Hatcheries to high seas: climate change connections to salmon marine survival

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Short running title: Climate connections to salmon survival

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Abstract

We investigated variations in the marine survival of Japanese hatchery chum salmon (*Oncorhynchus keta*) during 25 years of climate change (1998-2023). Japan is the world's largest hatchery salmon producer, and is located near the global southern distribution limit of chum salmon. Our goal was to identify local and context-specific metrics related to salmon survival (a climate-change indicator) for use in the adaptive management of hatchery salmon resources. We hypothesized multiple metrics in three categories of stressors: hatchery carryovers, ocean conditions, and predators and competitors. The hatchery carryovers are stressors related to hatchery rearing that affect survival at a different life stage. We collected, processed, and collated large publicly available datasets of metrics into a comprehensive open-access database encompassing the life cycle of Japanese chum salmon, from eggs to adult spawners. Multivariate regression models showed associations between stressor metrics and adult salmon return rate (marine survival) varied by coastal management region, salmon life stage, and seasonal high seas distribution area. Generalized additive models identified a shift to younger age at maturity and egg size decline in all management regions. Our analysis suggested that maternal traits (egg size, fecundity) and quality of juvenile hatchery salmon (body size at release) are particularly important for survival at later ocean stages. Our results support the hypothesis that whole life-cycle processes from anthropogenic selection in hatcheries to climate-driven changes in coastal predation, inter- and intra-specific high seas competition, and maternal effects during egg maturation at sea are responsible for the observed coastwide decline in survival of Japanese hatchery chum salmon over the past two decades. Our study highlights the need for an experimental approach to hatchery practices, including monitoring and analyses with updated information, leading to effective management decisions and policies for future sustainability and conservation of salmon resources.

KEYWORDS

adult returns, chum salmon, climate change, competition, predation, salmon survival, thermal habitat, age and size at maturity

1 | INTRODUCTION

Climate change influences the survival and abundance of many economically important marine and anadromous fish species, including Pacific salmon (*Oncorhynchus* spp.) (Springer & van Vliet, 2014; Cheung and Frölicher, 2020; Cheung et al., 2021; Crozier et al., 2021; Crozier & Siegel, 2023). Pacific salmon populations often consist of hundreds of subpopulations with diverse life history traits and local adaptations to environmental variation (Groot & Margolis, 1991; Hilborn et al., 2003; Larson et al., 2014; Quinn, 2018). Pacific salmon species are distributed in coastal marine waters and throughout the high seas (international waters) of the North Pacific Ocean and Bering Sea, where Asian and North American populations intermingle during seasonal feeding migrations (Myers et al., 2007; Beamish, 2018; Quinn, 2018). Their wide geographic range, long ocean migrations, and complex life histories expose salmon populations to multiple climate-driven stressors at both local and North Pacific-wide scales (Cline et al., 2019; Crozier et al., 2021). Global warming of 1.5°C above pre-industrial levels is projected to shift the ranges of many marine species to higher latitudes and increase damage to marine ecosystems such as rising temperatures, ocean acidification, heatwaves, decreases in sea ice, habitat loss, disruptions in food webs, and declining fish populations (Dahlke et al., 2018; Frölicher et al., 2018; Masson-Delmotte, 2022).

The effects of climate change, ocean acidification, and large-scale hatchery releases on the abundance and productivity of Pacific salmon populations have received increasing attention in recent years (Lewis et al., 2015; Jeffrey et al., 2017; Cunningham et al., 2018; Cline et al., 2019; Losee et al., 2019; Connors et al., 2020, 2024; Oke et al., 2020; Ohlberger et al., 2022, 2023; Malick et al., 2023). Declines in body size, primarily due to a shift in age structure towards younger ages at maturity, were found in chum, Chinook (*O. tshawytscha*), coho (*O. kisutch*), and sockeye (*O. nerka*) salmon from large-scale analyses across Alaska and were linked to climate change and 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). Pink salmon (*O. gorbuscha*) abundance increased since the mid-1970s to record highs in the 2000s, supported by climate change effects on the ocean environment and production processes, and may have affected abundance of salmon, other species, and their ecosystems (Springer & van Vliet, 2014; Connors et al., 2020; Ruggerone et al., 2023).

Ocean mortality of salmon is thought to be regulated initially by predation on juveniles soon after ocean entry, and is related to body size and density of salmon and abundance and type of predators. A later mortality phase is a consequence of growth rate in the early-ocean period and the ability of juvenile fish to survive the first ocean winter (Ricker, 1976; Beamish & Mahnken, 2001). Fisheries-oceanographic surveys in the western North Pacific, however, indicated that survival of salmon is related to ocean conditions (not growth rate) during the first fall and winter in the open ocean (Naydenko & Temnykh, 2016; Naydenko et al., 2016; Bugaev & Gerlits, 2023). Natural mortality of immature and maturing high seas salmon is generally thought to be low (Ricker 1976). Hypotheses about the mechanisms underlying high-seas salmon distribution and abundance in winter are varied (reviewed by Myers et al., 2016). Historical survey data indicated seasonal high-seas salmon distribution was related to sea surface temperature (SST) and salinity (Manzer et al., 1965; Welch et al., 1998; Azumaya et al., 2007; Abdul-Aziz et al., 2011; Langan et al., 2024). Salmon survey data in the Sea of Okhotsk and western North Pacific indicated the seasonal distribution of high-seas salmon reflects the climate-driven landscape (abiotic and biotic) of pelagic ecosystems, and interannual variation in high-seas salmon abundance is determined at earlier life stages (Naydenko & Temnykh, 2016; Naydenko et al.,

2016; Bugaev & Gerlits, 2024). Rapid seasonal climate-change events such as marine heatwaves are driving natural selection and adaptation of organisms in altered ecosystems (Bradshaw & Holzapfel, 2006). In our study, we expected survival of all life stages of chum salmon to be associated with climate change impacts on coastal and open ocean ecosystems.

Pacific salmon have a long history of artificial propagation beginning in the mid-1800s, and their management comprises the largest set of hatchery release programs (Naish et al., 2007), including chum salmon hatcheries in Japan that constitute the world's largest salmon hatchery release program (Amoroso et al., 2017; Kitada, 2018). Hatchery releases of juvenile chum in Japan increased rapidly in the 1970s, but gradually declined from a peak of 2 billion per year in 1983 to 1.3 billion per year in 2021 because of poor returns of adult spawners. Adult returns of Japanese hatchery chum increased rapidly since the 1970s, but declined sharply after the late 1990s (the historical maximum of 88 million in 1996 to the minimum of 19 million in 2021). Previous studies have reported higher spring SSTs in the coastal zone contributed to better survival of juvenile chum 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 and insufficient growth (Kaeriyama, 2022). Although it is generally accepted that a warming climate is affecting marine survival of salmon, the mechanisms underlying recent declines in Japanese hatchery chum salmon are largely unknown. The need for adaptive management is advocated for the long-term sustainability of chum salmon (Kaeriyama, 2008, 2022; Kaeriyama et al., 2012).

Development of adaptive management plans to address climate-change impacts on fish, fisheries, aquaculture, and associated habitats and ecosystems requires knowledge of "local and context-specific indicators associated with climate stressors" (FAO, 2022). Adaptive management is the design of management actions as experiments with feedback through monitoring, enabling an iterative process of learning and adapting to uncertainties and risks (Walters & Hilborn, 1978; Hilborn & Sibert, 1988; Bahri et al., 2021; Bryndum-Buchholz et al., 2021). A comprehensive review of literature addressed strengths and weaknesses of climate-change research by life stage and showed the complexity of whole life-cycle approaches to adaptive management strategies for anadromous salmonids (Crozier & Siegel, 2023). Here, we investigated associations between adult return rates (an indicator of marine survival) of Japanese hatchery chum salmon by life stage and a suite of hypothesized climate-change stressors. Our primary objective was to identify potential stressors along known coastal and high seas migration routes of Japanese chum salmon for use in regional adaptive management of salmon resources.

2 | MATERIALS AND METHODS

2.1 Ecological setting, study design, and methods overview

The ecological setting of our study encompasses the known geographic distribution and seasonal migration patterns of Japanese chum salmon in the North Pacific Ocean and adjacent seas (Figure 1; reviewed by Fisheries Agency of Japan, 1955; Sano, 1966, 1967; Shepard et al., 1968; Neave et al., 1976; Salo, 1991; Urawa et al., 2018). Juvenile chum salmon (age 0) are released from more than 260 coastal hatcheries in northern Honshu and Hokkaido in winter and spring and migrate rapidly through river estuaries (Figure 1a; Kobayashi, 1980; Kaeriyama, 1989; Saito & Nagasawa, 2009). After ocean entry, juveniles migrate northward in shallow coastal waters before moving offshore to summer feeding grounds in the southern Sea of Okhotsk (Figure 1b; Fukuwaka & Suzuki, 1998; Urawa et al., 2006; Kasugai et al., 2016;

Shubin & Akinicheva, 2016). Japanese chum salmon spend their first ocean winter (age 1) in the western North Pacific Ocean and in spring move northeastward to summer feeding grounds in the Bering Sea (Figure 1b; Mayama & Ishida, 2003; Urawa et al., 2018). At subsequent life stages (ages 2-4; immature and maturing), they make seasonal migrations between the Gulf of Alaska in winter and the Bering Sea in summer (Figure 1b; Beacham et al., 2009; Urawa et al., 2009, 2016). In spring, the northward migration of maturing chum salmon precedes that of immature fish (Neave et al., 1976; Nagasawa & Azumaya, 2009). In late summer and fall, maturing fish return to Japan from the Bering Sea through the western North Pacific (Figure 1b; Yonemori, 1975; Urawa et al., 2018).

A brief overview of our methodology for evaluating relationships between the indicator of salmon marine survival (return rates) and hypothesized stressors is provided below (see details in sections 2.2-2.8). We identified multiple *a priori* hypotheses about potential stressors driving marine survival of Japanese hatchery chum salmon at specific life stages and locations along their coastal and high seas migration routes (Table 1). We grouped hypothesized stressors into three broad categories: hatchery carryovers, ocean conditions (SST), and predators and competitors. Hatchery carryovers are stressors related to hatchery rearing that affect survival at a different life stage. We assembled available data sets for use as measures of hypothesized stressors in each category. We estimated annual adult return rates, stratified by salmon age group and year. We used multivariate regression models to evaluate relationships between return rates of salmon and hypothesized categories of stressors by coastal management region in Japan and seasonal high seas habitats in the Sea of Okhotsk, western North Pacific, central Bering Sea, and Gulf of Alaska. Readers are cautioned that our statistical modeling results are correlational, not causal.

2.2 Data sources, sample periods, sample sizes

We assembled available time-series datasets during 25 years of climate change (1998-2023) from public open-data websites. We assembled longer data time series to aid in interpreting results.

We obtained annual (1970-2023) numbers of adult salmon catches (coastal fishery and hatchery broodstock) and hatchery chum salmon juvenile releases from the Hokkaido Salmon Enhancement Association (HSEA, 2024), Fisheries Research and Education Agency (FRA, 2024), and the Aomori Prefectural Government (APG, 2024). FRA (2023) biological and reproductive trait data included time series of juvenile size at release and release month. We selected hatchery release events with juvenile body weight (BW) and fork length (FL) data (1998-2020, Hokkaido: 184 rivers, 37,886 release events, n = 21,332,093; Honshu: 171 rivers, 19,605 release events, n = 9,588,413). The data also included adult age composition at return (1997-2020, Hokkaido: 52 rivers; Honshu: 102 rivers; 1,902 surveys, n = 1,210,717 fish). Adult salmon trait data included egg weight, fecundity, fork length (FL), age at return, and gonad weight (1997-2020, Hokkaido: 10 rivers; Honshu: 14 rivers; n = 37,533 fish), and adult age at return (counts of annular marks on fish scales), including six age groups: age 2 (n = 25), age 3 (n = 2,892), age 4 (n = 20,643), age 5 (n = 13,118), age 6 (n = 846), and age 7 (n = 9). We used trait data such as fork length, egg weight, and fecundity of age–4 and age–5 fish for our analysis.

We obtained annual commercial catch data for all marine species in Japan (1980-2020) from the Japan Ministry of Agriculture, Forestry and Fisheries (MAFF, 2023). Catch statistics (1998-2022) for Canada, Russia, and USA pink and chum salmon were available from the North

Pacific Anadromous Fish Commission (NPAFC, 2023). For SST analyses, we downloaded Japan coastal 0.25°×0.25° daily mean SST data (1982 to 2020) from Hokkaido (18 areas) and Honshu (12 areas) from the Japan Meteorological Agency (JMA, 2022) and global 0.25°×0.25° monthly mean SST data (1982 to 2022) from the NOAA Optimum Interpolation (OI) SST V2 high-resolution dataset (NOAA, 2023a).

