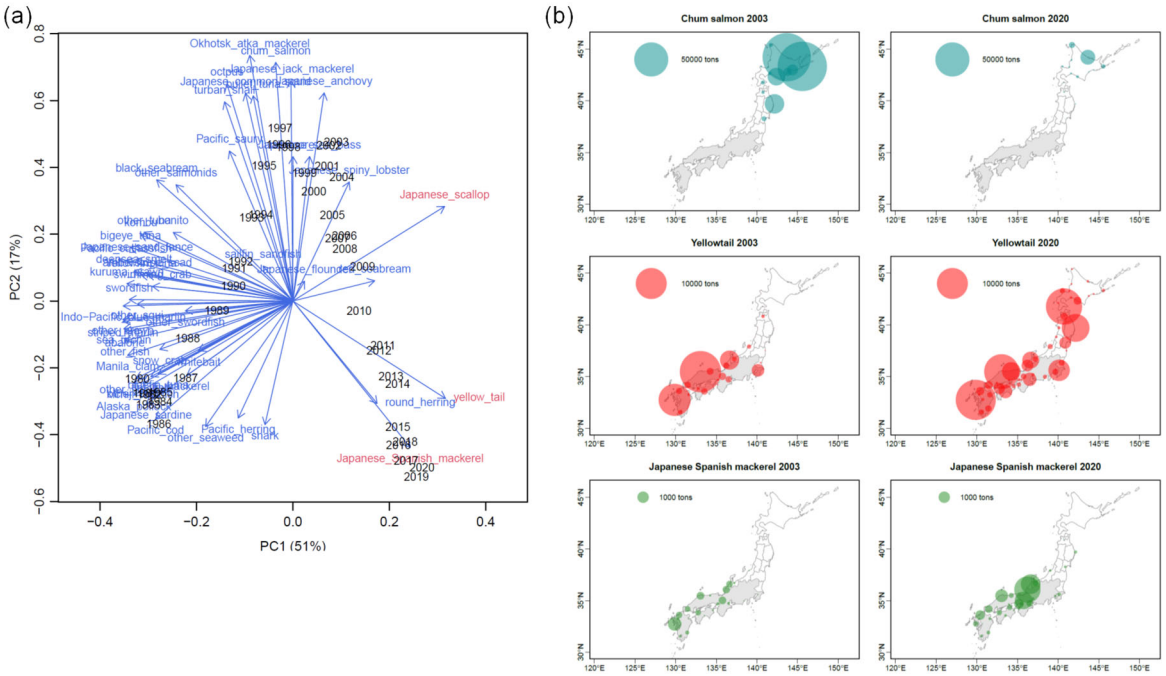

FIGURE 7 Changes in commercial catches of 56 marine species in Japan over four decades (1980-2020). (a) A biplot of the principal component analysis (PCA) based on the catch statistics. (b) Two decadal shifts in the commercial catch of chum salmon and two piscivores; yellowtail and Japanese Spanish mackerel.

