# 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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**CONFLICT OF INTEREST**
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**Abstract**

Anthropogenic climate change is driving survival of economically important marine and anadromous fish, including Pacific salmon (*Oncorhynchus* spp., Salmonidae). We investigated a 25-year (1998-2023) decline in marine survival of chum salmon (*O. keta*) in Japan, the world's largest hatchery salmon producer, located near the species' global southern distribution limit. Our objective was to identify local and context-specific indicators of climate-change effects on salmon survival for adaptive climate-change management. We hypothesized multiple indicators in three categories of stressors: hatchery carryovers, ocean conditions, and predator-competitor interactions. Mean annual survival of salmon released in 1998-2019 decreased from north (6.9%, Hokkaido Okhotsk) to south (0.6%, Honshu Sea of Japan). Survival decline corresponded to decadal-scale changes in chum optimal summer thermal habitat (8-12℃). Multivariate regression models showed survival indicators differed by management region. Hokkaido Okhotsk juvenile survival was related (negative) to a northward shift in migration of a piscivorous marine fish. Hokkaido and Honshu Pacific juvenile survival was related (negative) to hatchery carryovers (parental fecundity, fry size at release). Hokkaido Sea of Japan salmon survival was related to temperatures in coastal (negative) and high seas (negative in summer, positive in winter) habitats. Honshu Sea of Japan juvenile survival was related (negative) to sea temperature at time of release. High seas survival was related (negative) to abundance of Russian chum and pink (*O. gorbuscha*) salmon, indicating competitive interactions. A shift to younger age at maturity occurred in all management regions. Our results provide indicators and insights for adaptive salmon management in a changing climate.

**KEYWORDS**

adult returns, chum salmon, competition, predation, thermal habitat

## 1 | INTRODUCTION

Climate change is driving survival of many economically important marine and anadromous fish species, including Pacific salmon (*Oncorhynchus* spp., Salmonidae) (Cheung et al., 2020, 2021). Pacific salmon populations often consist of hundreds of subpopulations with diverse life history traits and local adaptations to environmental variation (Hilborn et al., 2003). 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 (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). 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 (FAO, 2022; IPCC, 2022). In the 2020s, abundances of naturally-produced high latitude Pacific salmon populations differ regionally, with record highs in southern Bering Sea populations (Russia and Alaska) and record lows in northern Bering Sea populations (Alaska) (Schoen et al., 2017; NPAFC, 2023).

Ocean mortality of salmon is thought to be regulated initially by predation on fry/smolt 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). Natural mortality of immature and maturing high seas salmon is generally thought to be low (Ricker 1976). We expected that climate change affects salmon survival at all marine life stages.

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 (*O. keta*) hatcheries in Japan that constitute the world's largest salmon hatchery release program (Amoroso et al., 2017; Kitada, 2018). Hatchery releases of chum fry in Japan increased rapidly in 1970s, reaching to ~2 billion per year in 1980s, but because of poor returns of adult spawners gradually declined to ~1 billion per year in 2021. Adult returns of Japanese hatchery chum increased dramatically since the 1970s, but declined sharply after the late 1990s (88 million in 1996 to 19 million in 2021). Previous studies have reported higher spring sea surface temperatures (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 (Kaeriyama, 2022). Although

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.

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). A comprehensive review of literature (meta-analysis across sub-disciplines) 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 marine survival (adult returns) of Japanese hatchery chum salmon at each life stage and a suite of hypothesized climate-change indicators. Our primary objective was to identify potential indicators along known coastal and high seas migration routes of Japanese chum salmon for use in regional adaptive management planning and hatchery and fishery management.

## 2 | MATERIALS AND METHODS

### 2.1 Ecological setting, study design, and methods overview

Due to extensive observational and experimental research over the past 75 years, our understanding of the ocean life history and ecology of Japanese chum salmon is arguably more complete than for any other Pacific salmon species or population. Urawa et al. (2018) reviewed what is known and needs to be known about the extensive ocean journeys (20,000 km), life history, and ecology of Japanese chum salmon. The freshwater distribution of Japanese chum is near the southern limit of Pacific salmon distribution in Asia. They are genetically distinct from other regional population groups in Russia and North America. After release from more than 260 coastal hatcheries in northern Honshu and Hokkaido in winter and spring (Figure 1a), juveniles (age 0) migrate rapidly (~10 days) through river estuaries, north and eastward in shallow coastal waters before moving offshore to summer feeding grounds in the southern Sea of Okhotsk (Figure 1b). They spend their first ocean winter (age 1) in the western North Pacific, and in spring move northeastward to summer feeding grounds in the Bering Sea (Figure 1b). 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. In late summer and fall, maturing fish return to Japan from the Bering Sea through the western North Pacific. In spring the northward migration of maturing fish precedes that of immature fish. Size at maturity is determined by growth in the final summer at sea. Distribution at sea is related SST. Growth at sea is density dependent. Survival (adult returns) is related to large-scale climatic drivers of ocean conditions and inter-and intra-specific interactions in summer feeding and overwintering grounds. Predation is likely the direct cause of most natural mortality of salmon at sea, but other

causes were considered.

We identified multiple *a priori* hypotheses about potential indicators of 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 indicators into three broad categories of stressors: hatchery carryovers, ocean conditions (SST), and predator-competitor interactions. 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 indicators in each stressor category. We stratified time series data of reproductive and biological traits of hatchery salmon and adult return rates (survival) by coastal Japan management region (Figure 1a). We created isotherm maps to illustrate decadal-scale trends in SST throughout the known ocean range of Japanese chum salmon. We estimated SSTs at ocean entry and along coastal and high seas migratory routes (Figure 1b). We developed measures of potential coastal marine fish predators and high seas salmon competitors of Japanese chum salmon. Investigation of coastal mammal and bird predators and high seas predators was beyond the scope of our study due to inadequate time-series data covering the period of our study. We estimated annual adult return rates (marine survival), stratified by salmon age group and year. We used multivariate regression models to evaluate relationships between marine survival 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**

Long time-series (~20-30 years) datasets are necessary for investigations of marine survival of salmon. We assembled available time-series datasets corresponding to the recent period of Japanese chum salmon decline (1998-2023) from public open-data websites. We assembled longer data time series to aid in interpreting results.

We obtained annual (1970-2022) numbers of adult salmon catches (fishery and hatchery broodstock) and hatchery chum salmon fry releases from the Hokkaido Salmon Enhancement Association (HSEA, 2023), Fisheries Research and Education Agency (FRA, 2023a), and the Aomori Prefectural Government (APG, 2023). FRA (2003b) biological and reproductive trait data (1998-2020) included time series of fry size at release and release month (Hokkaido: 184 rivers, 37,886 release events; Honshu: 171 rivers, 19,605 release events), adult age composition at return (1997-2019; Hokkaido: 52 rivers; Honshu: 102 rivers; 1,903 surveys, $n$=1,210,717 fish), adult salmon (egg weight, fecundity, fork length (FL), age, gonad weight; 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 selected hatchery release events with fry body weight (BW) and FL data. 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). We excluded marine mammals because catches are subject to strict limits, and catch data time-series fail to reflect relative abundance of marine mammal species. We also excluded species known not to be predators of salmon (e.g., sardine, smelt, algae, shellfish, and crustaceans). This resulted in catch data for 30 fishes out of 70 species. 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 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). The management regions coincide with genetic structure of the population (Beacham et al., 2008). Since number of individuals released ($n_l$) varied among release events ($l = 1, \ldots, L$), we calculated weighted mean 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. To estimate distribution of release times in Japan, we counted number of release events by month. We calculated the mean values of the traits and the relative fecundity (fecundity$/FL^3 \times 10^5$) 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 ($H = 1{,}903$), $p_{ah}$ is the proportion of age $a$ fish in survey $h$, $n_h$ is the sample size (individuals) ($\sum_{h=1}^{H} n_h = 1{,}210{,}717$) and $a$ refers to age at return ($a$=2,…,8<).

### 2.4 | Adult return rates

We used adult return rates as an index of marine survival of chum salmon (see discussion section). We assumed all adult chum salmon returning to Japan were hatchery reared. We estimated return rates for the current hatchery management regions (Figure 1a). We estimated 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 4-5, and few returns were older than age 6. We estimated age composition of returning adult chum salmon from available (1997-2020) data. We estimated 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 $1 - r_{jk}$ and illustrated distances by a neighbour-joining (NJ) tree in ape 5.7.1 package in R (ver. 4.3.2) (RCore Team, 2020), where $r_{jk}$ is the correlation coefficient between pairs of return rates.

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. We tested trends in younger age at maturity using the MannKendall function in Kendall 2.2.1 package in R.

### 2.5 | Long-term changes in chum salmon 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 in a similar way. We mapped the available temperature range of chum salmon (4-13°C), based on previous predictions: optimal growth and feeding (8-12°C), available for swimming and feeding (5-13°C), and overwintering temperature range (4-6°C) (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 coastal migration periods of chum salmon juveniles: 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; 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 1.0.15 package in R. We used monthly mean SSTs (1998-2022) in our regression model.