2.3 Catch, release, and reproductive traits

We summarized Japanese chum salmon catch, release, and reproductive traits data by seven management regions (Figure 1a). To estimate the distribution of release times in each region, we counted the number of release events by month. We also calculated the mean values of size at release, biological traits, and age composition by management region. Since the number of individuals released (n_k) varied among release events, we calculated the weighted mean size at release for BW (g) (1998-2020) as $\overline{BW} = (\sum_{k=1}^{K} BW_k\, n_k)/\sum_{k=1}^{K} n_k$. Here, the suffix for a region was omitted for simplicity. We calculated the mean values of the traits and the relative fecundity ($\mathrm{eggs}/FL(\mathrm{cm})^3 \times 10^5$) of the age_4 and age_5 fish from 1997 to 2020. The weighted mean proportion of age *a* fish was calculated as $\hat{p}_a = (\sum_{h=1}^{H} p_{ah}\, n_h)/\sum_{h=1}^{H} n_h$, where *h* refers to each survey, p_{ah} is the proportion of age *a* fish in survey *h*, n_h is the sample size (individuals), and *a* refers to age at return (*a* = 2,…,8).

2.4 | Adult return rates and age at maturity

We used adult return rates as an indicator of marine survival of chum salmon (James et al. 2023, see discussion section). We assumed all adult chum salmon returning to Japan were hatchery reared. Hatchery programs have been managed in five management regions in Hokkaido and by prefecture in Honshu, and previous studies have evaluated return rates in the seven management regions (Saito & Nagasawa, 2009; Miyakoshi et al., 2013; Kitada, 2014). The management regions coincide with the genetic structure of the population (Beacham et al., 2008). We estimated return rates for the current hatchery management regions (Figure 1a). We estimated the total number of fish returning from releases in year *t* (Y_t, coastal commercial catch plus river catch for hatchery broodstock) by

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

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 $t + a - 1$. We estimated return rate of juveniles released in year *t* by $\hat{R}_t = \hat{Y}_t/X_t$, where X_t is the number of hatchery-reared juveniles released in year *t*. We estimated age-specific return rate as $\hat{R}_{a,t} = \hat{Y}_{a,t}/X_t$. We summed the number of fish returned from ages 2–5 ($A_{min} = 2,\ A_{max} = 5$). Most returns were ages 2–5 fish, and few returns were age 6. There was no age–7 and age–8 fish in returns to any region except Hokkaido Okhotsk, where returns of these age groups were very low. We estimated the age composition of returning adult chum salmon from available (1997-2020) data (Figure S1). We estimated the age composition in 2021-2023 as a moving average of the previous three years. Based on age composition, we calculated the number of returning fish (ages 2–5) for each release year. Then, we estimated return rates and age-specific return rates from releases in 1998-2019. We measured distances between return rates in the management regions by $1 - r_{uv}$ and illustrated distances by a neighbor-joining (NJ) tree (Saitou & Nei, 1987) using the "MEGA11" package (Tamura et al., 2021), where r_{uv} is the correlation coefficient between pairs of return rates in regions *u* and *v*.

We also calculated the percentage of ages 2-4 chum salmon in the total number of adult returns (ages 2–5), used as an index of younger age at maturity. Excluding older fish (age 6 or older) should have a negligible effect on estimates of mean ages at maturity (Figure S1). To assess and visualize continuous changes in the percentage of ages 2–4 chum salmon, return rates, and other biological traits over the year, we fit general additive models (GAMs) to the data using the 'gam' function in the "mgcv" package (Wood, 2017) in R (R Core Team, 2024). As noted in the documentation of the mgcv package, 'gam' performs automatic smoothness selection based on a penalized regression spline approach (Wood, 2004, 2011).

2.5 | Long-term changes in chum salmon thermal habitat

To understand long-term changes in SST in the chum salmon habitats covered by our regression model (see below), we mapped monthly mean 1°×1° SST isoclines in the North Pacific Ocean for 1990, 2000, 2010, and 2022, using the Plot COBE Sea Surface Temperature system (NOAA, 2023b), based on the COBE2 SST dataset from JMA. The 1°×1° monthly mean SST isoclines around Japan for 2000, 2010, and 2022 were generated similarly. We mapped the available temperature range of chum salmon (4-13℃), based on previous predictions: optimal growth and feeding (8–12℃), available habitat for feeding (5–13℃), and overwintering temperature range (4–6℃) (Kaeriyama et al., 2012; Urawa et al., 2018).

2.6 | Japanese chum salmon migration route and SST

We calculated monthly mean SSTs for 30 coastal areas in Japan (JMA, 2022). From these we calculated monthly mean SSTs for the seven management regions (Figure 1b), and for release periods of chum salmon juveniles (Figure S2): Hokkaido Okhotsk (Apr-Jun), Hokkaido Nemuro (Mar-Jun), Hokkaido Pacific East (Mar-Jun), Hokkaido Pacific West (Mar-May), Hokkaido Sea of Japan (Mar-May), Honshu Pacific (Feb-May), and Honshu Sea of Japan (Feb-Apr).

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 abundance of juveniles is significantly correlated (positive) to 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 was between 8 and 13°C, and 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 released in all areas would migrate to the Sea of Okhotsk and disperse offshore in July (Figure 1a).

We identified the locations of four main offshore and high seas areas of Japanese chum salmon distribution (Figure 1b) based on information from previous studies (Myers et al., 2007; 2016; Nagata et al., 2007; Urawa et al., 2018, 2022). Using "sst.mnmean.nc" data (NOAA, 2023a), we calculated the monthly mean SSTs (1982-2022) for salmon distribution areas using the 'fldmean' function in the "cdo-2.1.1" package (Max Planck Institute, 2023). We mapped areas and migration routes using the "sf" package in R. We used monthly mean SSTs (1998-2022) in our regression model. To assess and visualize continuous changes in SSTs over the year, we fit GAMs to these variables by migration area using the 'gam' function in "mgcv" package in R.

2.7 | Potential predators of juvenile chum salmon

To characterize temporal changes in marine fish predator catch, we performed principal

components analysis (PCA) on the annual commercial catch data for the marine species in 1980-2020 (MAFF, 2023) using the 'prcomp' function in R. Because catches vary by geographic area and season, we obtained catch data of potential marine fish predator species by reporting area in Hokkaido and by prefecture in Honshu (MAFF, 2023), which should reflect their fishing seasons and migration patterns. Changes in chum salmon catch and catches of potential marine fish predators, identified by increasing catch in the chum salmon coastal distribution range, were mapped.

2.8 | Regression analysis of adult return rates (marine survival)

We created three subset models for our regression analysis of adult return rates and explanatory variables: (1) hatchery carryovers, (2) ocean conditions (SST), and (3) predators and competitors (see below). Our regression model describes the relationship between return rates of chum salmon juveniles released in year *t* across all ages ($\hat{R}_t$) and explanatory variables such as SSTs, size at release, and catch of potential predators and competitors. 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, and the explanatory variables are denoted by $\boldsymbol{z}$. The regression coefficients were denoted by $\boldsymbol{\beta}$ and $\varepsilon_t \sim N(0, \sigma^2)$ is the error that we assumed to be independently and normally distributed. We did not include interactions between explanatory variables. We selected the explanatory variables by AICc (Sugiura, 1978), which is the small sample correction of the Akaike Information Criterion (AIC, Akaike, 1973). We noted that the contributing variables vary among the regions. Ideally, linear mixed models with random effects of regions should estimate the common effects and their variance across regions. However, as is seen in the main result, not a few variables contribute in total. The time series with the 22 data points (1998-2019 releases) did not have enough information to estimate the random effects when we included all these variables in the linear mixed model.

We used the variance inflation factor (VIF) to diagnose multicollinearity among explanatory variables. We determined variables that could be included in a model by sequentially removing each explanatory variable with the highest VIF value until all remaining VIFs were less than the threshold of 3.0 (Zuur et al., 2010), using the 'VIF' function in “car” package in R. We estimated regression coefficients based on standardized explanatory variables, which allow for consistent comparison of different explanatory variables across management regions as done in salmon studies (e.g., Oke et al., 2020; Ohlberger et al., 2022). The use of an unstandardized measure (regression coefficient) is preferred to a standardized measure if the units of measurement (e.g., juvenile size at release, SST, and abundance of competitors) are used to describe effect sizes at a “practical” or “real world” level (Wilkinson, 1999). Therefore, we also estimated the regression coefficients using unstandardized explanatory variables, as done in Malick et al. (2023). In the latter, we define effect size as the effect of the unit change of an explanatory variable on the change in return rate. The effect size and 95% confidence intervals were calculated by $\exp\left(\hat{\beta}_i \pm 1.96 \times \mathrm{SE}(\hat{\beta}_i)\right)$ for coefficient *i*. We predicted return rates by region based on regression coefficients using the unstandardized measure and compared them to the observed return rates.

When many explanatory variables are included, the model selection procedure may select an inappropriate model as the best model due to complex multicollinearity. To avoid this problem,

we created three subset models of stressors, performed variable selection within each subset model, and compared the best models for combinations of the subset models and the full model, which included all subset models. In adaptive management terminology, our dependent variable (adult return rate) is an "indicator", and the explanatory variables are "metrics" (Rochet & Trenkel, 2009). We used 17 hypothesized metrics (s = 17) and: (1) hatchery carryover (three metrics), (2) ocean condition (five metrics), and (3) predators and competitors (nine metrics) (Table 1). The hypothesized hatchery carryover metrics included relative fecundity and egg size of females in year t-1, where t is the year of juvenile release, and juvenile size at release. Ocean-condition metrics included SST at juvenile release and in Japanese coastal management regions; summer SST in the southern Sea of Okhotsk and central Bering Sea, and winter SST in the western North Pacific and central Gulf of Alaska (see Figure 1). Predator and competitor metrics included predation in coastal Japan regions and competition in high seas areas (Table 1). We identified Yellowtail (*Seriola quinqueradiata*) as a potential predator of juvenile chum salmon (see Section 3.4). Age–4 chum salmon were the dominant age group in adult returns to Japan (Figure S1). We used annual commercial salmon catch (total number of fish) of chum salmon in Russia, the United States, and Canada in year t+3 as indices of 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 three years in the high seas and to compete when sharing the same environment. Pink salmon have a fixed life span of two years (Quinn, 2018). We used Russian, US, and Canadian catches in years t+1, t+2, and t+3 as indices of interspecific competition with Japanese chum salmon released in year t. The ocean distribution of chum and pink salmon overlaps throughout the North Pacific (Langan et al., 2024). We assumed cohorts of pink salmon compete with chum during the first (t+1), second (t+2) and third (t+3) ocean years. The dependent variable is return rates of juveniles released in 1998-2019.

We performed regression analysis for each subset model and combinations of subset models with explanatory variables less than 3.0 VIF. In each analysis, we selected the most parsimonious model (hereafter, best model) with the minimum AICc using the “MuMIn” package in R. We compared the subset models by their minimum AICc values. To summarize the result, we presented the regression coefficients of the best model for the selected subset models. In three of the four regions, the minimum of the minimum AICcs was achieved by multiple hierarchical subset models. In such cases, we chose the most parsimonious subset models. The estimated regression coefficients were compared with the results obtained by model averaging over all models with ΔAICc values less than 2 (Burnham & Anderson, 2002). A practical model averaging provides the weighted averages of the regression coefficients over the models. The weights represent the contributions of the models and are proportional to $\exp(-1/2 \times \mathrm{AICc})$. All data and the R script used for the regression analysis are available (see data availability statement).

3 | RESULTS

3.1 | Adult return rate and age at maturity

For Japan as a whole, the number of hatchery-released juveniles increased until the early 1980s, reaching 2 billion, and then decreased to about 1.3 billion at present (Figure 2). In the Honshu Pacific, there was a steady decline in releases since the mid-1990s and a rapid decline since 2021. Decreasing numbers of released juveniles were also observed in Hokkaido Pacific East and Honshu Sea of Japan, while stable numbers were observed in Hokkaido Nemuro, Hokkaido Pacific West, and Hokkaido Sea of Japan. Only in Hokkaido Okhotsk did the number of juveniles released increase slightly but continuously. Releases were largest in Honshu Pacific,

while other regions had similar release levels.