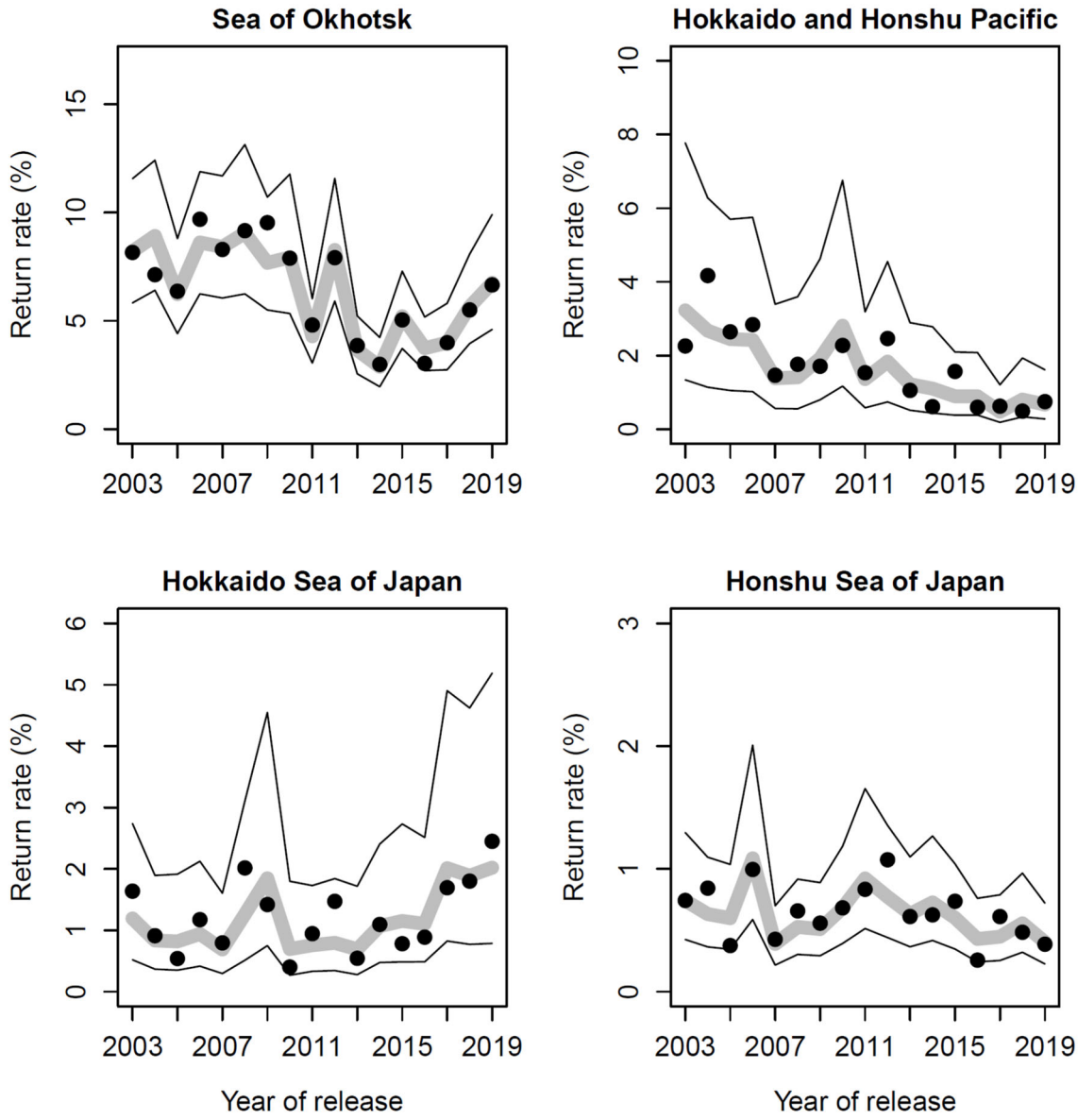

FIGURE 8 Predicted (gray line) and observed return rates (black dots) from Age 2 to Age 5 for the four geographic areas. The 95% prediction intervals are shown as black lines.

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

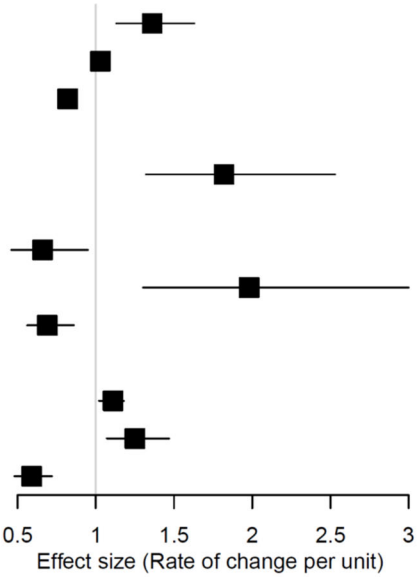

FIGURE 9 Effect size of the significant explanatory variables of the best models. The effect size indicates the rate of change per unit, calculated as the exponential of the regression coefficient.