### 2.7 | Potential predators of juvenile chum salmon

To characterize temporal changes in marine fish predator abundance, we performed principal components analysis (PCA) on commercial marine fish catch data (MAFF, 2023) using the prcomp function in R. Changes in chum salmon catch and catches of potential marine fish predator species, 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) predator-competitor interactions (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 $\beta_0$ 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 performed regression analyses for hatchery management regions (Figure 1a) that had a similar trend in return rates, using model selection by AICc (Sugiura, 1978), which is the small sample correction of the Akaike Information Criterion (AIC, Akaike, 1973). We used the results of the best model rather than model averaging, which may be unreliable in the presence of multicollinearity between explanatory variables (Cade, 2015). 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 3.1.2 package in R. We estimated regression coefficients based on standardized explanatory variables, which allow for consistent comparison of different explanatory variables across populations (e.g., Oke et al., 2020; Ohlberger et al., 2022). The use of an unstandardized measure is preferred to a standardized measure if the units of measurement are useful as effect sizes at a practical level (Wilkinson, 1999). We also estimated the regression coefficients using unstandardized explanatory variables, and return rates were predicted based on the regression coefficients. Here 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 created three subset models of stressors and used 17 hypothesized indicators (explanatory variables) ($s$=17) and: (1) hatchery carryover (three indicators), (2) ocean condition (five indicators), and (3) predator-competitor interaction (nene indicators) (Table 1). The hypothesized hatchery carryover indicators included relative fecundity and egg size of females in year $t$-1 where $t$ is the year of fry release, and fry size at release. Ocean-condition indicators included SST at fry 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-competitor-interaction indicators included predation in coastal Japan regions and competition in high seas areas (Table 1). We identified Yellowtail (*Seriola quinqueradiata*, Carangidae) 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. 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 shared high seas environment. Pink salmon have a fixed life span of two years (Quinn, 2018). We used

Russian, US, and Canadian catches in year $t$+1 as indices of interspecific competition with Japanese chum salmon released in year $t$. We assumed cohorts of pink salmon also compete with chum during the 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 in the MuMIn 1.47.5 package in R. All data and R script used for the regression analysis are available (see data availability statement).

## 3 | RESULTS

### 3.1 | Adult return rate

For Japan as a whole, total number of chum salmon adult returns increased substantially until 1996 as the number of hatchery-released fry increased (Figure 2). Mean adult return rate (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 (1.1 ± 0.7%), Hokkaido Sea of Japan (1.4 ± 0.7%), and Honshu Sea of Japan (0.6 ± 0.2%) (Figure 3a). Return rates of age 4 adults from 2019 fry (age 0) releases increased in Hokkaido Okhotsk and Hokkaido Sea of Japan regions, and age 5 return rates decreased slightly. A substantial increase in return rates of ages 2-4 adults from 1998-2019 fry (age 0) releases was observed in all management areas except Hokkaido Nemuro, particularly, after 2010 (Figure 3b; see supplementary information, Figure S1).

NJ tree analysis showed that the Hokkaido Sea of Japan, Hokkaido Okhotsk, and Honshu Sea of Japan adult return rates were distinct, and the Hokkaido Nemuro, Hokkaido Pacific East and West, and Honshu Pacific return rates were similar (see supplementary information, Figure S2). As a result, we used four coastal areas in Japan in our regression models: (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 habitat

Decadal-scale maps of SST isoclines showed that until 2000, the summer and winter thermal habitat of chum salmon was stable (Figure 4). 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) (see supplementary information, Figures S3-S6). Around Japan, optimal 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 (see supplementary information, Figure S7). Optimal habitat in June shifted to northern Hokkaido.

### 3.3 | Japanese chum salmon migration route and SST

In Hokkaido Nemuro the mean SST at hatchery fry release in 1998-2019 increased, and trends were indiscernible in other management regions (see supplementary information, Figure S8). The summer and winter SSTs (mean ± standard deviation), used in our regression analysis (1998-2022) as common explanatory variables for all offshore (southern Sea of Okhotsk) and high seas regions (Figure 1b), were: southern Sea of Okhotsk July SST (12.7 ± 1.1°C), western North Pacific January-April SST (5.3 ± 0.5°C), central Bering Sea August-September SST (9.7 ± 0.8°C), and central Gulf of Alaska January-April SST (5.6 ± 0.8°C) (see supplementary information, Figure S9). An increasing trend in July SST after 2018 was notable in the southern Sea of Okhotsk but the trend was not significant due to large variability in the time series (1998-2022). Western North Pacific winter SST in January-April increased after 2016, but the trend was not significant. A strong increase in August-September SST was observed in the central Bering Sea after 2012, but SST decreased after 2015 with large interannual variability, and the increasing trend was not significant. In the central Gulf of Alaska, an increasing trend was observed in January-April SST, and the trend was not significant.

### 3.4 | Potential predators of juvenile chum salmon

The PCA biplot identified differences in commercial fishery catch levels (biomass of landed fish) as the primary component (PC1, 46% variance), and the second component (PC2, 18% variance) corresponded to catch trends before and after 1998 (Figure 5a). The PCA confirmed that changes in commercial catches of 30 marine species in Japan after 1998 were largely characterized by two highly piscivorous fish species that increased in recent decades, yellowtail and Japanese Spanish mackerel (*Scomberomorus niphonius*, Scombridae). There was a northward shift of yellowtail landings into the range of Japanese chum salmon (Figure 5b). 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

All models used explanatory variables with a VIF less than the threshold of 3.0. For Hokkaido Okhotsk, the best subset model was predator-competitor interactions. For Hokkaido and Honshu Pacific, the best model was the subset model of carryover effects and predator-competitor interactions. For Hokkaido Sea of Japan and Honshu Sea of Japan, the subset model of ocean conditions and predator-competitor interactions was selected as the best model.

The best models from the regression analysis are summarized in Table 2. For Hokkaido Okhotsk, the negative effect of yellowtail catch in the fry release year (*t*), and Russian pink salmon (adult, age 1) catch in years *t*+2 explained 58% of the variation in return rates. For Hokkaido and Honshu Pacific, the positive effect of fry size at release, the negative effect of relative fecundity (age 4 in year *t*-1), and the negative effect of Russian pink salmon catch in years *t*+2 and *t*+3 explained 79% of the variation in return rates; age 4 relative fecundity had a smaller AICc (30.0) than that of age 5 (38.2), and we identified the best model using age 4 relative fecundity. For Hokkaido Sea of Japan, 54% of variation in return rates was explained by the positive effect of winter SST (Feb-Apr) in the Gulf of Alaska (year *t*+3) and the negative effect of summer SST (July) in the Sea of Okhotsk (year *t*) and the Bering Sea (Aug-Sep) (year *t*+2); Russian chum salmon catches in years *t*+3 had a negative effect. For Honshu Sea of Japan, 57% of variation in return rates was explained by the positive effect of winter SST (Jan-Apr) in the western North Pacific in years *t*+1, and the negative effects of SST at release, summer SST (July) in the southern Sea of Okhotsk, and Russian pink salmon catch in year *t*+2. No evidence of competition between Japanese chum salmon and US and Canadian chum and pink salmon was found.

The standardized effects of explanatory variables on adult returns were positive for winter SST and size at release and negative for SST at release, summer SST, relative fecundity, yellowtail, and Russian chum and pink salmon abundance (Figure 6). The effect size for each regression coefficient, measured by $\exp(\hat{\beta}_i)$, represents the rate of change per practical unit in each coastal management area (see supplementary information, Figure S10). The effect of winter SST in the western North Pacific and Gulf of Alaska was positive in two management areas. A 1°C increase in winter SST in the Gulf of Alaska increased the return rate by 50% 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. In Honshu Sea of Japan, SST at release reduced the return rate by 38%. A 100-egg increase in the relative fecundity of parent females (age 4) reduced return rate by 61%, while size at release had a positive effect, with a 0.1 g increase in hatchery fry BW increasing the return rate by 63%

in Hokkaido and Honshu Pacific. Yellowtail had a negative effect on Hokkaido Okhotsk adult returns, and an increase in biomass of yellowtail landings of 100 tons predicted 19% reduction in the adult return rate of chum salmon. 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 management 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 regression models predicted trends in observed chum salmon adult return rates to all four management regions, and observed values were within the 95% prediction interval (Figure 7).

## 4 | DISCUSSION

### 4.1 Marine survival

Our regional estimates of marine survival (return rate) of chum salmon decreased from north (Hokkaido Okhotsk, 7%) to south (Honshu Sea of Japan, <1%) in Japan. A meta-analysis of published salmon survival estimates indicated average smolt-to-adult survival of wild or naturally-reared chum salmon populations was 1.4%, and was lower than other Pacific salmon species: 2.8% pink salmon, 3.1% Chinook salmon (*O. tshawytscha*), 10.4% coho salmon (*O. kisutch),* 13.0% steelhead (*O. mykiss*), and 13.1% sockeye salmon (*O. nerka*) (Quinn, 2018). Given their comparatively low natural marine survival rate, chum salmon may be more vulnerable to climate change effects than other salmon species.

Our regression model results indicated stressors related to marine survival Japanese chum salmon varied by coastal management region, salmon life stage, and seasonal high seas distribution area. Our survival estimates should be regarded as indices because little is known about freshwater mortality of Japanese hatchery chum salmon fry 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 30%-40% of 238 non-enhanced streams in Hokkaido (Miyakoshi et al., 2012), and in 90% of 47 hatchery-enhanced streams and 75% of

47 non-enhanced streams along the northern Honshu Sea coast of Japan (Iida et al., 2018; Iida et al., 2021). Hatchery fish are stocked in most large rivers, while naturally spawning chum salmon populations persist in many small (short) rivers in Hokkaido (Miyakoshi et al., 2013; Kitada, 2014). Escapement of hatchery chum salmon returns to natural spawning grounds is infrequent in Hokkaido. In Honshu Sea of Japan, salmon are collected in approximately half of the broodstock streams by small nets or hooks to avoid interfering with the upstream migration of chum salmon (Iida et al., 2018). Relative reproductive success of hatchery-reared salmon is approximately 50% of that of wild-origin naturally spawning fish (Shedd et al., 2022), with considerable variation (Kitada et al., 2011). We expected low survival from egg to size at ocean entry of wild fish in natural streams in Japan. The magnitude of recruitment from natural reproduction may be insubstantial relative to the number of juveniles released (1-1.5 billion juveniles nationwide). Our regression analysis overestimates the intercept proportional to the magnitude of natural recruitment, but regression coefficients are expected to be robust.