The total number of adult chum salmon returns throughout Japan increased rapidly until 1996 (88 million fish), and then declined to the current level of 20 million fish (Figure 2). The highest regional returns were in the Honshu Pacific in 1996 (31 million), and then declined continuously to the historical regional minimum (~10 thousand). Among other regions, adult returns were highest in northern Hokkaido regions (Okhotsk and Nemuro) and lowest in Sea of Japan regions (Hokkaido and Honshu). Since approximately 2008, adult returns decreased in all management regions except Hokkaido Okhotsk and Hokkaido Sea of Japan, and the decrease was most severe in Hokkaido and Honshu Pacific regions.

Mean adult return rate ± standard deviation (including ages 2–5) for 1998-2019 releases was highest in Hokkaido Okhotsk (6.9 ± 2.4%), followed by Hokkaido Nemuro (4.5 ± 3.0%), Hokkaido Pacific East (2.3 ± 1.7%) and Hokkaido Pacific West (2.3 ± 1.2%), Honshu Pacific (1.2 ± 0.7%), Hokkaido Sea of Japan (1.4 ± 0.7%), and Honshu Sea of Japan (0.6 ± 0.2%) (Figure S3a). The GAMs showed that return rates decreased over time in all management regions, except in Hokkaido Okhotsk and Hokkaido Sea of Japan, where return rates increased recently (Figure S4).

The percentage of age 2–4 adults in the total number of adult returns from 1998-2019 juvenile (age 0) releases was very high in all management regions: Honshu Sea of Japan (81.8 ± 7.1%), Hokkaido Sea of Japan (73.4 ± 7.6%), Honshu Pacific (71. 3 ± 9.7%), Hokkaido Pacific West (70.7 ± 10.9%), Hokkaido Nemuro (66.7 ± 7.1%), Hokkaido Okhotsk (64.4 ± 9.4%), and Hokkaido Pacific East (59.7 ± 8.0%) (Figure S3b). The GAMs confirmed that after approximately 2008 the percentage of returning age 2-4 adults generally increased over time in all management regions: Hokkaido Okhotsk (p = 0.000, R^2 = 0.61), Hokkaido Nemuro (p = 0.244, R^2 = 0.24), Hokkaido Pacific East (p = 0.000, R^2=0.73), Hokkaido Pacific West (p = 0.003, R^2 = 0.51), Hokkaido Sea of Japan (p = 0.008, R^2 = 0.57), Honshu Pacific (p = 0.021, R^2 = 0.32), and Honshu Sea of Japan (p= 0.078, R^2 = 0.11) (Figure 3).

The NJ tree analysis showed that Hokkaido Okhotsk, Honshu Sea of Japan, and Hokkaido Sea of Japan adult return rates were distinct, and the Hokkaido Nemuro, Hokkaido Pacific East and West, and Honshu Pacific return rates were similar (Figure 4). As a result, we used four coastal regions in Japan in our regression analysis: (1) Hokkaido Okhotsk, (2) Hokkaido and Honshu Pacific (combined returns to Hokkaido Nemuro, Hokkaido Pacific East and West, and Honshu Pacific), (3) Hokkaido Sea of Japan, and (4) Honshu Sea of Japan.

3.2 | Long-term changes in chum salmon thermal habitat

Decadal-scale maps of SST isoclines showed that until 2000, the summer and winter thermal habitat of chum salmon was stable (Figure 5). After 2010, optimal summer habitat for chum salmon growth and feeding (especially, 8–11°C isotherms) shifted north and contracted longitudinally, and winter habitat remained relatively stable. Evaluation of intra-seasonal changes in spring and summer thermal habitat revealed a progressive northward shift in optimal habitat, from a slight shift in early spring (March and April) to a larger shift in early summer (May and June), northward longitudinal contraction in late summer (August and September), and a slight northward shift in fall (October and November) (Figures S5–S8). In coastal Japan, optimal thermal habitat for juvenile chum salmon migrating to the Sea of Okhotsk shifts northward in spring and early summer (April-June), especially in the Sea of Japan (Figure S9).

3.3 | Japanese chum salmon migration route and SST

In Hokkaido Okhotsk and Hokkaido Sea of Japan, the mean SST at hatchery juvenile release was relatively stable from 1998 to 2019 (Figure S10). In Hokkaido Nemuro, the mean SST increased. Hokkaido and Honshu Pacific showed a similar pattern; the mean SST decreased until around 2010 and then slightly increased. In the Honshu Sea of Japan, the mean SST remained stable until around 2010 and then increased.

The summer and winter SSTs used in our regression analysis (1998-2022) as common explanatory variables for all offshore (southern Sea of Okhotsk) and high seas areas (Figure 1b) were: southern Sea of Okhotsk July SST, western North Pacific January-April SST, central Bering Sea August-September SST, and central Gulf of Alaska January-April SST (Figure S11a). A GAM (Figure S11b) showed that July SST in the southern Sea of Okhotsk increased after the early 2000s, and a strong increase was observed after around 2015. In the western North Pacific, winter SST in January-April increased after around 2015. In the central Bering Sea, August-September SST continued to increase since the late 1990s but decreased after around 2015. In the central Gulf of Alaska, a strong increasing trend in January-April SST was observed after around 2010, but SST decreased after around 2015. Similar trends were observed in the western and eastern North Pacific.

3.4 | Potential predators of juvenile chum salmon

We excluded marine mammals because catches are subject to strict limits, and catches were not recorded by species but by total marine mammals. This resulted in catch data for 56 of 70 species, including 39 fish, six crustaceans, five shellfish, two squids, an octopus, a sea urchin, and two algae. The PCA biplot identified differences in commercial fishery catch levels as the primary component (PC1, 51% variance), and the second component (PC2, 17% variance) corresponded to catch trends before and after 1998 (Figure 6a). The PCA confirmed that changes in commercial catches of 56 marine species in Japan after 1998 were largely characterized by three species that increased in recent decades: yellowtail and Japanese Spanish mackerel (*Scomberomorus niphonius*) and Japanese scallop (*Mizuhopecten yessoensis*). We visualized trends in catches of 56 species (1980-2020) and confirmed that catches increased only in the three species identified by the PCA analysis (unpublished figure, S. Kitada). Among these, yellowtail and Japanese Spanish mackerel are strong piscivores. There was a northward shift of yellowtail landings into the range of Japanese chum salmon (Figure 6b). In contrast, increased landings of Japanese Spanish mackerel occurred only in the eastern area of Japan, with slight increases in the Honshu North Pacific area. Based on these results, we identified yellowtail as a possible new predator of juvenile (age 0) chum salmon.

3.5 | Regression analysis of adult return rates (marine survival)

All models used explanatory variables with a VIF less than the threshold of 3.0. Model selection results for all subset models are shown in Table S1. The full model results and the best subset model results were the same for all management regions except for the Hokkaido Sea of Japan (Table 2; Tables S1 and S2). The results of the model averaging (Table S3) were qualitatively the same as the best models (Table 2) for all regions. The explanatory variables selected in the best models were region-specific or common to some areas, or both. For ocean conditions, SST at release (year t) and summer SST (July) in the Sea of Okhotsk (year t) and the Bering Sea (August-September) (year t+1) were negatively associated with return rates. In contrast, winter SST (January-April) in the western North Pacific (year t+1) and the Gulf of Alaska (year t+2)

were positively associated with return rates. For predators and competitors, we found negative associations between Japanese chum salmon return rates and yellowtail catch in the year of juvenile release. Russian chum salmon catch in year *t*+3, and Russian pink salmon (adult, age 1) catch in years *t*+2 and *t*+3 were negative. No associations between Japanese chum salmon return rates and US and Canadian chum and pink salmon catches were found. For hatchery carryovers, juvenile size at release was positively associated with salmon return rates, while relative fecundity was negatively associated with return rate. The relative fecundity of age–4 salmon had a smaller AICc (30.0) than age–5 salmon (38.2). We used the relative fecundity of age–4 salmon to identify the best model.

The standardized effects of explanatory variables on adult returns allow comparison of the magnitude of the effects across the four regions (Figure 7). The largest positive effect was winter SST (January-April) in the Gulf of Alaska (year *t*+2), followed by size at release and winter SST (January-April) in the western North Pacific (year *t*+1). On the other hand, yellowtail catch had the largest negative effect, followed by SST at release, summer SST in the Bering Sea (August-September) (year *t*+1) and in the Sea of Okhotsk (July) (year *t*), and parental relative fecundity (year *t*-1). The negative effect of intraspecific and interspecific competition was relatively small and similar in all areas.

The practical effect size in a regression model describes how much of a change in the dependent variable is expected for a given change in the independent variable. The effect size for each regression coefficient, measured by exp $(\hat{\beta}_i)$, represents the rate of change per practical unit in each coastal area (Figure S12). The area-specific practical effect sizes showed that a 1°C increase in winter SST in the Gulf of Alaska increased the return rate by 50% $(\exp(0.405) = 1.5)$ in Hokkaido Sea of Japan, and a 1°C increase in winter SST in the western North Pacific increased the return rate by 30% in Honshu Sea of Japan. In contrast, summer SST in the southern Sea of Okhotsk decreased return rate by 27% in Hokkaido Sea of Japan, and by 13% in Honshu Sea of Japan. SST at release reduced the return rate by 38% in Honshu Sea of Japan. An increase of 100 eggs (relative fecundity) of parent females (age 4) reduced the return rate by 61%, while juvenile size at release had a positive effect; a 0.1 g increase in hatchery juvenile BW increased the return rate by 63% in Hokkaido and Honshu Pacific. An increase in biomass of yellowtail landings of 100 tons predicted a 19% reduction in the adult return rate of chum salmon in Hokkaido Okhotsk. An increase in Russian pink salmon abundance (100 million fish) in year *t*+2 reduced return rates by 12% in Hokkaido Okhotsk, 27% in Hokkaido and Honshu Pacific, and 13% in Honshu Sea of Japan areas. An increase in abundance of Russian pink salmon (100 million fish) in year *t*+3 reduced return rates by 20% in Hokkaido and Honshu Pacific. An increase in abundance of Russian chum salmon (10 million fish) reduced return rates by 14% in Hokkaido Sea of Japan.

The correlation between predicted and observed adult return rates was high in all four coastal regions: Hokkaido Okhotsk $(r = 0.79, t = 5.75, p = 0.0000)$, Hokkaido and Honshu Pacific $(r = 0.91, t = 9.98, p = 0.0000)$, Hokkaido Sea of Japan $(r = 0.79, t = 5.78, p = 0.0003)$, and Honshu Sea of Japan $(r = 0.81, t = 6.17, p = 0.0000)$. Our best models with few (2–4) explanatory variables provided good fits to the four coastal regions and the annual variations in chum return rates, although the 95% prediction intervals are large (Figure 8).

4 | DISCUSSION

4.1 Thermal habitat ranges and marine survival indicator

Since 2010, the high seas thermal habitat of Japanese chum salmon in summer shifted northward and contracted; winter habitat remained relatively stable (Figure 5). The frequency of annual marine heatwaves increased in the western and central Bering Sea, and heatwaves in the eastern Bering were longer and more intense (Carvalho et al., 2021). The SST indices used in our regression model represent the thermal habitat of Japanese chum salmon at ocean entry and along coastal and high seas migration routes. We assumed all Japanese chum salmon occupied the same geographic location of summer and winter habitat throughout the period of our study. Ranges of chum salmon thermal habitat used in our analysis were narrower (thermal limits, 4–13°C) than previously published estimates, based largely on historical high seas salmon survey data collected before the winter 1976-1977 climate regime shift (preferred spring-summer SST range, 1.3–12.6°C ; Langan et al., 2024). The pre-regime shift period (1948-1975) was characterized by low ocean productivity, cold winter SSTs in the Gulf of Alaska, and a low abundance of salmon populations that overwinter in the Gulf of Alaska, including Japanese chum salmon. During periods of low ocean productivity, optimal temperatures for salmon growth decline (Beauchamp, 2009).

Our results show correlations between return rates (marine survival) of salmon and multiple climate-driven stressors that varied by coastal management region, salmon life stage, and seasonal high seas distribution area. Our marine survival estimates should be regarded as indices because little is known about freshwater mortality of Japanese hatchery chum salmon juveniles after release or population mixtures in landed commercial catches (Nagata et al., 2016). We assumed all chum salmon returning to Japan were hatchery reared. The total proportion of naturally produced chum salmon in Japan is largely unknown. Field studies provide evidence that natural reproduction of chum salmon occurs in Hokkaido (Miyakoshi et al., 2012) and in the Honshu Sea coast of Japan (Iida et al., 2018; Iida et al., 2021). Relative reproductive success (RRS) of hatchery-reared salmon is approximately 50% of the RRS of wild-origin naturally spawning fish (Araki et al., 2007; Christie et al., 2014; Shedd et al., 2022), with considerable variation (Kitada et al., 2011). Reduced RRS can be carried over to the next generation (Araki et al., 2009). We expected low survival from egg to size at ocean entry of wild-born fish in natural streams in Japan. Our marine survival estimates should be overestimated depending on the magnitude of recruitment of wild-born fish, which was expected to be very low compared to the number of hatchery-released fish (100-200 million juveniles per year in each management region, Figure 2). Our regression analysis overestimated the intercept proportional to the magnitude of natural recruitment, but regression coefficients were expected to be robust if natural recruitment was constant over the period of our analysis.

