

RESEARCH ARTICLE

Temporal trends in geographic clines of chum salmon reproductive traits associated with global warming and hatchery programmes

Koh Hasegawa¹  | Yasutaka Okamoto^{1,2} | Kentaro Morita^{1,3} 

¹ Salmon Research Department, Fisheries Resources Institute, Japan Fisheries Research and Education Agency, Nakanoshima, Toyohira, Sapporo, Japan

² Fisheries Agency, Kasumigaseki, Chiyoda, Tokyo, Japan

³ Uryu Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, Moshiri, Horokanai, Japan

Correspondence

Koh Hasegawa, Salmon Research Department, Fisheries Resources Institute, Japan Fisheries Research and Education Agency, Nakanoshima, Toyohira, Sapporo 062-0922, Japan
Email: hasegawa_koh43@fra.go.jp

Funding information

Research Council of Norway project "Global trout, Grant/Award Number: 287438

Handling Editor: Olivier Morissette

Abstract

1. Geographic clines in life-history traits are often recognized as adaptations to the associated transitional environments. As life-history traits evolve in response to anthropogenic processes, these geographic clines can change over time.
2. The geographic and temporal trends of reproductive traits in Japanese chum salmon *Oncorhynchus keta* were analysed. Data were collected from 23 rivers located between 36° and 45° north latitude and 136° and 146° east longitude from 1994 to 2010.
3. We confirmed the geographic clines of reproductive traits: relative gonad weight increased in more northeasterly locations, and females had fewer, but larger, eggs in more northeasterly locations after standardization by body size.
4. The geographic clines changed over the years. The northeastward geographic trend of increasing gonad weight became more pronounced over time. Temporal trends towards smaller but more numerous eggs were evident, especially in northeasterly locations.
5. Under natural and sexual selection, gonadal investment should be constrained by the energetic demands of the cost of migration, particularly in southwesterly locations (which are farthest from the feeding grounds), and by breeding competition during natural reproduction. In addition, females should have fewer but larger eggs owing to a constraint on growth opportunities for their offspring in more northeasterly regions of Japan, which are colder and have less available food. However, global warming may mitigate this constraint on growth opportunities in northeastern Japan by increasing river water temperatures. Moreover, we consider that relaxation of the effects of natural and sexual selection on intense breeding competition and early growth conditions has occurred through domestication selection by hatchery programmes. These may have caused temporal shifts in geographic clines.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Authors. *Ecological Solutions and Evidence* published by John Wiley & Sons Ltd on behalf of British Ecological Society

6. We should consider several co-occurring anthropogenic impacts on natural and sexual selection when evaluating the life-history traits of organisms. For the sustainable use of biological resources, maintaining geographically adapted life-history traits during adaptation to climate change is essential. Therefore, the conservation of wild salmon populations formed by natural selection is preferable to the stocking of hatchery-reared fry.

KEYWORDS

climate change, domestication selection, egg size, fecundity, gonad, latitudinal cline, natural selection, Pacific salmon

1 | INTRODUCTION

Geographic clines in life-history traits are often recognized as evidence for adaptation through natural and sexual selection to the transitional environments associated with these clines (Mayr, 1956; Tamate & Maekawa, 2006). In addition to showing patterns related to climate and geography, life-history traits vary with time owing to both natural and anthropogenic effects (Garant, 2020). Climate change is the major global concern associated with anthropogenic effects (Thuiller, 2007). For example, global warming because of increases in atmospheric greenhouse gas has caused shifting latitudinal clines in the body sizes of some Australian avian species over the past 100 years (Gardner et al., 2009). Brakefield and de Jong (2011) demonstrated that the longitudinal cline in two-spot ladybird *Adalia bipunctata* melanism has decayed over 25 years in the Netherlands because of warming. There are also additional causes of temporal trends in life-history traits, such as the selective harvest of mammals (e.g. trophy hunting for large horns or antlers decreases horn or antler size: Pigeon et al., 2016; Rivrud et al., 2013). Understanding how these anthropogenic effects temporally modify geographic clines is important for the management of wild organisms and to maintain their original life-history traits in the Anthropocene. Furthermore, Thuiller (2007) points out that anthropogenic effects such as warming and artificial selection sometimes interact with each other. However, studies integrating geographic and temporal trends of life-history traits while considering interacting anthropogenic impacts have not been conducted.