### 4.2 Hatchery carryovers

Our regression model coefficients (effect size) indicated that a 0.1 g increase in hatchery chum salmon fry body weight at release increased marine survival by 63% in the Hokkaido and Honshu Pacific regions. After release, Pacific region juveniles chum migrate long distances northward to their summer feeding area in the Sea of Okhotsk. On the Sanriku Coast, Honshu Pacific region, 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). Our model effect size for fry body weight at release (positive) and parental relative fecundity (negative) suggested that quality of juvenile hatchery fish at release is particularly important for survival at later ocean stages for Honshu Pacific region chum salmon. Relative fecundity was negatively correlated with egg size except in the Hokkaido Sea of Japan region, suggesting that larger eggs (lower relative fecundity) result in better survival (Einum et al., 2002). Over the past 25 years, egg size of 4-year-old chum salmon declined (see supplementary information, Figure S11); adult body size of 4-year-old chum salmon was relatively stable (see supplementary information, Figure S12). Our result is consistent with the hypothesis that unintentional selection in captivity may lead to change in important life-history traits such as egg size and may reduce the success of hatchery release programs (Heath et al., 2003).

In Japanese hatcheries, fertilized eggs are generally kept in incubators for about 2 months until hatching in a very dark environment with calm water flow. The daily oxygen consumption was correlated with sunrise and day length (Maxime et al., 1989). The blind, cave-dwelling form of

the Mexican tetra (*Astyanax mexicanus*, Characidae), which lives in complete darkness, consumes far less oxygen than the surface morph, and uses ~27% less energy per day (reviewed by Boggs & Gross, 2021). The evidence suggests that the egg incubation environment may reduce oxygen consumption in hatchery chum salmon. Total oxygen consumption is higher for larger eggs (Rollinson & Hutchings, 2011), and it is more difficult for large eggs to get the oxygen they need to meet their metabolic needs (Einum et al., 2002). The evidence suggests that the hatchery rearing environment may contribute to the decline in egg size found in our analysis.

### 4.3 Predator-competitor interactions

There are many known salmonid, fish, bird, and marine mammal predators of Japanese chum salmon（Okado & Hasegawa, 2024). We focused on identifying potential new marine fish predators of juvenile chum salmon to use as indicators of climate-driven changes in predator interactions. Young yellowtail and mahi-mahi (*Coryphaena hipposesus*, Coryphaenidae) were found in chum salmon landings in the Sea of Okhotsk in September 2012. Since 2014, yellowtail have been caught along the coast of the Sea of Okhotsk in May-June (Hoshino & Fujioka, 2021). In May 2023, schools of yellowtail were often observed on the sea surface near the central Sea of Okhotsk coast (pers. comm., Takashi Ichikawa). May-June coincides with the release period of Japanese chum salmon, suggesting that yellowtail are juvenile chum salmon predators. Our analysis of predator interactions was too limited in scope to identify potential indices of climate-driven predator interactions in high seas areas of chum salmon distribution. The use of commercial marine fishery stock assessment data is a promising approach for developing new indices of climate-driven predator interactions, especially if predator diet information is available.

Competitive interactions between Russian pink salmon and chum salmon, as well as many other species, are increasingly evident (Ruggerone et al., 2023). Pink salmon spend only one winter in the ocean before maturing fish return to spawning streams in spring and summer. Pink salmon adult returns in odd- and even-numbered years never intermix on the spawning grounds, and the populations are genetically distinct. The Karaginsky region of northeastern Kamchatka in the Russian Far East borders the southwestern Bering Sea and is host to world's largest natural-spawning population of pink salmon. Maturing Karaginsky region pink salmon return to the Bering Sea in June from spring feeding areas in the North Pacific Ocean, and the returns in odd-numbered years usually dominate the two-year abundance cycle. Many researchers have used this odd-year dominance cycle as a "natural experiment" to detect competitive interactions between Russian pink salmon and other species (Ruggerone et al., 2023).

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 meta-analysis of salmon trophic ecology showed that chum, pink, and sockeye salmon have similar diet composition throughout the North Pacific, with diet overlap of 31.8% between chum and pink and 30.9% between chum and sockeye. Diet overlap was highest between pink and sockeye salmon at 46.6% (Graham et al., 2021). Our regression model indicated survival of immature (age 1) Japanese chum salmon during 1998-2019 was not related to abundance of Russian pink salmon but was related (negative) to survival of older (ages 2-3) chum salmon. Thus, despite the odd-year dominance cycle of Karaginsky Bay pink salmon, maturing Russian pink salmon appear to compete with Japanese chum salmon in both even-and odd-numbered years. 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) in winter the Gulf of Alaska (Urawa et al., 2016).

**4.4 Ocean conditions**

Since 2010, high seas thermal habitat of Japanese chum salmon in summer shifted northward and contracted; winter habitat remained relatively stable (Figure 4). The frequency of annual marine heatwaves in the western and central Bering Sea increased, lasted longer, and were even more intense in the eastern Bering Sea (Carvalho et al., 2021). Reduced growth was associated with warm summer SST in Alaskan Chinook salmon and sockeye salmon (Yasumiishi et al., 2020; Ohlberger et al., 2023). Improved growth and younger age at maturity were associated with warm winter SST in Alaskan sockeye salmon (Ohlberger et al., 2023). Increases in winter SST were observed in the western North Pacific and Gulf of Alaska since about 2010 (see supplementary information, Figure S9b), and may have resulted in improved growth and younger age at maturity of Japanese chum salmon.

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). Survival of juveniles released from Sea of Japan hatcheries in Honshu was related to SST at time of release (negative), during their first summer in the Sea of Okhotsk (negative), and their first winter in the western North Pacific (positive). In contrast, marine survival of northern (Hokkaido) Sea of Japan releases was related to SST (negative) during their first summer in the Sea of Okhotsk. The pattern of relationships between Sea of Japan chum salmon survival and SST at different life stages suggests carryover effects

from SSTs at hatchery release. There was no relationship between survival and SST at any marine life stage for Hokkaido Okhotsk and Hokkaido and Honshu Pacific hatchery releases.

The SST indices used in our regression model represent 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. We consider this a reasonable assumption because migratory behavior in salmon is inherited (Putman, 2015; Thompson et al., 2020). Ranges of chum salmon thermal habitat used in our analysis were narrower (thermal limits, 4.0-13°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 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).

**4.5 Age at maturity**

Younger maturing salmon grow faster than older maturing salmon (Ricker, 1981). The peak in adult returns of Japanese chum salmon observed in 2022 in the Hokkaido Sea of Japan and Okhotsk was driven by an increase in 4-year-old fish released in 2019. We observed a trend towards younger age at maturity in all hatchery management regions in Japan (see supplementary information, Figure S1).

Coastal thermal habitat (4-13°C) available to Japanese chum salmon shifts northward in spring and early summer, especially in the Sea of Japan (see supplementary information, Figure S7), and juveniles (age 0) must arrive by late June or early July in the southern Sea of Okhotsk, where they spend their first summer growth season. In July 2019, optimal thermal habitat (<10°C) was widely distributed in the Sea of Okhotsk (see supplementary information, Figure S13), and in September 2020 in the central Bering Sea, where they spend their second summer growing season (age 1). Expansion of optimal habitat in the first and second summers likely improved growth and survival of immature chum salmon in 2020 and 2021, resulting in the peak of adult returns in 2022. This suggests that SSTs warmer than 10°C in summer negatively affect growth of chum salmon.

Decrease in age at maturity in Japanese hatchery chum salmon may be related to hatchery practices. For example, steelhead grow significantly faster in hatcheries than in the wild (Blouin et al., 2021). Growth of Japanese hatchery chum fry is accelerated by feeding them formulated

diets before release. Growth hormone in some of these diets may have a significant effect on age at maturation. For example, juvenile Atlantic salmon (*Salmo salar*; Salmonidae) have a size threshold for greater sensitivity of growth hormone and cortisol axes to changes in the environment, and these hormones affect survival, ion homeostasis, growth, and swimming performance at ocean entry (McCormick, 2009).

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). The geographic distribution of growth hormone (GHII3129), gonadotropin-releasing hormone (GnRH373), and the combined mtDNA3 single-nucleotide polymorphism (SNP) allele frequencies of chum salmon (Seeb et al., 2011) showed significant deviations of Japanese chum from the geographic pattern (Kitada & Kishino, 2021, see supplementary information, Figure S14). Unintentional and intentional selection in hatchery rearing may alter these gene frequencies above Pacific Rim levels, possibly resulting in slower swimming speeds (Hasegawa et al., 2021a) and younger age at maturity. These interpretations are consistent with domestication selection in hatcheries (Araki et al., 2008). The mechanisms of genetic selection in hatcheries and their effects on fitness remain largely unknown and are one of the most important topics for future study.