4.2 Size at release and egg size

Our regression model coefficients (effect size) indicated that a 0.1 g increase in size of juvenile hatchery chum salmon at release increased return rates by 63% in the Hokkaido and Honshu Pacific region. The average return rate over the last five years was 0.74% in this region, and a 0.1g increase in size at release would be expected to increase the return rate to 1.2% (= 0.74 × (1+0.63)) from current levels. After release, Honshu Pacific region juvenile chum migrate long distances northward to their summer feeding area in the Sea of Okhotsk. On the Sanriku Coast, Honshu Pacific region, where the decline in abundance was most severe (Figure 2), juvenile chum salmon reared under low food availability (1% body weight) allocated less than half of their energy to growth at high temperatures (14℃) compared to juveniles reared under high food availability (4% body weight; Iino et al., 2022). In the high-diet group, 32–47% of the energy consumed by the fish should be used for daily growth (Iino et al., 2022). Japanese

hatchery chum salmon larger than 2 g (BW) significantly increased long-distance swimming performance and reduced the metabolic cost of swimming against the southward current at 8-12°C SST (Iino et al., 2024). Our model effect size for juvenile size at release and relative fecundity suggested that size at release and quality of juvenile hatchery fish are particularly important for survival at later ocean stages for Honshu Pacific region chum salmon. The GAMs indicated that size at release has continued to decrease in all regions after around 2010, except Hokkaido Pacific West, and the decline in size at release was substantial in the Honshu Pacific region (Figure S13). The reasons for the continuous decline in juvenile size at the time of release were unknown.

Relative fecundity of parent females was negatively associated with return rates in the Honshu Pacific region. Negative relationships between egg size and fecundity have been reported for Pacific salmon (Beacham & Murray, 1993; Fleming & Gross, 1990). Relative fecundity was negatively correlated with egg size in all management regions except in the Hokkaido Sea of Japan region (unpublished figure, S. Kitada). Egg size is an important fitness trait, and larger eggs have a positive effect on juvenile survival and growth in salmonids (Hutchings, 1991; Einum & Fleming, 1999, 2000). Our results suggested that higher relative fecundity (smaller eggs) could contribute to reduced survival rate of Hokkaido and Honshu Pacific region chum salmon. GAMs confirmed that egg size for 4-year-old fish has decreased over the last two decades in all regions, except Hokkaido Okhotsk (Figure 9). Similar decreasing trends in egg size for 5-year-old fish were also observed (Figure S14). Selection in hatcheries could impact fecundity and egg size (Heath et al., 2003), although egg size or fecundity was not found to differ between hatchery and natural-origin fish in other populations (Beacham & Murray, 1993; Quinn et al., 2004; Beacham, 2010). Hasegawa et al. (2021a) showed that the egg size of 5-year-old Japanese chum salmon in 2010 was smaller in more northeasterly locations than in 1994 and 2001, and hypothesized that domestication selection in hatcheries affected by global warming may have caused the temporal shifts in egg size. Our finding of a nationwide decline in egg size in Japanese chum salmon over the past two decades is striking, and suggests that anthropogenic selection in hatchery practices (Ford, 2002; Araki et al, 2008) may be contributing to the decline in egg size. An alternative process might be maternal effects, whereby environmental variation (e.g., ocean temperature during egg development; maternal diet) experienced by the mother is translated into phenotypic variation in reproductive traits of offspring (e.g., egg size, age at maturation) (reviewed by Mousseau & Fox 1998; Thorn et al. 2019). The mechanisms of decline in egg size are unknown and require further investigation.

4.3 Predators and competitors

There are many known fish, bird, and marine mammal predators of Japanese chum salmon (Okado et al., 2020; Hasegawa et al., 2021b; Okado & Hasegawa, 2024). We used commercial catch as a metric of predator species abundance because annual stock assessments covering the period of our study were unavailable. Stock abundance (biomass) or relative abundance (catch per unit effort), derived from annual stock assessments, would be much more appropriate metrics, especially when considering many potential predator species (e.g., Pauly et al., 2013; Thorson et al., 2020; Punt, 2023). We focused on identifying potential new marine fish predators of juvenile chum salmon to use as metrics of climate-driven changes in predator exposure.

We identified Japanese yellowtail, also known as Japanese amberjack (*Seriola quinqueradiata*), as a potential marine fish predator of juvenile chum salmon. Japanese yellowtail are a

subtropical species distributed from Japan and the eastern Korean Peninsula to the Hawaiian Islands (Robins et al., 1991), and are one of the most commercially important marine predatory fish in Japan. A climate regime shift (warming) during the late 1980s was associated with the northward extension of yellowtail distribution in the Tsushima Warm Current off northwestern Honshu and Hokkaido (Figure 1a), and global warming was projected to further expand suitable thermal habitat of yellowtail northward (Tian et al. 2012). In September 2012, young adult yellowtail were observed in chum salmon landings in the Sea of Okhotsk. Since 2014, yellowtail have been caught along the coast of the Sea of Okhotsk in May-December by a setnet fishery targeting yellowtail, adult salmon (September-December), and other marine fish species (Hoshino & Fujioka, 2021). The catch by setnets should reflect the seasonal migration and abundance of yellowtail. In May 2023, the peak month of hatchery release of juvenile Japanese chum salmon in the Sea of Okhotsk (Figure S2), schools of yellowtail were often observed on the sea surface near the central Sea of Okhotsk coast (pers. comm., Takashi Ichikawa). Adult yellowtail feed on small pelagic fish and invertebrates (Robins et al., 1991), but stomach contents surveys are necessary to confirm predation of chum salmon juveniles by yellowtail. Yellowtail was identified by PICES as a potential indicator of human pressure due to the rapid increase in salmon setnet catches in recent years in Japan (Hunsicker et al., 2022).

Our analysis of predator exposure was too limited in scope to identify potential predators in high seas areas of chum salmon distribution. The use of stock assessment data is a promising approach for developing new indices of climate-driven predator exposure, especially if predator diet information is available. A similar approach for high seas regions may be possible through future scientific collaborations among international treaty organizations. For example, an international scientific collaborative agreement has prioritized climate change research in the North Pacific focused on the use of high seas commercial fishery stock assessment data and an ecosystem approach to conservation of vulnerable marine ecosystems (PICES-NPFC, 2019).

Competitive interactions between Russian pink salmon and chum salmon, as well as many other species, are increasingly evident (Ruggerone et al., 2023). Our regression model indicated survival of immature (age 1) Japanese chum salmon during 1998-2019 was not related to the abundance of Russian pink salmon but was related (negative) to the survival of older (age 2 and age 3) chum salmon. Pink salmon spend only one winter in the ocean before maturing fish return to spawning streams in spring and summer. Little is known about interannual variation in the relative abundance and overlap in high seas distribution of Japanese, Russian, and North American chum and pink salmon, due to infrequent and costly high-seas salmon research. A reanalysis of coastal and high seas salmon gillnet and longline survey data (1953-2022) confirmed the results of earlier studies showing that distributions of chum, pink, and sockeye salmon overlap throughout the North Pacific (Langan et al., 2024). A meta-analysis of salmon trophic ecology data showed that chum, pink, and sockeye salmon have similar diet composition throughout the North Pacific, with a diet overlap of 31.8% between chum and pink and 30.9% between chum and sockeye, and diet overlap was highest between pink and sockeye salmon at 46.6% (Graham et al., 2021). Our results suggest that Russian pink and chum salmon compete for food with Japanese chum salmon (ages 2-3) in the central Bering Sea in summer and Gulf of Alaska in winter, while competition with immature (age 1) chum salmon could be weak or negligible in the Sea of Okhotsk and western North Pacific (Nadenko & Temnykh, 2016; Nadenko et al., 2016; Bugaev & Gerlits, 2023). Inter- and intra-specific competition for prey resources may not be a limiting factor for salmon in the western subarctic North Pacific because the climatic connections to the ecosystem differ from those in the Gulf of Alaska

(reviewed by Radchenko et al. 2018; Somov et al. 2024).

We do not know if bycatch in Russian commercial salmon fisheries could negatively affect the survival of Japanese chum salmon. Annual Russian surveys of juvenile pink and chum salmon biomass in the Sea of Okhotsk and oceanographic data (e.g., Radchenko et al., 2013; Shuntov et al., 2019) could provide information on changes in survival of Japanese chum during their first summer at sea, but we did not have access to these data. In contrast, marine survival of Japanese chum salmon was not related to abundance of North American pink and chum salmon. This is likely because of latitudinal differences in distribution of Japanese chum salmon (southern latitudes) and North American chum salmon (northern latitudes) during winter in the Gulf of Alaska (reviewed by Myers et al., 2016; Urawa et al., 2016).

4.4 Ocean conditions

The effects of ocean conditions (positive or negative) were inferred only for juveniles released in the Hokkaido and Honshu Sea of Japan. The largest positive effect on return rates was winter SST (January-April) in the Gulf of Alaska (year *t*+2), followed by winter SST (January–April) in the western North Pacific (year *t*+1). The largest negative effect on return rates was SST at release in the Sea of Japan, followed by summer SST in the Bering Sea (August-September) (year *t*+1) and in the Sea of Okhotsk (July) (year *t*) (Figure 7). In contrast, there was no relationship between survival and SST at any marine life stage for Hokkaido Okhotsk and Hokkaido and Honshu Pacific hatchery releases.

The Sea of Japan, where northwestern Honshu and western Hokkaido hatchery chum salmon are released, is a global hotspot for long-term declines in marine fisheries productivity (Free et al., 2019). After a brief (1998-1999) natural cooling event, anthropogenic climate change became the principal driver of extreme warming events in the Sea of Japan, particularly in southern regions (Hayashi et al., 2022). Juveniles (age 0) were released along the coasts of Honshu (mainly in Feb-Mar) and Hokkaido Sea of Japan (Mar-Apr) (Figure S2). Coastal thermal habitat (4–13°C) available to Japanese chum salmon shifts northward in spring and early summer, especially in the Sea of Japan (Figure S9), and to survive, juveniles must arrive by late June or early July in the southern Sea of Okhotsk, where they spend their first summer growth season (Figure 1). The peak release month in the Hokkaido Okhotsk region was May, when SSTs were below ~6°C (Figures S9, S10). The negative association with SST during the first summer in the Sea of Okhotsk may be related to the delayed arrival at their nursery area in the Sea of Okhotsk.

4.5 Age and body size at maturity

We observed a trend towards younger age at maturity in all hatchery management regions in Japan (Figure 3). This trend was strongest after around 2008, and the rates of change differed among regions. In the Hokkaido Sea of Japan and Okhotsk regions, the peak in adult returns of in 2022 (Figure 2) was related to an increase in age–4 fish released as juveniles in 2019 and increased total return rates of all age groups (Figure S15), indicating better growth and survival of the 2019 year class. In contrast, total return rates decreased in other regions (Figure S15), despite the generally increasing proportion of age–2, age–3, and age–4 fish in all regions after approximately 2008 (Figure 3).

Optimal thermal habitat for growth and feeding (8–12°C) of chum salmon was widely distributed in the Sea of Okhotsk in July 2019 and in the central Bering Sea in September 2020,

(Figure S16), where Japanese chum salmon spend their second summer growing season (age 1). Expansion of optimal thermal habitat during the first and second summers likely improved the growth of immature chum salmon in 2020 and 2021, and may have resulted in the peak returns of age–4 fish in 2022. Summer SST (August–September) in the Bering Sea (range, 8.3–11.4°C) was within the optimal growth and feeding range, while winter SST (January–April) increased after 2010 in the western North Pacific (range, 4.6–6.1°C) and the Gulf of Alaska (range, 4.6–7.2°C) (Figure S11b). The summer SSTs within the optimal range for growth and feeding and the warming winter SST are consistent with the increasing trend in younger age at maturity of Japanese chum salmon after 2008 (Figure 3). The GAMs confirmed that body size (FL) of age–4 and age–5 hatchery chum salmon generally remained at similar levels after 2008 in all regions, though the variation was particularly large in age–5 fish in the Hokkaido Sea of Japan region (Figures S17, S18). The observed younger age at maturity and the relatively constant trends in body size after 2008 suggest increasing growth rates in Japanese chum salmon. Summer SST within the optimal growth and feeding range in the Bering Sea and increased winter SST in the western North Pacific and the Gulf of Alaska (Figure S11b) might contribute to increasing growth rates in Japanese chum salmon. Our result is consistent with improved growth of Alaskan sockeye salmon that was associated with warm winter SST (Ohlberger et al., 2023). However, warm summer SST was associated with reduced growth of Alaskan Chinook and sockeye salmon (Yasumiishi et al., 2020; Ohlberger et al., 2023).