Among life-history traits, those reproductive traits directly related to individual fitness have attracted researchers as a means of testing geographic and temporal trends. In oviparous animal species, for example, both positive and negative latitudinal trends in egg number and size have been found in many taxa (Armbruster et al., 2001; Forsman & Shine, 1995; B. Gollman, & G. Gollman, 1996; Martin et al., 2006). Anthropogenic effects have also induced temporal trends in reproductive traits, such as enlarged ovaries of urban-dwelling spiders, by providing warm and preferable growth conditions through the heat island effect (Lowe et al., 2014).

Pacific salmon *Oncorhynchus* spp. are distributed widely around the North Pacific rim, and they show interpopulation geographic clines in reproductive traits (Beacham & Murray, 1993; Fleming & Gross, 1990;

McGurk, 2000; Morita et al., 2009; Tamate & Maekawa, 2000) with adaptation to the specific local environments of their spawning rivers (Taylor, 1991). Precise homing generates and maintains local adaptations (e.g. Quinn et al., 1995). Juveniles migrate from their natal rivers to an offshore feeding area for growth, and they experience common oceanic environments regardless of the origin of the populations in each region (Groot, 1991). Salmonids, including Pacific salmon, occur in cold waters, and previous studies have suggested that their life-history traits in both riverine and marine environments are susceptible to the effects of global warming (e.g. Richter & Kolmes, 2005; B. Jonsson & N. Jonsson, 2009).

The life history of Pacific salmon has also been greatly affected by the hatchery programmes that stock captive-reared juveniles into natural environments to feed, grow, and return; this has been conducted over most of their distribution area (McNeil, 1980; Naish et al., 2007). As a result, their reproductive traits, such as gamete formation and secondary sexual development, have temporally changed owing to adaptation to captivity (Hendry et al., 2000; Heath et al., 2003). Therefore, the reproductive traits of Pacific salmon are an ideal model to test integrated geographic and temporal trends in relation to these anthropogenic impacts, namely global warming and hatchery programmes.

The geographic trends in salmon reproductive traits have often been explained by the geographic gradients in offspring habitat productivity and in the parental migration cost, which is often estimated by the migration distance from the offshore feeding area to the freshwater spawning area. First, there is a trade-off of energy allocation between gonadal investment and migration energy; this is often illustrated by the negative relationship between gonad mass and migration distance (Beacham & Murray, 1993; Kinnison et al., 2001). Thus, populations with spawning areas farther away from feeding areas are expected to have smaller gonads. Gonad mass is the product of egg number (fecundity) and average egg mass. There is another trade-off between fecundity and average egg mass because energetic constraints do not allow a large number of large eggs, and selection does not favour a small number of small eggs in semelparous species such as Pacific salmon (Fleming & Gross, 1990; Einum et al., 2003). Fewer eggs of larger size are favoured under severe environmental conditions, such as low water temperatures, that restrict growth (Hutchings, 1991; Einum & Fleming,

1999). Therefore, two geographic trends can be expected: Populations whose spawning areas are farther from their feeding areas should have less gonadal investment and therefore less gonad mass, and females should have fewer, but larger, eggs in northerly populations because water temperatures are lower and offspring growth conditions are less favourable for these populations (e.g. Neuheimer & Taggart, 2007).