We conclude that anthropogenic climate change is driving unprecedented changes in salmonid ecosystems and salmon survival across the North Pacific Ocean and marginal seas. We used long-term data series collected from world's largest hatchery salmon program to investigate potential climate-change stressors and indicators related to 25-year decline in marine survival of Japanese chum salmon (1998-2023). We found that stressors and indicators related to declines in coastal and high seas survival differed by coastal management region in Japan. Our results highlight the importance of hatchery carryovers (parental relative fecundity, fry size at release) on salmon survival in the Pacific region of Japan, where the decline in abundance was most severe during the period of our study. Our results suggest that larger eggs (lower relative fecundity) provide better growth and survival of juveniles migrating long distances against the Oyashio current. Over the past 25 years, Japanese chum salmon egg size declined and adult body size was stable, consistent with the hypothesis that unintentional selection in captivity may change important life-history traits that reduce the success of hatchery programs. A temporary increase in salmon adult returns to Japan in 2022, was driven by a shift toward younger age at maturity in all management regions, especially after 2010, and is consistent with shifts observed in North American salmon populations. Our results provide local and context-specific indicators of marine survival of salmon and insights for future use in regional adaptive management planning, hatchery and fishery management, and

research.

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**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 are available at https://doi.org/10.5281/zenodo.12741306.

**REFERENCES**

Akaike, H. (1973). Information theory as an extension of the maximum likelihood principle. In B. N. Petrov & F. Csaki (Eds.), *Second international symposium on information theory* (pp. 267–281). Budapest: Akademiai Kiado.

Amoroso, R. O., Tillotson, M. D., & Hilborn, R. (2017). Measuring the net biological impact of fisheries enhancement: Pink salmon hatcheries can increase yield, but with apparent costs to wild populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 74, 1233–1242. https://doi.org/10.1139/cjfas-2016-0334

APG (Aomori Prefectural Government) (2023). Chum salmon catch statistics, Aomori Prefectural Government, Aomori. https://www.pref.aomori.lg.jp/soshiki/nourin/sshinko/sake.html (accessed 8 August 2023).

Araki, H., Berejikian, B. A., Ford, M. J., & Blouin, M. S. (2008). Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications*, 1, 342–355. https://doi.org/10.1111/j.1752-4571.2008.00026.x

Beacham, T. D., Sato, S., Urawa, S., Le, K. D., & Wetklo, M. (2008). Population structure and stock identification of chum salmon *Oncorhynchus keta* from Japan determined by microsatellite DNA variation. *Fisheries Science*, 74, 983–994. https://doi.org/10.1111/j.1444-2906.2008.01616.x

Beamish, R. J., editor (2018), *The Ocean Ecology of Pacific Salmon and Trout*. Bethesda,

Maryland: American Fisheries Society. https://doi.org/10.47886/9781934874455

Beamish, R. J., & Mahnken, C. (2001). A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography*, 49, 423–437. https://doi.org/10.1016/S0079-6611(01)00034-9

Beauchamp, D. (2009). Bioenergetic ontogeny: linking climate and mass specific feeding to life-cycle growth and survival of salmon. *In* C. Krueger & C. E. Zimmerman (Eds.), *Pacific salmon: ecology and management of western Alaska's populations* (Symposium 70, pp. 53–72). American Fisheries Society. https://doi.org/10.47886/9781934874110

Blouin, M. S., Wrey, M. C., Bollmann, S. R., Skaar, J. C., Twibell, R. G., & Fuentes, C. (2021). Offspring of first-generation hatchery steelhead trout (*Oncorhynchus mykiss*) grow faster in the hatchery than offspring of wild fish, but survive worse in the wild: Possible mechanisms for inadvertent domestication and fitness loss in hatchery salmon. *Plos One*, 16, e0257407. https://doi.org/10.1371/journal.pone.0257407

Boggs, T., & Gross, J. (2021). Reduced oxygen as an environmental pressure in the evolution of the blind Mexican cavefish. *Diversity*, 13, 26. https://doi.org /10.3390/d13010026

Cade, B. S. (2015). Model averaging and muddled multimodel inferences. *Ecology*, 96, 2370–2382. https://doi.org/10.1890/14-1639.1

Carvalho, K. S., Smith, T. E., & Wang, S. (2021). Bering Sea marine heatwaves: Patterns, trends and connections with the Arctic. *Journal of Hydrology*, 600, 126462. https://doi.org/10.1016/j.jhydrol.2021.126462.

Cheung, W. W., & Frölicher, T. L. (2020). Marine heatwaves exacerbate climate change impacts for fisheries in the northeast Pacific. *Scientific Reports*, 10, 6678. https://doi.org/10.1038/s41598-020-63650-z

Cheung, W. W., Frölicher, T. L., Lam, V. W., Oyinlola, M. A., Reygondeau, G., Sumaila, U. R., ... & Wabnitz, C. C. (2021). Marine high temperature extremes amplify the impacts of climate change on fish and fisheries. *Science Advances*, 7, eabh0895. https://doi.org/10.1126/sciadv.abh0895

Cline, T. J., Ohlberger, J., & Schindler, D. E. (2019). Effects of warming climate and competition in the ocean for life-histories of Pacific salmon. *Nature Ecology & Evolution*, 3, 935–942. https://doi.org/10.1038/s41559-019-0901-7

Crozier, L. G., & Siegel, J. E. A. (2023). Comprehensive review of the impacts of climate change on salmon: strengths and weaknesses of the literature by life stage. *Fishes*, 8, 1–50. https://doi.org/10.3390/fishes8060319

Einum, S., Hendry, A. P., & Fleming, I. A. (2002). Egg-size evolution in aquatic environments: does oxygen availability constrain size?. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269, 2325–2330.

https://doi.org/10.1098/rspb.2002.2150

FAO (2022). The state of world fisheries and aquaculture. *Towards blue transformation*. United Nations Food and Agriculture Organization, Rome, FAO. https://digitallibrary.un.org/record/3978694?v=pdf (accessed 5 July 2024).

FRA (Japan Fisheries Research and Education Agency) (2023a). Chum salmon catch and release statistics, Japan Fisheries Research and Education Agency, Yokohama. https://www.fra.go.jp/shigen/salmon/index.html (accessed 5 March 2024).

FRA (Japan Fisheries Research and Education Agency) (2023b). Salmon Data Base, Japan Fisheries Research and Education Agency, Yokohama. https://www.fra.go.jp/shigen/salmon/sdb.html (accessed 9 December 2023).

Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., & Jensen, O. P. (2019). Impacts of historical warming on marine fisheries production. *Science*, 363, 979–983. https://doi.org/10.1126/science.aau175

Graham, C., Pakhomov, E. A., & Hunt, B. P. (2021). Meta-analysis of salmon trophic ecology reveals spatial and interspecies dynamics across the North Pacific Ocean. *Frontiers in Marine Science*, 8, 618884. https://doi.org/10.3389/fmars.2021.618884

Hasegawa, K., Honda, K., Yoshiyama, T., Suzuki, K., & Fukui, S. (2021a). Small biased body size of salmon fry preyed upon by piscivorous fish in riverine and marine habitats. *Canadian Journal of Fisheries and Aquatic Sciences*, 78(5), 631–638. https://doi.org/10.1139/cjfas-2020-0339

Hasegawa, K., Okamoto, Y., & Morita, K. (2021b). Temporal trends in geographic clines of chum salmon reproductive traits associated with global warming and hatchery programmes. *Ecological Solutions and Evidence*, 2(4), e12107. https://doi.org/10.1002/2688-8319.12107

Hayashi, M., Shiogama, H., & Ogura, T. (2022). The contribution of climate change to increasing extreme ocean warming around Japan. *Geophysical Research Letters*, 49, e2022GL100785. https://doi.org/10.1002/grl.62465

Heath, D. D., Heath, J. W., Bryden, C. A., Johnson, R. M., & Fox, C. W. (2003). Rapid evolution of egg size in captive salmon. *Science*, 299, 1738–1740. https://doi.org/10.1126/science.1079707

Hilborn, R., Quinn, T. P., Schindler, D. E., & Rogers, D. E. (2003). Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences*, 100, 6564–6568. https://doi.org/10.1073/pnas.1037274100

Honda, K., Kawakami, T., Suzuki, K., Watanabe, K., & Saito, T. (2017). Growth rate characteristics of juvenile chum salmon *Oncorhynchus keta* originating from the Pacific coast of Japan and reaching Konbumori, eastern Hokkaido. *Fisheries Science*, 83, 987–996. https://doi.org/10.1007/s12562-017-1137-6

Honda, K., Sato, T., Kuroda, H., & Saito, T. (2021). Initial growth characteristics of poor-return stocks of chum salmon *Oncorhynchus keta* originating from the Okhotsk and Nemuro regions in Hokkaido on the basis of scale analysis. *Fisheries Science*, 87, 653–663. https://doi.org/10.1007/s12562-021-01538-1

Hoshino, N., & Fujioka, T. (2021). Characteristics of yellowtail catch in Hokkaido, Japan in the 2010s. *Scientific Report of Hokkaido Fisheries Research Institute*, 100, 71–82. (in Japanese)

HSEA (Hokkaido Salmon Enhancement Association) (2023). Chum salmon catch and release statistics, Hokkaido Salmon Enhancement Association, Sapporo. http://www.sake-masu.or.jp/ (accessed 21 July 2023).