Declines in body size, shifts to younger age at maturity, and decreased size-at-age were reported in chum, Chinook, coho, and sockeye salmon from large-scale analyses across Alaska, and were associated with climate and competition with other salmon at sea (Lewis et al., 2015; Oke et al., 2020; Ohlberger et al., 2023). Body size of adult salmon has declined in British Columbia (Freshwater et al., 2023) and in Washington State since the 1970s (Losee et al., 2019). Competition with other salmon is considered an important driver of size declines in salmon (Oke et al., 2020; Ohlberger et al., 2023). When populations of wild and hatchery salmon are abundant, increased competition at sea could lead to reductions in body size by reducing the availability or quality of food resources (Bigler et al., 1996; Jeffrey et al., 2017).

Body size at maturity of Japanese hatchery chum salmon declined from the 1970s to the 1980s, possibly due to density-dependent effects related to the carrying capacity of Japanese chum salmon in the open ocean (Ishida et al., 1993; Hayashizaki & Ida, 1993; Kaeriyama, 1998; Morita & Fukuwaka, 2007). A United Nations' worldwide moratorium on large-scale high-seas driftnet fishing (1989) and the closure of the U.S. 200-nautical mile Exclusive Economic Zone (EEZ) to large-scale driftnet fishing went into effect in 1992. The Convention for the Conservation of Anadromous Stocks in the North Pacific Ocean, an intergovernmental treaty closing all directed commercial fishing for Pacific salmon in international waters of the North Pacific Ocean and its adjacent seas, went into effect in 1993. The large-scale high-seas driftnet fishing gear was highly size-selective for salmon. After 1992, the body size at maturity of Japanese chum salmon increased, possibly the result of natural selection and phenotypic plasticity induced by environmental changes after the relaxation of high-seas driftnet fishing pressure (Fukuwaka & Morita, 2008). Our analysis showed that adult body size (age-specific FL) of Japanese chum salmon increased from 1997 to around 2003, and then decreased until the mid-2000s (Figures S17, S18). Until the mid-2000s, the trends in adult body size of Japanese chum salmon agreed with those of Alaskan chum, coho, and sockeye salmon (Oke et al., 2020). After 2003, the positive effect of the relaxation of high-seas fishing pressure on size at maturity might have been masked or reduced by density-dependent effects related to climate change

effects on oceanic thermal habitats of salmon.

Our regression analysis showed a negative association between Russian chum and pink salmon and survival of Japanese chum salmon (Table 2), but body size-at-maturity was relatively stable after the mid-2000s (Figures S17, S18). The estimated proportion of hatchery chum salmon was 60% of the total maturing ocean population (Ruggerone & Irvine, 2018). The substantial decrease in catches of Japanese chum salmon after the mid-2000s (Figure 2) may have reduced inter- and intra-specific competition for prey resources, contributing to an increased growth rate. The lack of an association between Russian pink salmon catch and survival of age–1 Japanese chum salmon might also indicate improved growth in the Sea of Okhotsk. However, even when catches of Japanese chum salmon were low, their survival (age–2 and age–3 fish) was negatively correlated with Russian chum and pink salmon catches. Water temperature is an important regulator of physiological processes in fish (Powers et al., 1991; Somero, 2022). Water temperature and body size influence swimming performance in salmon, but swimming performance has been least studied in adult chum salmon and Chinook salmon (reviewed by Kraskura et al., 2024). Comparison of the swimming performance of Japanese chum salmon with Russian chum and pink salmon is a topic for further study.

4.6 Management implications

Hatchery experiments to test appropriate juvenile size and time of release and nearshore monitoring of SSTs might provide an adaptive approach for improving adult returns of Japanese chum salmon (Saito & Nagasawa, 2009; Nagata et al., 2016; Iida et al., 2021). For example, in the most successful management region (Hokkaido Okhotsk), the peak time of release is in May (SST, 4.7–6.2°C). In the Sea of Japan region, SST at release and summer SST (July) in the Sea of Okhotsk were negatively associated with return rate. Adjustment of release timing to allow juveniles to arrive in the Sea of Okhotsk in May or early June or both might improve nearshore survival. In the Pacific region of Japan, parental fecundity (negative) and juvenile size at release (positive) were associated with salmon survival. Size at release declined in most regions after around 2010. Smaller juveniles are easy prey for nearshore birds, fish, and marine mammal predators due to their slow swimming speed (Hasegawa et al., 2021b).

Our finding of a nationwide decline in egg size in Japanese hatchery-reared chum salmon populations over the past decade suggests that anthropogenic selection in hatchery practices is contributing to the decline in egg size and other traits related to fitness. The geographic distribution of chum salmon single nucleotide polymorphism (SNP) allele frequencies (Seeb et al., 2011) showed significant deviations of Japanese chum from the geographic pattern (Kitada & Kishino, 2021), some of which were associated with growth, reproduction, and aerobic metabolism (Figure S19). Population genomics studies will be useful for understanding adaptation and anthropogenic selection on salmon fitness (Waples et al., 2020).

Efforts in Japan to increase the early-run chum salmon population since the early 1980s have induced changes in adult run-timing distribution, and late-run populations have almost disappeared in Hokkaido (Miyakoshi et al., 2013). Run timing is known to have a genetic basis for salmon, and a small genomic region is associated with spawning run timing (O'Malley et al., 2007; Brieuc et al., 2015; Thompson et al., 2020). The practice of selecting for earlier run timing could certainly have an impact on run timing. Efforts should be made to restore late-run populations in Hokkaido.

Climate change, reduced competition with Russian chum and pink salmon due to the lower abundance of Japanese chum salmon, and increased growth rate all may have contributed to the younger age at maturity of chum salmon observed in all management regions of Japan after 2008. A study of annular growth history on the scales of adult (age-4) Japanese chum salmon showed that growth during the 2nd and 3rd years is more strongly associated with the probability of maturation than age or age-specific body size, which is affected by environmental conditions (Morita & Fukuwaka, 2006). Summer SSTs in the Bering Sea and winter SSTs in the Gulf of Alaska, where immature age-2 and age-3 Japanese chum salmon are distributed, were warmer after 2010 (Figure S11b), possibly resulting in increased growth rates of immature age-2 and age-3 fish.

Currently, hatchery managers, fishermen, and scientists are aware of the importance of natural spawning. In Kitami, Hokkaido Okhotsk, upstream escapement of adult salmon has been implemented since 2008 by redesigning fish weirs (Kitada, 2014; Miyakoshi, 2021). In Hidaka, Hokkaido Pacific West, the removal of fish weirs has been initiated since 2008 to allow returning fish to spawn in natural streams (Kaeriyama & Sakaguchi, 2023). Such efforts are admirable and can serve to raise awareness of the importance of salmon conservation to fishermen and society. There is evidence that the key to success in mitigating the genetic effects of captive breeding and increasing the abundance of wild fish is a high proportion of wild (or wild-born) fish in the target population with healthy spawning and nursery habitat (Kitada et al., 2019). Very high gene flow between demes (Kitada, 2020) may work against mitigating the genetic effects of captive breeding in current chum salmon hatchery programs, as almost all chum salmon returning to Japan are hatchery fish (Kaeriyama, 1999; Kaeriyama & Sakaguchi, 2023). Restoration or reconstruction of healthy spawning and nursery habitat cannot be achieved without support from the central and prefectural governments. Continued monitoring is needed to demonstrate the effectiveness of natural spawning in increasing the number of returning salmon.

Investigations of many other potentially important stressors beyond the scope of our study remain to be addressed. For example, relationships between marine survival of salmon and climate-driven changes in marine fisheries operating along high seas salmon migration routes and within the 200-mile EEZs of other nations. In Alaska, genetic analyses show that Asian (Russia and Japan) populations dominate early (June) catches by salmon fisheries targeting sockeye salmon along the south side of the Alaska Peninsula in early (June), when chum salmon are migrating from winter (North Pacific) to summer (Bering Sea) feeding grounds (Dann et al. 2023). Asian stocks of chum salmon also dominate prohibited species bycatch of salmon in the US walleye pollock (*Gadus chalcogrammus*) fishery in the eastern Bering Sea in early summer (Barry et al., 2023). Interesting to note are the unexpectedly high bycatches of Asian chum salmon (ocean-age-3 and age-4; unknown maturity stage) by both fisheries in 2021 (Barry et al., 2023; Dann et al., 2023). The Alaska bycatch of Asian chum salmon preceded the spike in adult returns to Japan in 2022. Seeking predictive (vs. retrospective) indices would benefit preseason forecasting of adult salmon returns. In the absence of quantitative marine stock assessment surveys of salmon, potentially predictive indices might be used in a qualitative "stoplight" approach to pre-season forecasting (Caddy, 2002; NOAA 2024). This method requires an adaptive approach because relationships between salmon survival and index variables change over time (non-stationarity; Litzow et al. 2018; Ohlberger et al. 2022).

5 | SUMMARY AND CONCLUSIONS

This study assessed stressors on the survival of hatchery-reared chum salmon along known coastal and open ocean migration routes in the context of climate change. We used long-term data series collected from the world's largest hatchery salmon program to investigate potential stressors of hatchery practices, ocean conditions (SST), and predators and competitors related to the 25-year population dynamics of Japanese chum salmon (1998-2023). Our results highlighted the regional differences in stressor metrics associated with the decline in marine survival of Japanese chum salmon. Parental fecundity and size at release were associated with survival in the Pacific region, where the decline in abundance was most severe. The northward migration shift of a piscivorous marine fish indicated a possible new predator in Hokkaido Okhotsk, the most successful management region. Effects of sea temperature were inferred for juveniles released in the Sea of Japan, while no effects of sea temperature were found at any life stage for hatchery releases in other regions. Russian chum and pink salmon abundance was negatively associated with survival of Japanese chum salmon in all regions. Importantly, we observed a trend toward younger age at maturity in all hatchery management regions of the country after around 2008, while body size at maturity generally remained at similar levels, indicating that growth rates are increasing. Moreover, egg size decreased over the past two decades in all regions. The nationwide decline in egg size suggests that anthropogenic selection in hatchery practices and maternal effects on transgenerational phenotypic plasticity are contributing to the decline in egg size and other traits related to fitness. Age at maturity, fecundity, and egg size are key demographic parameters that contribute to the productivity of salmon populations, and the decadal-scale changes observed herein could result in significant ecosystem, fishery, and societal losses. The results of this study highlight the need for monitoring and analysis with updated information to rethink the role of hatcheries and develop adaptive management plans for future sustainability and conservation of salmon in a changing climate.

AUTHOR CONTRIBUTIONS

Shuichi Kitada: Conceptualization (lead); data curation; formal analysis (lead); funding acquisition; investigation; methodology; software; validation; visualization (lead); writing – original draft; writing – review and editing. Katherine W. Myers: Conceptualization; writing – review and editing (lead). Hirohisa Kishino: Conceptualization; formal analysis; funding acquisition; methodology (lead); validation (lead); visualization; writing – review and editing. All authors approved the final version of the manuscript.

ACKNOWLEDGMENTS

We sincerely acknowledge the thousands of biologists, fishery and hatchery managers, and fishers who contributed to collection of data analyzed in our manuscript. The efforts of APG, FRA, HSEA, JMA, MAFF, NOAA, and NPAFC to create public open use databases made our study possible. We thank the reviewers for their constructive comments, which significantly improved earlier versions of the manuscript. Takashi Ichikawa provided information on chum salmon and yellowtail. This study was supported by Japan Society for the Promotion of Science Grants-in-Aid for Scientific Research KAKENHI No. 18K0578116 for SK and 22K11950 for HK.

CONFLICT OF INTEREST STATEMENT

The authors declare that no conflict of interest exists.

DATA AVAILABILITY STATEMENT

The data generated or analyzed in this study are fully described in the published article and its Supplementary Information. Analysis scripts and data will be available at https://doi.org/10.5281/zenodo.14064278 on acceptance.

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TABLE 1 Three subset models of stressors related to chum salmon marine survival (adult return rates) of fry released in year *t* (1998-2019) and explanatory variables (metrics) considered in a regression model and hypothesized directional relationship. Sea surface temperature (SST); Western North Pacific (WN Pacific); Gulf of Alaska (GOA).