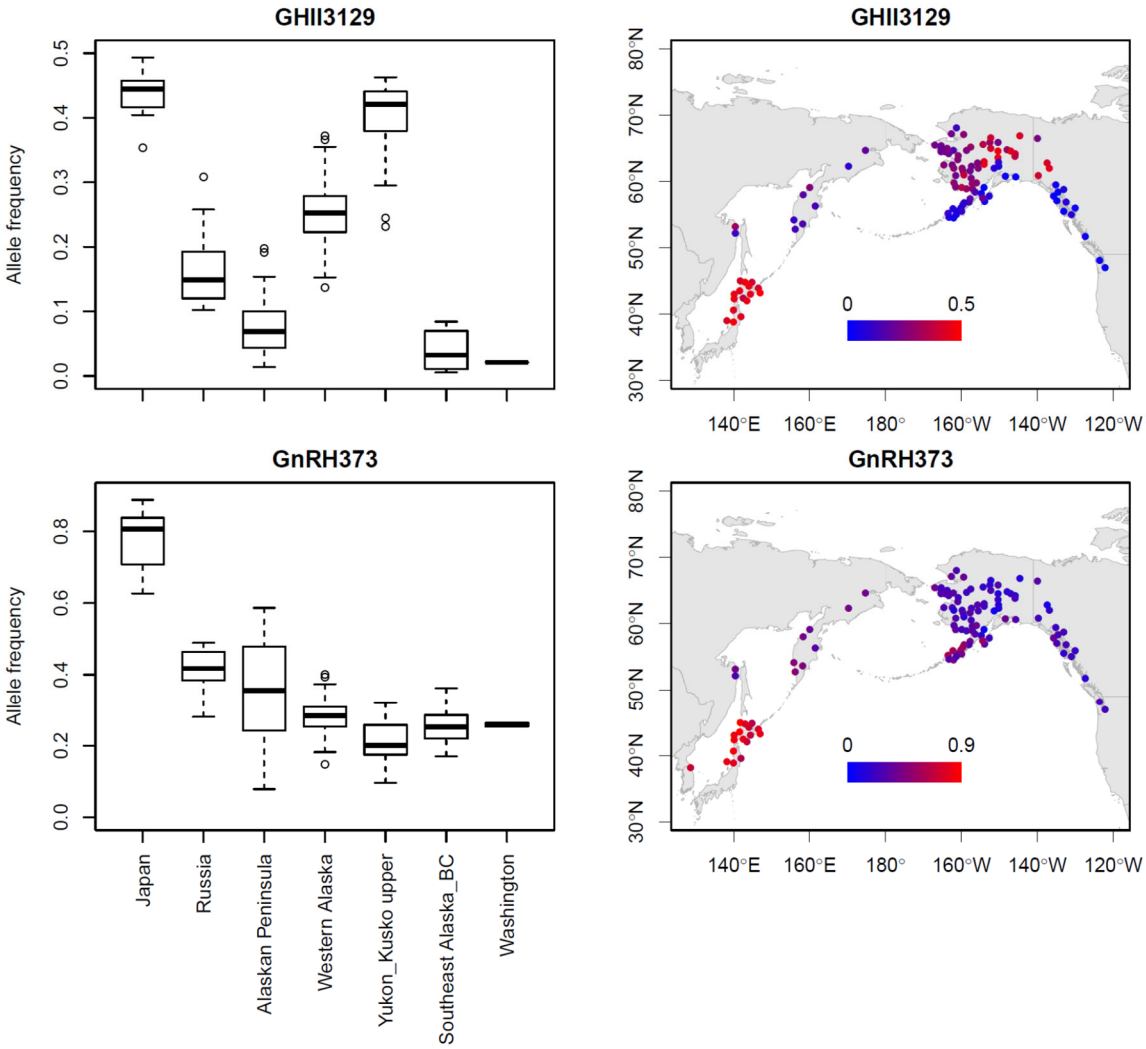

FIGURE 10 Growth hormone 2 (GHII3129) and gonadotropin-releasing hormone (GnRH) SNP allele frequencies characterizing the distinctiveness of Japanese chum salmon populations. Based on data from Seeb et al. (2011). Figures for GnRH redrawn from Kitada & Kishino (2021). The dots on the maps show sampling locations and allele frequencies with a continuous color gradient from blue to red for the lowest and highest allele frequencies. All Japanese samples were collected from hatcheries and weirs for broodstock collection and were therefore hatchery fish and/or hatchery descendants.

TABLE 1 Explanatory variables included in the regression model and hypothesized mechanism. All data including the response variable (return rate from release in year *t*), are available in the Supplementary Tables and Supplementary Data.

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	°C	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.	°C	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. Feb.-Apr.	°C	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.	°C	During the feeding migration, SSTs affect the survival of young chum salmon.
Winter SST in the GoA in year *t*+2 when Age 2 fish over winter	Gulf of Alaska	Age 2	Jan. Feb.-Apr.	°C	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.

TABLE 2 Summary of the best models with minimum AICc values out of 2^{14} (=16,384) models for each geographic area. Bold indicates significance. a) Jan., b) Feb.-Apr. (mean). c) Jul.

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 [a)]	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 [b)]	0.682	0.213	3.20	**0.007**		
	Sea of Okhotsk summer SST [c)]	-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 [a)]	0.223	0.081	2.76	**0.016**		
	SST at release	-0.529	0.105	-5.05	**0.000**		