Iida, M., Yoshino, K., & Katayama, S. (2018). Current status of natural spawning of chum salmon *Oncorhynchus keta* in rivers with or without hatchery stocking on the Japan Sea side of northern Honshu, Japan. *Fisheries science*, 84, 453–459. https://doi.org/10.1007/s12562-018-1192-7

Iida, M., Yagi, Y., & Iseki, T. (2021). Occurrence of wild chum salmon fry in the surf zone, and spawning and emergence timing in the adjacent nonstocked river in Niigata Prefecture, Japan. *Fisheries Science*, 87, 549–557. https://doi.org/10.1007/s12562-021-01535-4

Iino, Y., Kitagawa, T., Abe, T. K., Nagasaka, T., Shimizu, Y., Ota, K., ... & Kawamura, T. (2022). Effect of food amount and temperature on growth rate and aerobic scope of juvenile chum salmon. *Fisheries Science*, 8, 397–409. https://doi.org/10.1007/s12562-022-01599-w

IPCC (Intergovernmental Panel on Climate Change) (2022). *Global Warming of 1.5°C.* IPCC special report on impacts of global warming of 1.5°C above pre-industrial levels in context of strengthening response to climate change, sustainable development, and efforts to eradicate poverty. Cambridge University Press. https://www.ipcc.ch/sr15/ (accessed 5 July 2024).

JMA (Japan Meteorological Agency) (2022). Coastal sea surface temperature information, Japan Meteorological Agency, Tokyo. https://www.jma-net.go.jp/ (accessed 23 August 2022).

Kaeriyama, M. (2022). Warming climate impacts on production dynamics of southern populations of Pacific salmon in the North Pacific Ocean. *Fisheries Oceanography*, 32, 121–132. https://doi.org/10.1111/fog.12598

Kaeriyama, M., Seo, H., Kudo, H., & Nagata, M. (2012). Perspectives on wild and hatchery salmon interactions at sea, potential climate effects on Japanese chum salmon, and the need for sustainable salmon fishery management reform in Japan. *Environmental Biology of Fishes*, 94, 165–177. https://doi.org/10.1007/s10641-011-9930-z

Kitada, S. (2014). Japanese chum salmon stock enhancement: current perspective and future challenges. *Fisheries Science*, 80, 237–249. https://doi.org/10.1007/s12562-013-0692-8

Kitada, S. (2018). Economic, ecological and genetic impacts of marine stock enhancement and sea ranching: A systematic review. *Fish and Fisheries*, 19, 511–532. https://doi.org/10.1111/faf.12271

Kitada, S., & Kishino, H. (2021). Population structure of chum salmon and selection on the markers collected for stock identification. *Ecology and Evolution*, 11, 13972–13985. https://doi.org/10.1002/ece3.8102

Kitada, S., Kishino, H., & Hamasaki, K. (2011). Bias and significance of relative reproductive success estimates based on steelhead trout (*Oncorhynchus mykiss*) data: a Bayesian meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 1827–1835. https://doi.org/10.1139/f2011-087

Kuroda, H., Saito, T., Kaga, T., Takasuka, A., Kamimura, Y., Furuichi, S., & Nakanowatari, T. (2020). Unconventional sea surface temperature regime around Japan in the 2000s-2010s: Potential influences on major fisheries resources, *Frontiers in Marine Science*, 7, 574904. https://doi.org/10.3389/fmars.2020.574904

Langan, J. A., Cunningham, C. J., Watson, J. T., & McKinnell, S. (2024). Opening the black box: New insights into the role of temperature in the marine distributions of Pacific salmon. *Fish and Fisheries*. https://doi.org/10.1111/faf.12825

Max Planck Institute (2023). Climate Data Operators, Max Planck Institute für Meteorologie, Hamburg. https://code.mpimet.mpg.de/projects/cdo (accessed 14 June 2023).

MAFF (2023). Annual statistics of fisheries and aquaculture production, Ministry of Agriculture, Forestry and Fisheries, Tokyo. https://www.jfa.maff.go.jp/j/kikaku/toukei/ (accessed 11 January 2023).

Maxime, V., Boeuf, G., Pennec, J. P., & Peyraud, C. (1989). Comparative study of the energetic metabolism of Atlantic salmon (*Salmo salar*) parr and smolts. *Aquaculture*, 82(1–4), 163–171. https://doi.org /10.1016/0044-8486(89)90405-5

McCormick, S. D. (2009). Evolution of the hormonal control of animal performance: insights from the seaward migration of salmon. *Integrative and Comparative Biology*, 49, 408–422. https://doi.org/10.1093/icb/icp044

Miyakoshi, Y., Urabe, H., Saneyoshi, H., Aoyama, T., Sakamoto, H., Ando et al. (2012). The occurrence and run timing of naturally spawning chum salmon in northern Japan. *Environmental Biology of Fishes*, 94, 197–206. https://doi.org/10.1007/s10641-011-9872-5

Miyakoshi, Y., Nagata, M., Kitada, S., & Kaeriyama, M. (2013). Historical and current hatchery programs and management of chum salmon in Hokkaido, northern Japan. *Reviews in Fisheries Science*, 21, 469–479.

https://doi.org/10.1080/10641262.2013.836446

Myers, K. W., Klovach, N. V., Gritsenko, O. F., Urawa, S., & Royer, T. C. (2007). Stock-specific distributions of Asian and North American salmon in the open ocean, interannual changes, and oceanographic conditions. *North Pacific Anadromous Fish Commission Bulletin*, 4, 159–177. https://www.npafc.org/wp-content/uploads/Bulletins/Bulletin-4/159-177Myers.pdf (accessed 5 July 2024).

Nagata, M., Miyakoshi, Y., Ando, D., Fujiwara, M., Sawada, M., Shimada, H., & Asami, H. (2007). Influence of coastal seawater temperature on the distribution and growth of juvenile chum salmon, with recommendations for altered release strategies. *North Pacific Anadromous Fish Commission Bulletin*, 4, 223–235. https://www.npafc.org/wp-content/uploads/Bulletins/Bulletin-4/223-235Nagatachum.pdf (accessed 5 July 2024).

Nagata, M., Miyakoshi, Y., Fujiwara, M., Kasugai, K., Ando, D., Torao, M., ... & Irvine, J. R. (2016). Adapting Hokkaido hatchery strategies to regional ocean conditions can improve chum salmon survival and reduce variability. *North Pacific Anadromous Fish Commission Bulletin*, 6, 73-85. https://doi.org/10.23849/npafcb6/73.85

Naish, K. A., Taylor III, J. E., Levin, P. S., Quinn, T. P., Winton, J. R., Huppert, D., & Hilborn, R. (2007). An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. *Advances in Marine Biology*, 53, 61–194. https://doi.org/10.1016/S0065-2881(07)53002-6

NOAA (NOAA Physical Sciences Laboratory) (2023a). NOAA Optimum Interpolation SST V2 high-resolution dataset (OISST V2), National Oceanic and Atmospheric Administration, Silver Spring. https://downloads.psl.noaa.gov/Datasets/noaa.oisst.v2/ (accessed 14 June 2023).

NOAA (NOAA Physical Sciences Laboratory) (2023b). Plot: COBE Sea Surface Temperature, National Oceanic and Atmospheric Administration, Silver Spring. https://psl.noaa.gov/mddb2/makePlot.html?variableID=1570 (accessed 18 March 2024).

NPAFC (North Pacific Anadromous Fish Commission) (2023). NPAFC Pacific salmonid catch statistics (24 July 2023), North Pacific Anadromous Fish Commission, Vancouver. https: //npafc.org (accessed 7 August 2023).

Ohlberger, J., Ward, E. J., Brenner, R. E., Hunsicker, M. E., Haught, S. B., Finnoff, D. et al. (2022). Non-stationary and interactive effects of climate and competition on pink salmon productivity. *Global Change Biology*, 28, 2026–2040. https://doi.org/10.1111/gcb.16049

Ohlberger, J., Cline, T. J., Schindler, D. E., & Lewis, B. (2023). Declines in body size of sockeye salmon associated with increased competition in the ocean. *Proceedings of the Royal Society B*, 290, 20222248. https://doi.org/10.1098/rspb.2022.2248

Okado, J., & Hasegawa, K. (2024). Exploring predators of Pacific salmon throughout their life history: the case of Japanese chum, pink, and masu salmon. *Reviews in Fish Biology and Fisheries*, 1–23. https://doi.org/10.1007/s11160-024-09858-y

Oke, K. B., Cunningham, C. J., Westley, P. A. H., Baskett, M. L., Carlson, S. M., Clark et al. (2020). Recent declines in salmon body size impact ecosystems and fisheries. *Nature Communications*, 11, 4155. https://doi.org/10.1038/s41467-020-17726-z

Putman, N. F, (2015). Inherited magnetic maps in salmon and the role of geomagnetic change, *Integrative and Comparative Biology*, 55, I396–405, https://doi.org/10.1093/icb/icv020

Quinn, T. P. (2018). *The behavior and ecology of Pacific salmon and trout, 2nd edition*. University of Washington Press, Seattle.