Subset model	Explanatory variable (year)	Age [†]	Spatial scale [‡]	Hypothesized relationship to chum salmon survival (source)
Hatchery carryovers	Parental relative fecundity (*t* -1)	0	Japan coast	Survival related (negative) to higher fecundity (Hasegawa et al., 2021a)
	Egg size (*t*)	0	Japan coast	Survival related (positive) to larger eggs (Hasegawa et al., 2021a)
	Fry size at release (*t*)	0	Japan coast	Survival related (positive) to size at release (Hasegawa et al., 2021b)
Ocean conditions	SST at release (*t*)	0	Japan coast	Survival related (negative) to SST (Nagata et al., 2007)
	Okhotsk coast Jul SST (*t*)	0	Okhotsk	1st summer survival related (negative) to SST (Nagata et al., 2007)
	N. Pacific Jan-Apr SST (*t*+1)	1	WN Pacific	1st winter survival related (positive) to SST (this study)
	Bering Sea Aug-Sep SST (*t*+1)	1	Bering Sea	2nd summer survival related (negative) to SST (Kaeriyama, 2022)
	GOA Jan-Apr SST (*t*+2)	2	Gulf of Alaska	2nd winter survival related (positive) to SST (this study).
Predators and competitors	Yellowtail catch (*t*)	0	Japan coast	1st year survival related (negative) to predation (Beamish, 2018)
	Russia chum catch (*t*+3)	0-4	Okhotsk, North Pacific	1st - 3rd year survival related (negative) to Russian chum (this study).
	Russia pink catch (*t*+1)	0-1	Okhotsk, WN Pacific	1st year survival related (negative) to Russian pink (this study)
	Russia pink catch (*t*+2)	1-2	Bering Sea	2nd year survival related (negative) to Russian pink (Ruggerone et al., 2023
	Russia pink catch (*t*+3)	2-3	Gulf of Alaska, Bering Sea	3rd year survival related (negative) to Russian pink (Ruggerone et al., 2023)
	US & Canada chum catch (*t*+3)	1-4	North Pacific	2nd - 3rd year survival related (negative) to US & Canadia chum (this study)
	US &Canada pink catch (*t*+1)	0-1	Okhotsk, WN Pacific	1st year survival related (negative) to US & Canada pink (this study)
	US & Canada pink catch (*t*+2)	1-2	Bering Sea	2nd year survival related (negative) to US & Canada pink (this study)
	US and Canada pink catch (*t*+3)	2-3	Gulf of Alaska, Bering Sea	3rd year survival related (negative) to US & Canada pink (this study)

[†] Age of Japanese chum salmon released in year *t* (=1998,…,2019). [‡] See Japanese salmon migration route (Fig. 1).

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TABLE 2 Best regression models of Japanese chum salmon survival in four coastal regions in Japan and regression coefficients with their *p*-values in parentheses. Bold indicates significant relationship ($\alpha = 0.05$). *t* = ocean entry year of chum salmon fry. SST = sea surface temperature. See Figure 1a for management region locations.

Subset model	Explanatory variable (year)	Management region			
		Hokkaido Okhotsk	Hokkaido & Honshu Pacific	Hokkaido Sea of Japan	Honshu Sea of Japan
Hatchery carryovers	Relative fecundity[†] [‡] (*t*-1)	–	**–0.931 (0.0009)**	–	–
	Egg size[†] (*t*-1)	–	–	–	–
	Size at release (*t*)	–	**0.486 (0.0009)**	–	–
Ocean conditions	SST at release (*t*)	–	–		**-0.483 (0.0033)**
	Okhotsk Jul SST (*t*)	–	–	**-0.315 (0.0042)**	**-0.138 (0.0452)**
	North Pacific Jan-Apr SST (*t*+1)	–	–	–	0.259 (0.0647)
	Bering Sea Aug-Sep SST (*t*+1)	–	–	**-0.383 (0.0153)**	–
	Gulf of Alaska Jan-Apr SST (*t*+2)	–	–	**0.405 (0.0051)**	–
Predators and competitors	Yellowtail catch in year (*t*)	**-0.093 (0.0001)**	–	–	–
	Russia chum catch (*t*+3)	–	–	-0.151 (0.0504)	–
	Russia pink catch (*t*+1)	–	–	–	–
	Russia pink catch (*t*+2)	-0.127 (0.0559)	**-0.311 (0.0025)**	–	-0.139 (0.0605)
	Russia pink catch (*t*+3)	–	**-0.225 (0.0138)**	–	–
	USA & Canada chum catch (*t*+3)				
	USA & Canada pink catch (*t*+1)	–	–	–	–
	USA & Canada pink catch (*t*+2)	–	–	–	–
	USA & Canada pink catch (*t*+3)	–	–	–	–
	Adjusted R^2 (*p*-value)	**0.58**	**0.79**	**0.54**	**0.57**

The three subset models were fitted to log return rates for 1998-2019 releases and variable selection was performed using the Akaike Information Criterion corrected for small sample sizes (AICc). Multicollinearity of explanatory variables was checked using the variance inflation factor (VIF), and those with VIF < 3.0 were used for variable selection.

[†] Egg sizes and relative fecundity of age 4 and age 5 fish were examined. [‡] Age 4 had a smaller AICc (30.0) than that of age 5 (38.2).

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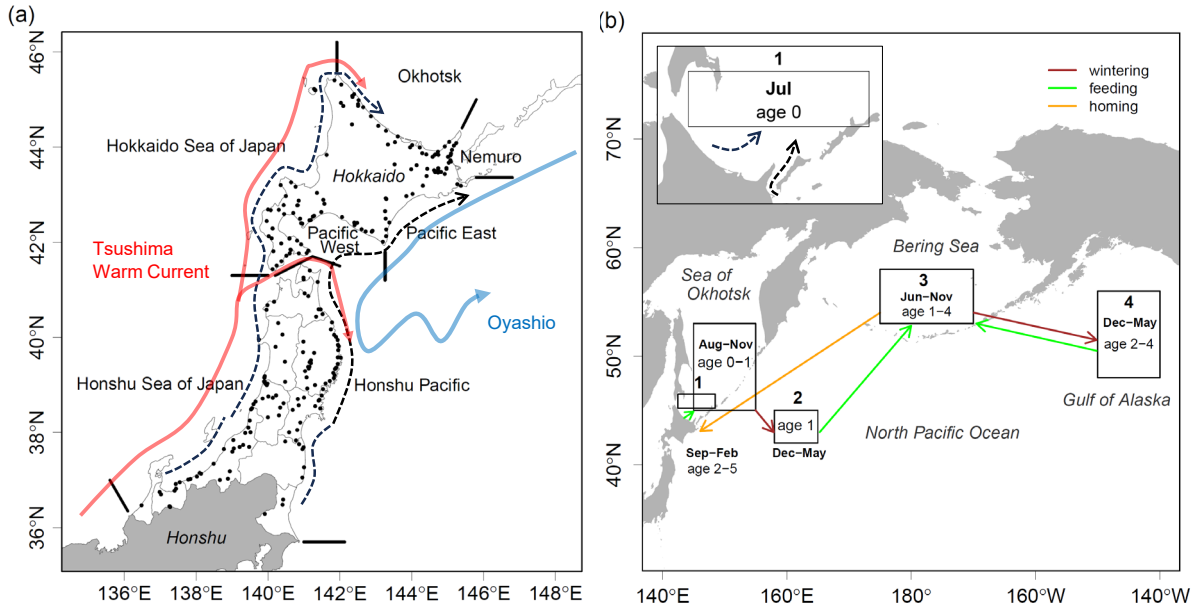

FIGURE 1 Japanese chum salmon management regions, coastal migration routes, and high seas distribution areas. (a) Seven management regions (delineated by black bars) and hatcheries (black dots) in Japan. Migration paths of hatchery-released juveniles (age 0, dashed lines) were modified from Saito et al. (2009, Figure 1). Schematic sea surface currents were redrawn from Kuroda et al. (2020, Figure 1). (b) principal areas of high seas distribution (boxes), month(s), age group(s), and seasonal direction of wintering, feeding and homing migrations (arrows), numbered areas are: 1.Southern Sea of Okhotsk (45.2°N-46.5°N, 142.5°E-148.5°E), 2. Western North Pacific (42°N-45°N, 158°E-165°E), 3. Central Bering Sea (53°N-58°N, 175°E-170°W), 4. Central Gulf of Alaska (48°N-56°N, 140°W-150°W). Migration routes of Japanese chum salmon estimated from long-term field surveys, modified from Myers et al. (2007, Figure 1) and Urawa et al. (2018, Figure 37).

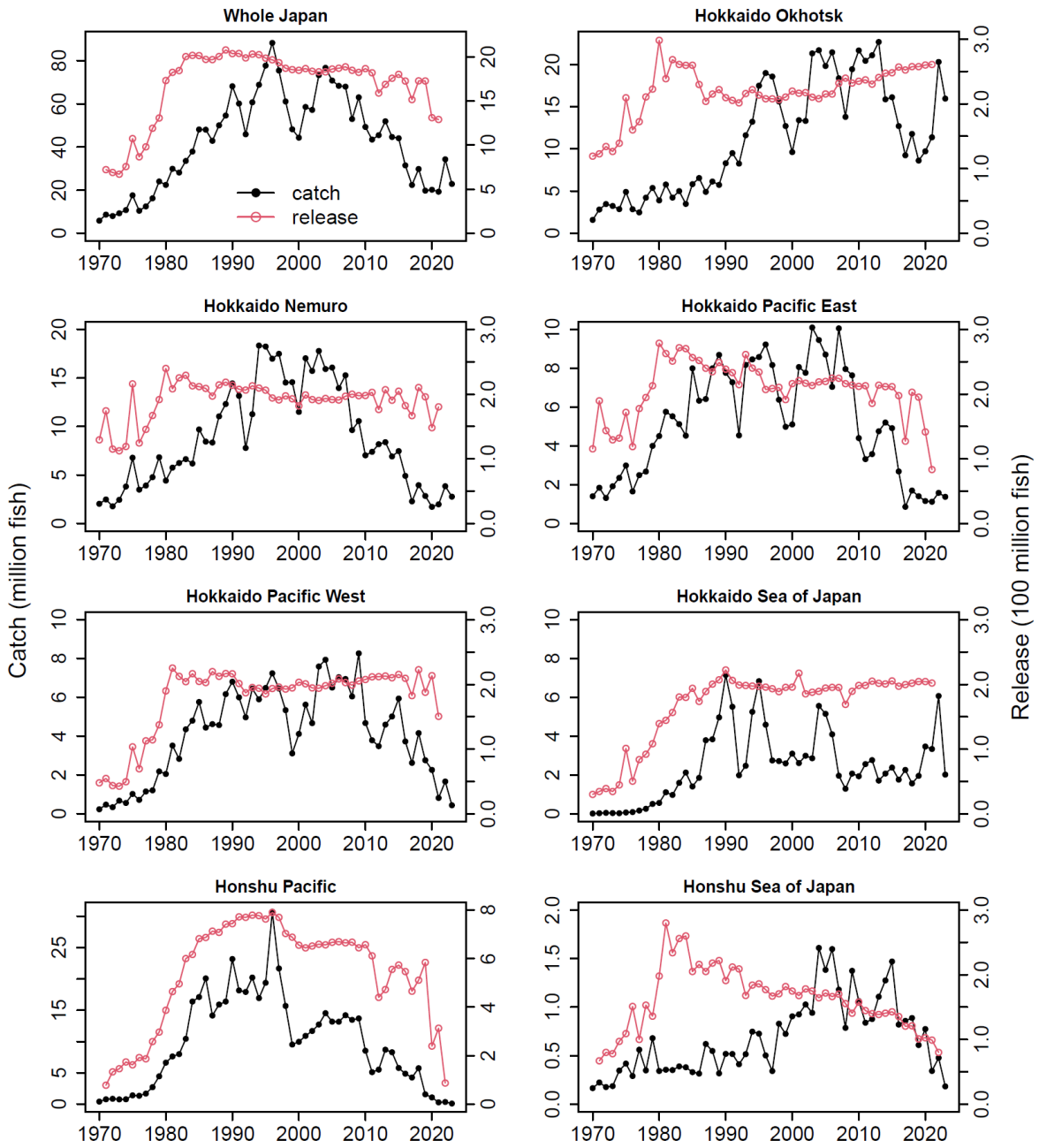

FIGURE 2 Number of juvenile hatchery chum salmon released (red line) and adult returns (coastal catch plus hatchery broodstock catch; black line) in seven management regions in Japan (1970-2023; Figure 1a).