R Core Team (2024). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Ricker, W. E. (1976) Review of the rate of growth and mortality of Pacific Salmon in salt water, and noncatch mortality caused by fishing. *Journal of the Fisheries Board of Canada*, 33. https://doi.org/10.1139/f76-191

Ricker, W. E. (1981). Changes in the average size and average age of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 38, 1636–1656. https://doi.org/10.1139/f81-213

Rollinson, N., & Hutchings, J. A. (2011). Why does egg size of salmonids increase with the mean size of population spawning gravels?. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 1307–1315. https://doi.org/10.1139/f2011-069

Ruggerone, G. T., Springer, A. M., van Vliet, G. B., Connors, B., Irvine, J. R., Shaul, L. D., ... & Atlas, W. I. (2023). From diatoms to killer whales: impacts of pink salmon on North Pacific ecosystems. *Marine Ecology Progress Series*, 719, 1–40. https://doi.org/10.3354/meps14402

Saito, T., & Nagasawa, K. (2009). Regional synchrony in return rates of chum salmon (*Oncorhynchus keta*) in Japan in relation to coastal temperature and size at release. *Fisheries Research*, 95, 14–27. https://doi.org/10.1016/j.fishres.2008.07.004

Schoen, E. R., Wipfli, M. S., Trammell, E. J., Rinella, D. J., Floyd, A. L., Grunblatt, J., ... & Witmer, F. D. (2017). Future of Pacific salmon in the face of environmental change: Lessons from one of the world's remaining productive salmon regions. *Fisheries*, 42, 538–553. https://doi.org/10.1080/03632415.2017.1374251

Seeb, L. W., Templin, W. D., Sato, S., Abe, S., Warheit, K., Park, J. Y., & Seeb, J. E. (2011). Single nucleotide polymorphisms across a species' range: Implications for conservation studies of Pacific salmon. *Molecular Ecology Resources*, 11(Suppl. 1), 195–217. https://doi.org/10.1111/j.1755-0998.2010.02966.x

Shedd, K. R., Lescak, E. A., Habicht, C., Knudsen, E. E., Dann, T. H., Hoyt, H. A., … & Templin, W. D. (2022). Reduced relative fitness in hatchery-origin pink salmon in two streams in Prince William Sound, Alaska. *Evolutionary Applications*, 15, 429–446. https://doi.org/10.1111/eva.13356

Sugiura, N. (1978). Further analysis of the data by Akaike's information criterion and the finite corrections. *Communications in Statistics, Theory and Methods*, A7, 13–26._ https://doi.org/10.1080/03610927808827599

Thompson, N. F., Anderson, E.C., Clemento, A. J., M. A. Campbell, & Garza, J. C. (2020). Complex phenotype in salmon controlled by a simple change in migratory timing. *Science* 370, 609-613. https://doi.org/10.1126/science.aba9059

Urawa, S., Beacham, T., Sato, S., Kaga, T., Agler, B. A., Josephson, R., & Fukuwaka, M. A. (2016). Stock-specific abundance of chum salmon in the central Gulf of Alaska during winter. *North Pacific Anadromous Fish Commission Bulletin*, 6, 153–160. https://doi.org/10.23849/npafcb6/153.160.

Urawa, S., & Bugaev, A. V. (2021). Survival of Japanese chum salmon during early ocean life in 2011–2017. *North Pacific Anadromous Fish Commission Technical Report*, 17, 60–62. https://doi.org/10.23849/npafctr17

Urawa, S., Beacham, T. D., Fukuwaka, M., & Kaeriyama, M. (2018). Ocean ecology of chum salmon. In R. J. Beamish (Ed.), *The Ocean Ecology of Pacific Salmon and Trout* (pp. 161–317). Bethesda, Maryland: American Fisheries Society. https://doi.org/10.47886/9781934874455.ch3

Urawa, S., Beacham, T., Sutherland, B., & Sato, S. (2022). Winter distribution of chum salmon in the Gulf of Alaska: a review. *North Pacific Anadromous Fish Commission Technical Report*, 18, 83–87. https://doi.org/10.23849/npafctr18

Wilkinson, L. (1999). Statistical methods in psychology journals: Guidelines and explanations. *American Psychologist*, 54, 594. https://psycnet.apa.org/doi/10.1037/0003-066X.54.8.594

Yasumiishi, E. M., Farley Jr, E. V., Maselko, J., Aydin, K. Y., Kearney, K. A., Hermann, A. J., ... and Strasburger, W. W. (2020). Differential north–south response of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) marine growth to ecosystem change in the eastern Bering Sea, 1974–2010. *ICES Journal of Marine Science*, 77, 216–229. https://doi.org/10.1093/icesjms/fsz166

Zuur, A. F., Ieno, E. N., and Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

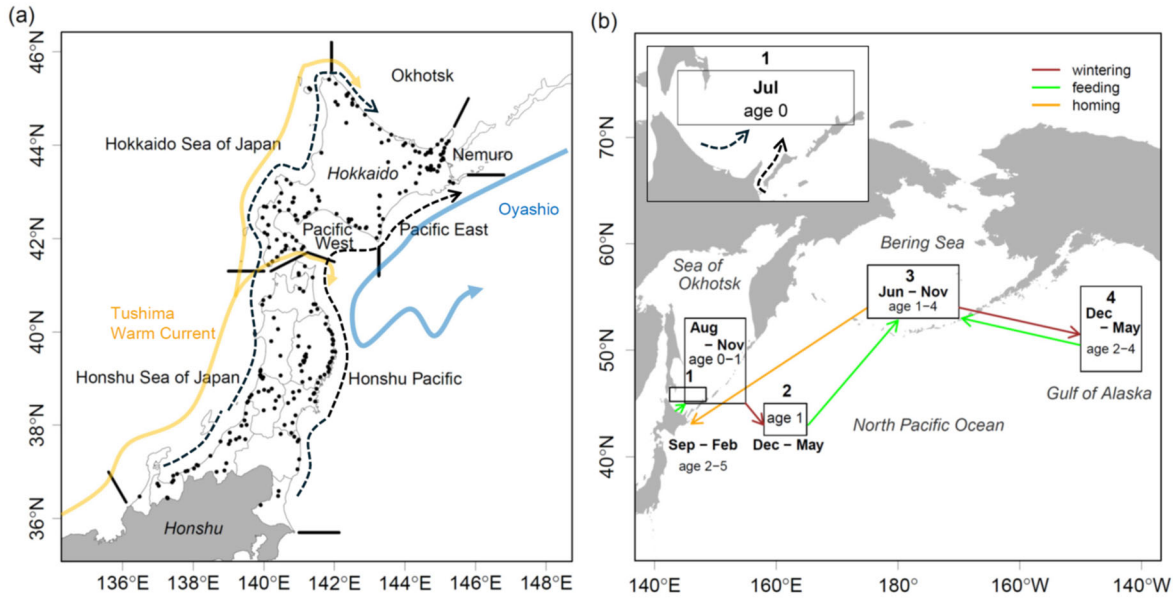


**FIGURE 1 Japanese chum salmon management regions, coastal migration routes, and high seas distribution areas.** (a) Seven management regions (delineated by black bars) and hatcheries (black dots) in Japan. Migration paths of hatchery-released juveniles (age 0, dashed lines) were modified from Saito 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).

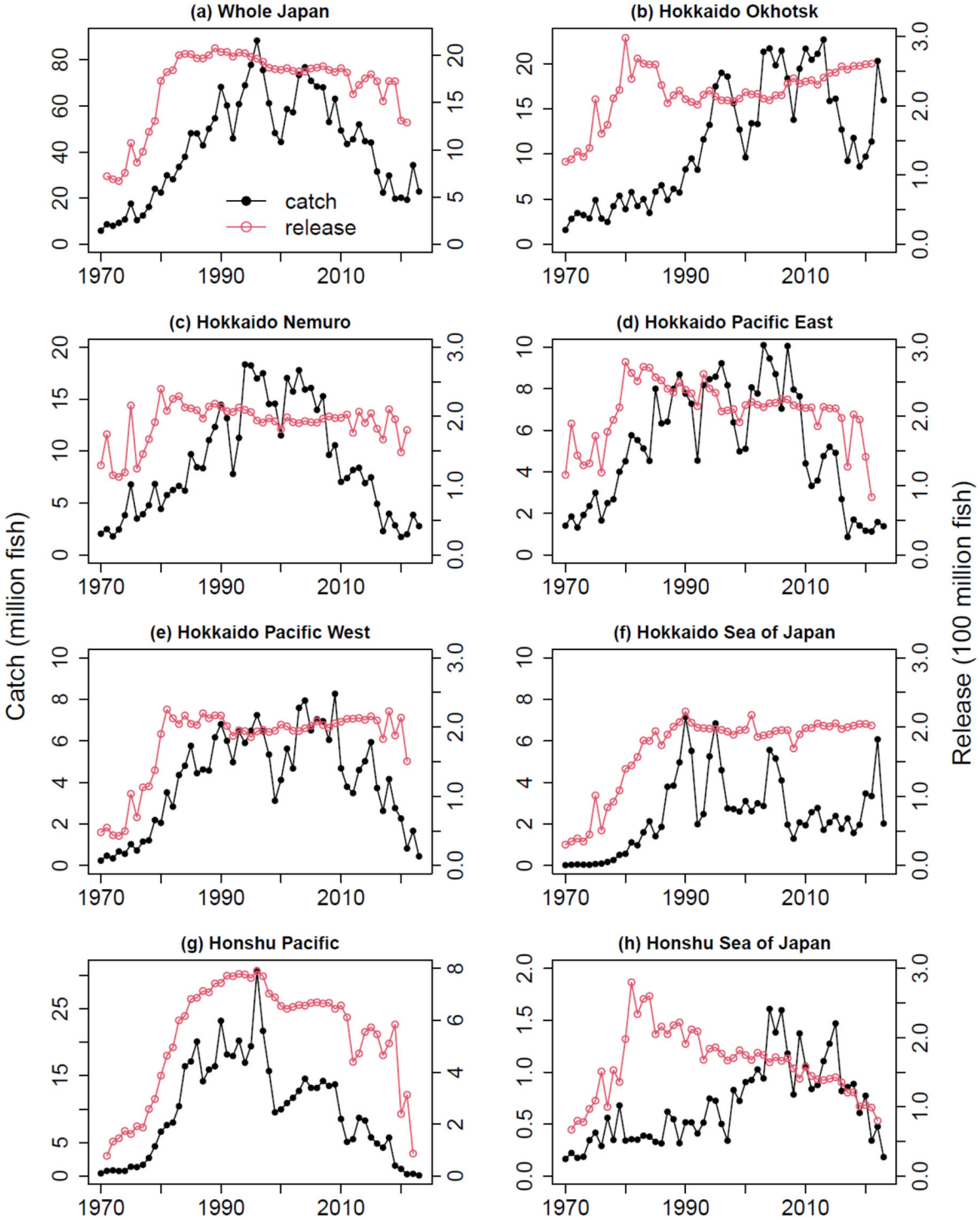


**FIGURE 2 Number of chum salmon released (red line) and returned (coastal catch plus hatchery broodstock catch; black line) in seven management regions in Japan (1970-2023).**

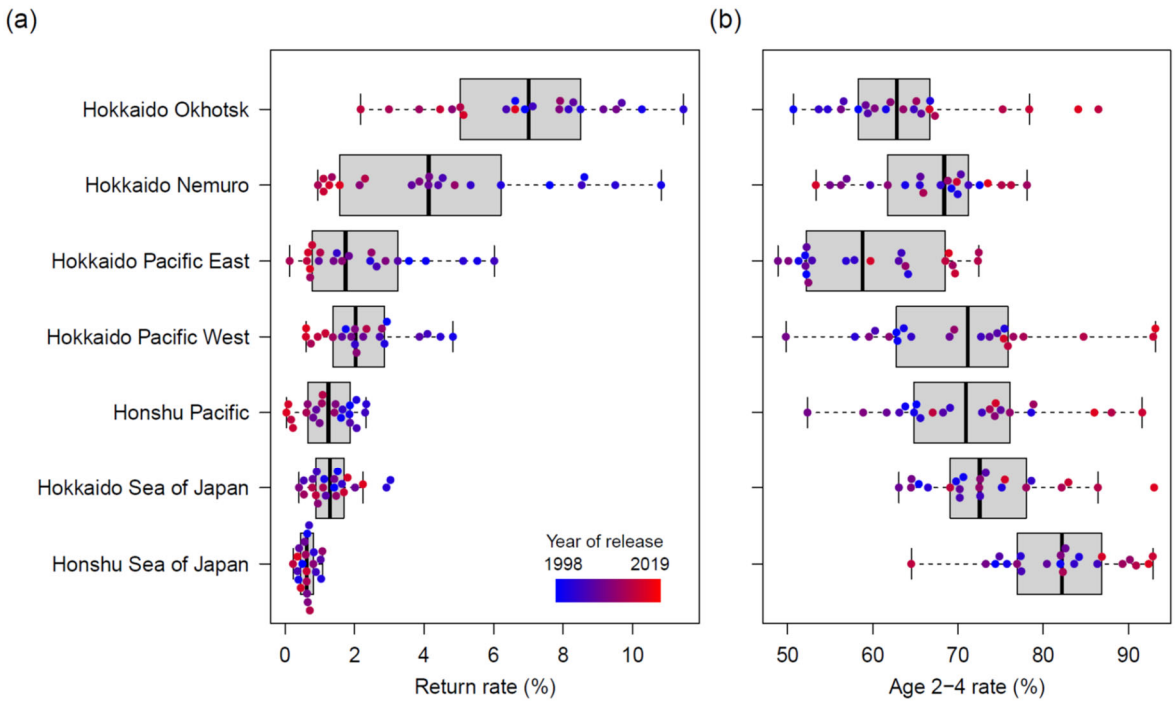


**FIGURE3 Chum salmon marine survival (adult return rate) and age at maturity (younger, age 2 - 4) vary by management region in Japan.** (a) Adult return rates calculated for age 2 - 5 returns to seven management regions in Japan fry (age 0) releases in 1998-2019. (b) Percentages of age 2 - 4 fish in the total number of adult returns from 1998-2019 hatchery releases. Return rates of younger (age 2 – 4) fish increased significantly in all regions except Hokkaido Nemuro: Hokkaido Okhotsk ($\tau$=0.58, $p$=0.000), Hokkaido Pacific East ($\tau$=0.36, $p$=0.021) and Hokkaido Pacific West ($\tau$=0.46, $p$=0. 003), Hokkaido Sea of Japan ($\tau$=0.33, $p$=0.037), Honshu Pacific ($\tau$=0.36, $p$=0.021), and Honshu Sea of Japan ($\tau$=0.34, $p$=0.028), and Hokkaido Nemuro ($\tau$=0.03, $p$=0.866). Continuous color gradient from blue (1998) to red (2019). See Figure 1a for management region locations.

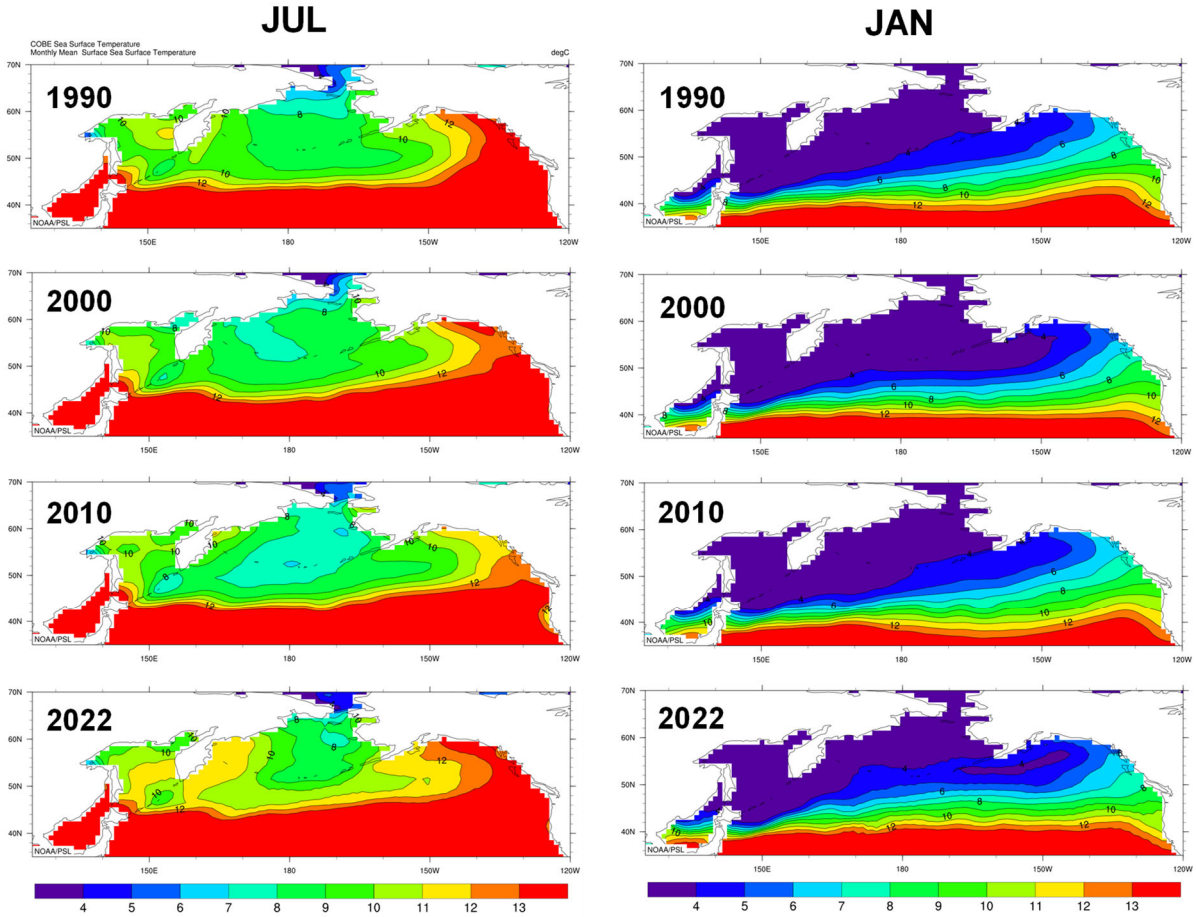


**FIGURE 4 Sea surface temperature (SST) isotherms in recent decades (1990-2022) showed a northward shift and longitudinal contraction of chum salmon summer (July) thermal habitat in the North Pacific Ocean, while winter (January) habitat was relatively stable.** Blue, green and orange show the range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