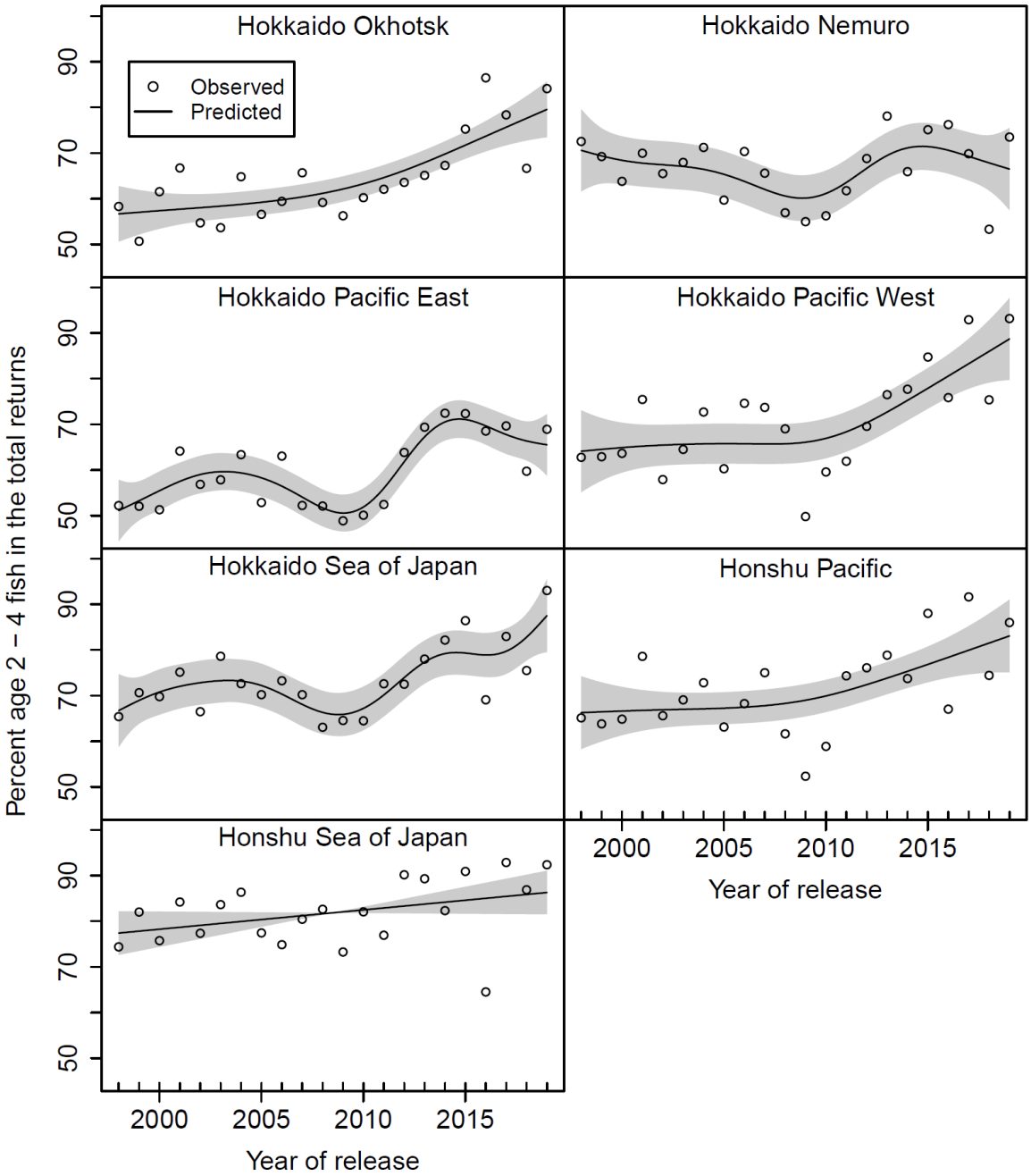

FIGURE 3 Percentage of age 2 - 4 Japanese chum salmon in the total number of adult returns for 1998-2019 hatchery releases generally increased in all regions after around 2008, as shown by the nonlinear and linear year effect from GAMs: Hokkaido Okhotsk (p=0.000, R^2=0.61), Hokkaido Nemuro (p=0.244, R^2=0.24), Hokkaido Pacific East (p=0.000, R^2=0.73), Hokkaido Pacific West (p=0.003, R^2=0.51), Hokkaido Sea of Japan (p=0.008, R^2=0.57), Honshu Pacific (p=0.021, R^2=0.32), Honshu Sea of Japan (p=0.078, R^2=0.11).

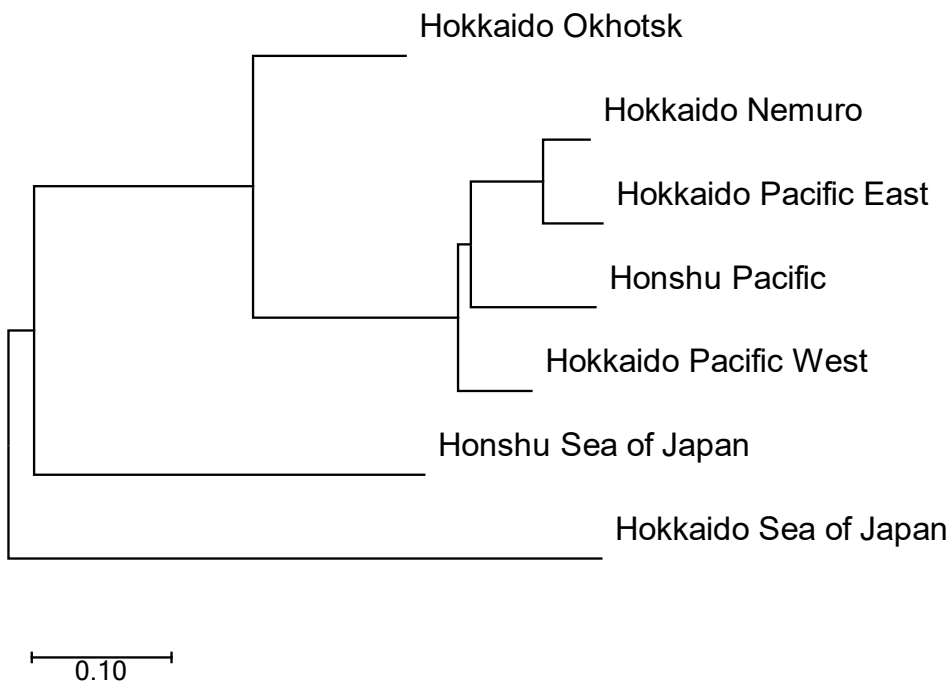

FIGURE 4 Neighbor-joining tree based on correlation coefficients of chum salmon adult return rates between pairs of seven management regions in Japan, 1998-2019.

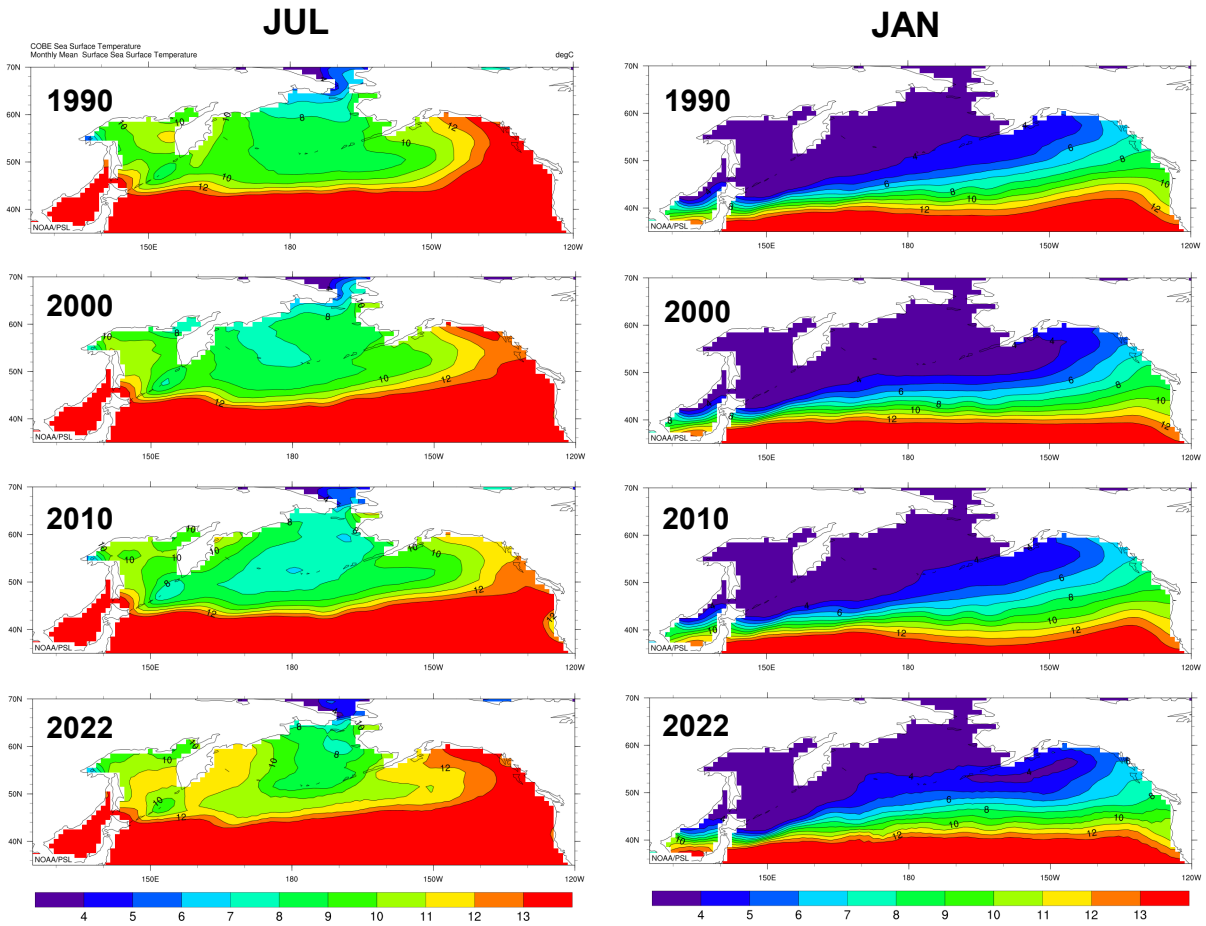

FIGURE 5 Sea surface temperature (SST) isotherms in recent decades (1990-2022) showed a northward shift and longitudinal contraction of chum salmon summer (July) thermal habitat in the North Pacific Ocean, while winter (January) habitat was relatively stable. Blue, green and orange show the range of Japanese chum salmon thermal limits (4-13°C): optimal growth and feeding habitat (8-12°C), swimming and feeding habitat (5-13°C), and overwintering habitat (4-6°C) (Kaeriyama et al., 2012; Urawa et al., 2018). Red (>13°C) and purple (<4°C) indicate critical habitat, lost to ocean production of Japanese chum salmon.

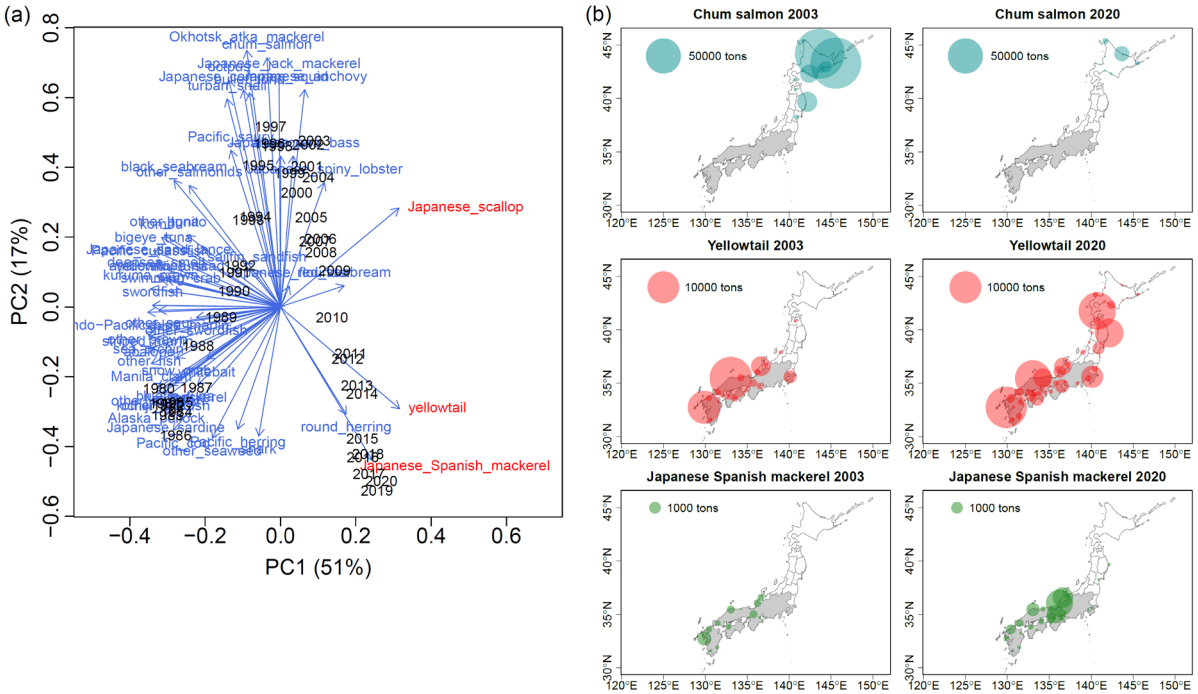

FIGURE 6 Northward shifts of two marine piscivorous fishes in Japan. (a) Principal component analysis biplot based on catch statistics of 56 marine species (1980 - 2020) showed increasing catches of yellowtail and Japanese Spanish mackerel. (b) Two-decadal shifts in commercial catches of chum salmon and two piscivores.