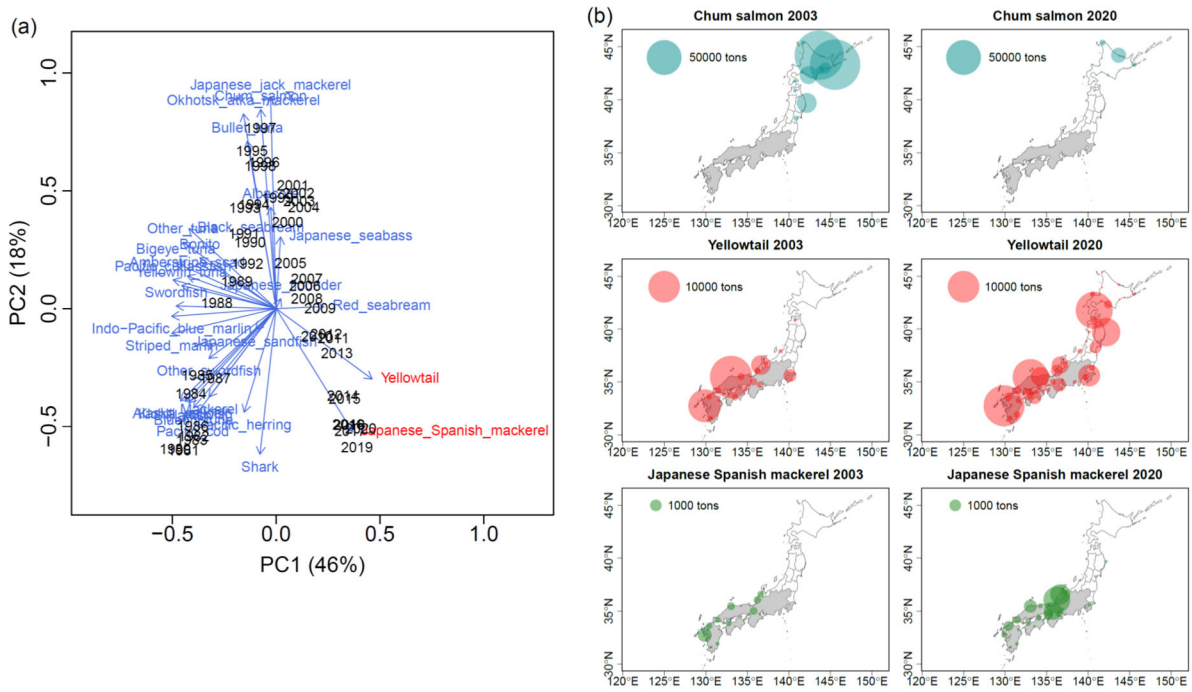


**FIGURE 5 Northward shifts of two marine piscivorous fishes in Japan.** (a) Principal component analysis biplot based on catch statistics of 30 marine fish species (1980 - 2020) showed increasing catches of yellowtail and Japanese Spanish mackerel. (b) Two-decadal shifts in commercial catches of chum salmon and two piscivores.

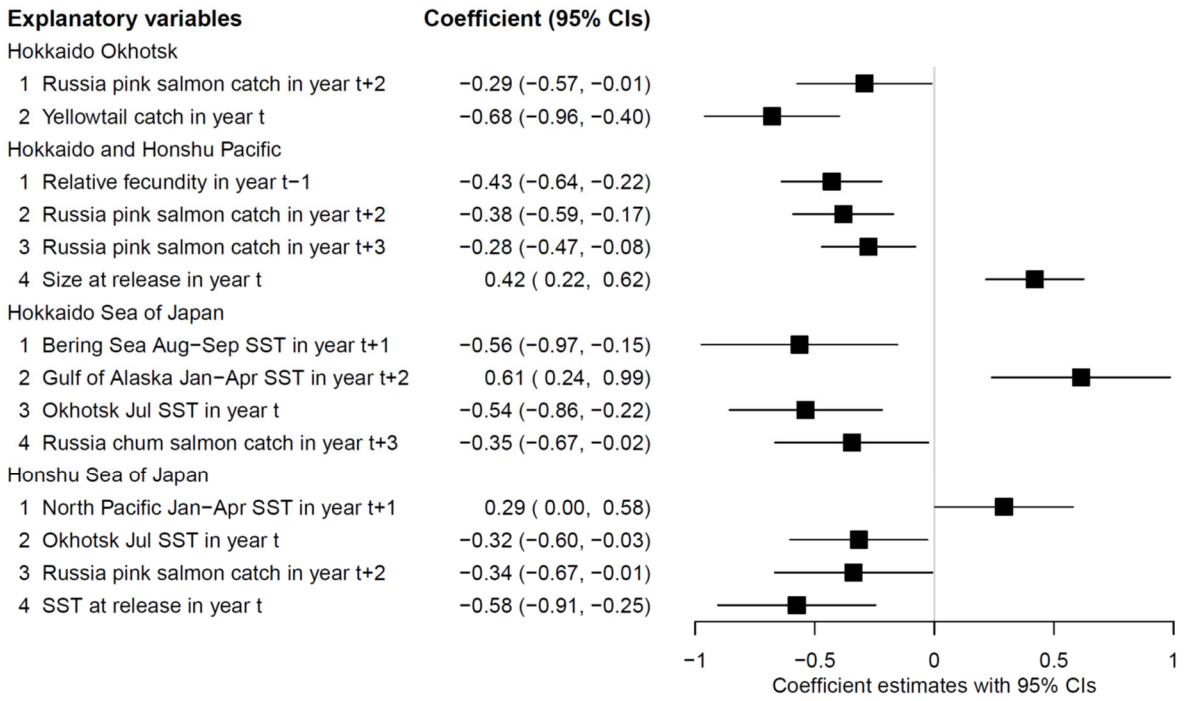


**FIGURE 6 Standardized effects of hypothesized indicators (explanatory variables) on Japanese chum salmon marine survival (adult return rates across regions).** Regression coefficients of best regression models with 95% confidence intervals in four management regions in Japan, estimated using standardized explanatory variables.

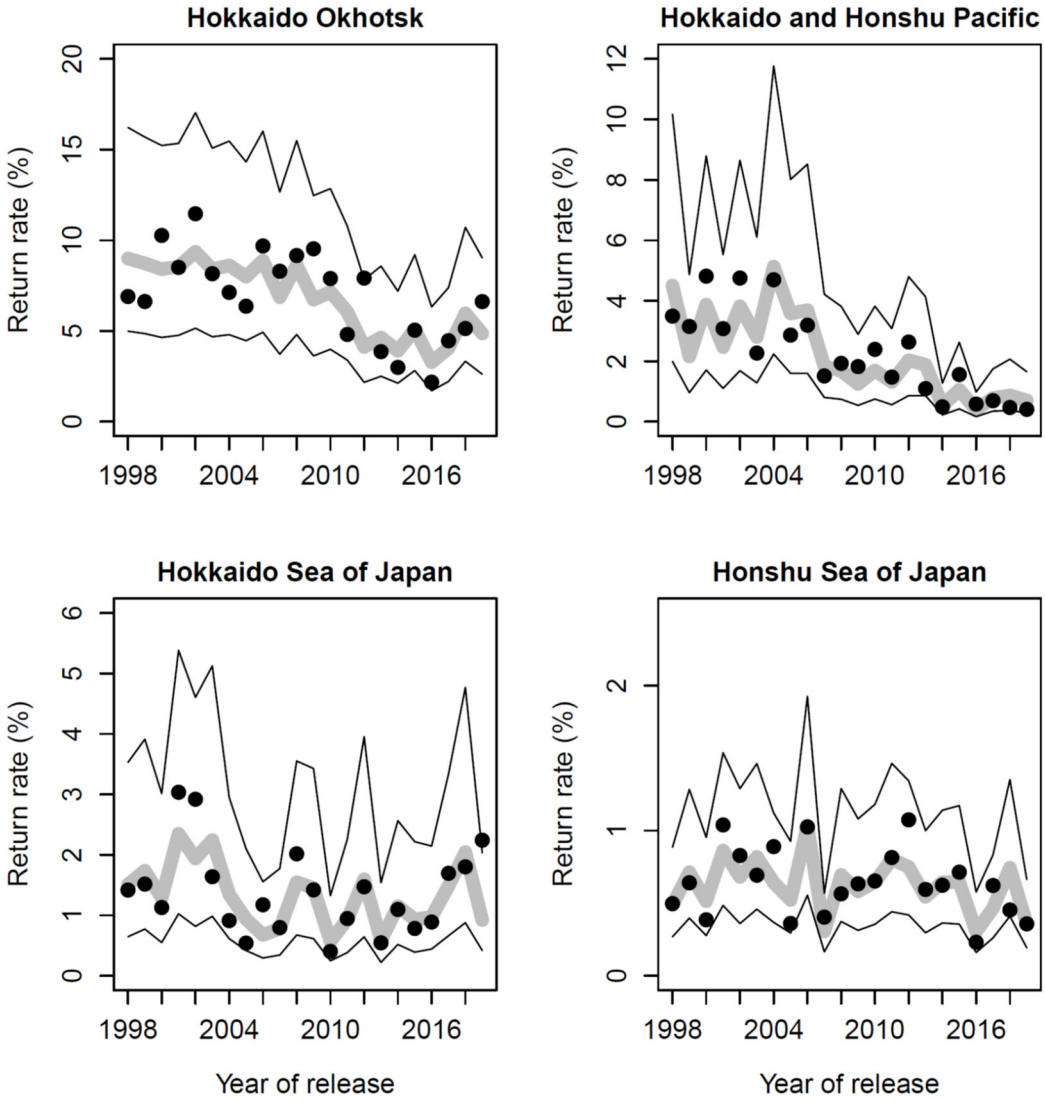


**FIGURE 7 Predicted and observed chum salmon marine survival (adult return rates) by management region in Japan.** Predicted return rates (grey line), observed return rates (black dots), and 95% prediction intervals (black lines). Note that scales on return rate axis differ by region. Figure updated

**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 (indicators) 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 (positive) to fewer eggs (Hasagawa et al., 2021b) |
| | Egg size (*t*) | 0 | Japan coast | Survival related (positive) to larger eggs (Hasagawa et al., 2021b) |
| | Fry size at release (*t*) | 0 | Japan coast | Survival related (negative) to size at release (Hasagawa et al., 2021a) |
| 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). |
| Predator - competitor interactions | 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. 2a).

**TABLE 2** Best regression models of Japanese chum salmon survival in four management 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.

| 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)** | – |
| Predator - competitor | 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 (0.0001)** | **0.79 (0.0000)** | **0.54 (0.0015)** | **0.57 (0.0008)** |

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

† 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).