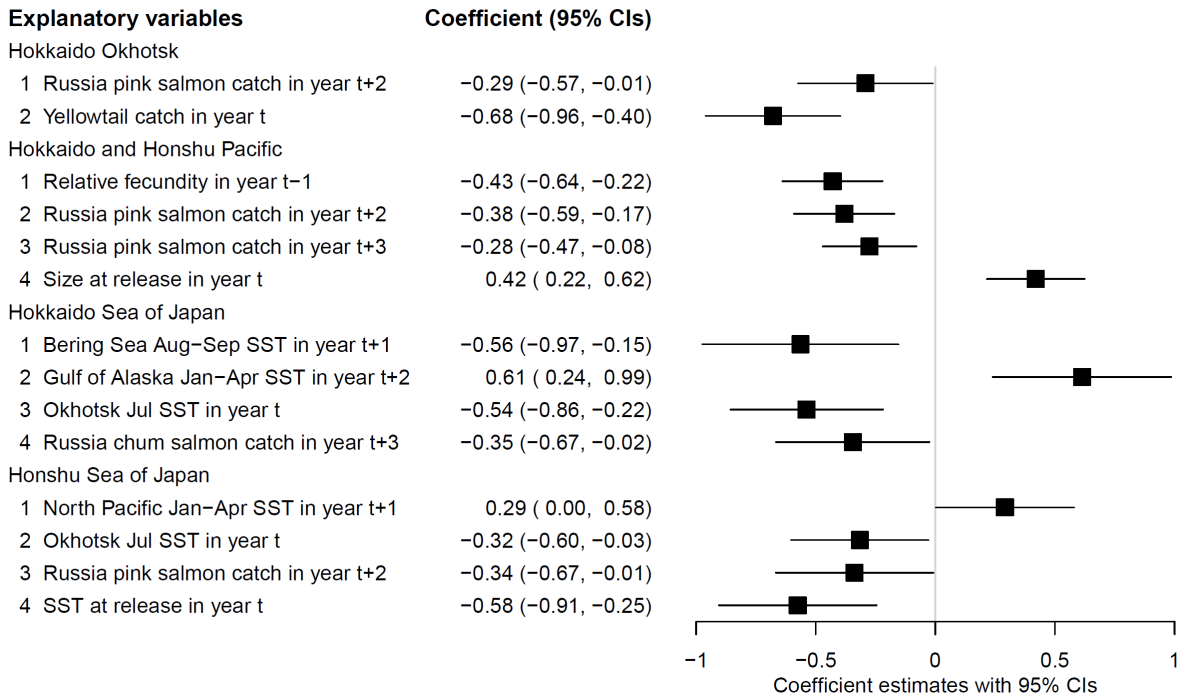

FIGURE 7 Standardized effects of hypothesized metrics (explanatory variables) on Japanese chum salmon marine survival (adult return rates across regions). Regression coefficients of best regression models with 95% confidence intervals in four coastal regions in Japan, estimated using standardized explanatory variables.

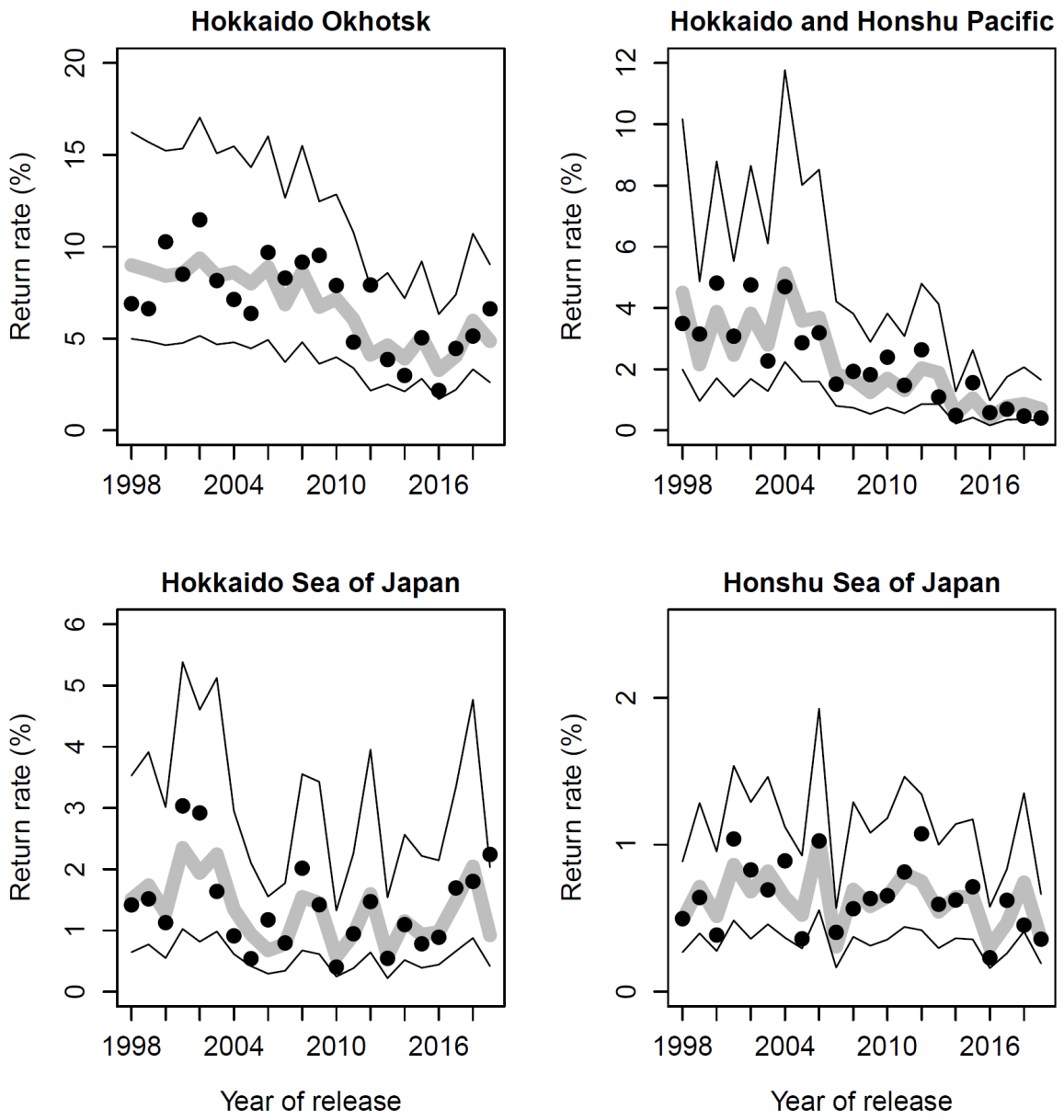

FIGURE 8 Predicted and observed chum salmon marine survival (adult return rates) by management region in Japan. Predicted return rates (grey line), observed return rates (black dots), and 95% prediction intervals (black lines). Note that scales on return rate axis differ by region.

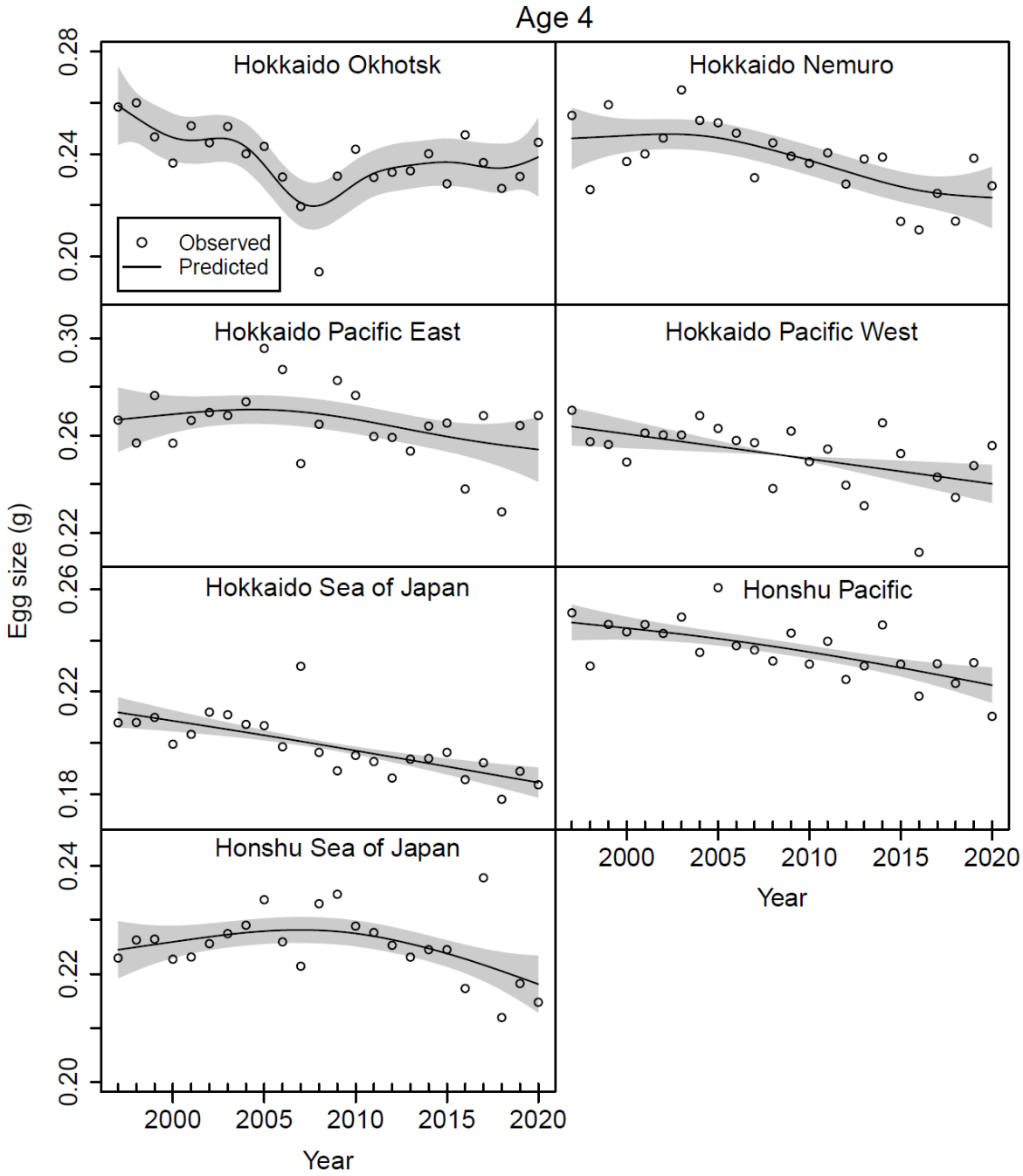

FIGURE 9 Egg size of age–4 chum salmon has generally decreased in all regions, as shown by the nonlinear and linear year effect from GAMs (1997-2020): Hokkaido Okhotsk (p=0.016, R^2=0.50), Hokkaido Nemuro (p=0.046, R^2=0.44), Hokkaido Pacific East (p=0.024, R^2=0.19), Hokkaido Pacific West (p=0.007, R^2=0.26), Hokkaido Sea of Japan (p=0.000, R^2=0.52), Honshu Pacific (p=0.001, R^2=0.44), Honshu Sea of Japan (p=0.045, R^2=0.27). Open circles show observed values. The black lines show predicted values with shaded areas of 2×standard errors.