Increasing water temperature owing to global warming often alters the reproductive traits of fishes through both practical and evolutionary processes (Johnston & Leggett, 2002; Sheridan & Bickford, 2011). Some salmon have been found to be thinner and have lower condition factor associated with increasing temperatures (Todd et al., 2008; Morita et al., 2010). As a low condition factor indicates low migration energy stockpiling (Chellappa et al., 1995), salmon experiencing high water temperatures may plastically reduce their gonadal investment and decrease their final egg mass. Numerous eggs of smaller size may become more favourable in northerly salmon populations if the severity of the growth environment is mitigated by increasing temperatures (Hutchings, 1991; Einum & Fleming, 1999). In contrast, B. Jonsson and N. Jonsson (2009) suggest that selection favours larger egg size in warmer temperatures because high water temperatures reduce the efficiency of yolk conversion for the growth of alevins.

Domestication selection through hatchery programmes that artificially fertilize eggs and rear fry in ponds before stocking has helped salmon adapt to captivity (Christie et al., 2012). Thus, domestication selection has the potential to alter salmon reproductive traits (Hendry et al., 2000; Heath et al., 2003; Hagen et al., 2019; but see Quinn et al., 2004, and Beacham, 2010, for evidence to the contrary). For example, gonad mass may increase under hatchery programmes because females can convert a larger portion of energy to gonadal investment and a smaller portion to behavioural costs associated with breeding (e.g. redd construction; breeding competition: Fleming & Gross, 1989; Hendry et al., 2000). Moreover, Heath et al. (2003) suggested that downsizing of eggs with increased egg numbers, which results in numerous small fry, is an adaptation to a hatchery environment that provides high survival rates, even for small fry, through abundant food and no predation pressure (but see criticism of this study by Beacham, 2003, and Fleming et al., 2003). Therefore, we may expect the following temporal trends caused by domestication selection: (1) hatchery-reared salmon increase their gonadal investment by reducing the energy needed for breeding behaviour; and (2) hatchery-reared females sacrifice egg size for increased egg number.

The reproductive traits of Pacific salmon should therefore show both geographic trends brought about by natural and sexual selection and temporal trends due to global warming and domestication selection through hatchery programmes. Moreover, these geographic and temporal trends will not necessarily be independent of each other, potentially complicating the detection of the impacts of global warming and domestication selection in specific areas. It is important to identify the integrated geographic and temporal trends of anthropogenically influenced life-history traits. In this study, we addressed geographic and temporal trends contemporaneously with ongoing global warming and domestication selection by analysing monitoring datasets of Japanese hatchery-reared chum salmon *Oncorhynchus keta*.

2 | MATERIALS AND METHODS

2.1 | Japanese chum salmon and its hatchery programme

All chum salmon originating from various natal rivers of the Japanese archipelago migrate to the North Pacific Ocean, including the Sea of Okhotsk and the Gulf of Alaska, and move to the Bering Sea in their final summer before returning to their natal rivers in autumn, as revealed by genetic analysis and studies of the distribution of marked fish in the Bering Sea (e.g. Urawa et al., 2018). In the Bering Sea, the feeding areas of Japanese chum salmon from different rivers overlap in time and space (Urawa et al., 2012). The chum salmon is semelparous, and they migrate from the Bering Sea to their natal rivers via the Kamchatka Peninsula in autumn and winter for spawning (Yonemori, 1975). Their fry migrate towards the sea in next spring. The locations of the spawning rivers in the Japanese archipelago range from northeast to southwest (Figure 1: Okazaki, 1982). Thus, their migration distance to the more southerly and westerly river mouths is longer, and geographical coordinates at the river mouths could be proxies for the cost of migration on gonadal investment (Figure 1; Supporting Information 1). The climate of northeastern Japan is categorized as subarctic, and air and river water temperatures tend to become colder with increasing latitude (Beck et al., 2018). A warming trend in winter is apparent in northeastern Japan: mean air temperature increased by about 0.8°C from the 1970s to the 2000s (Schaefer & Domroes, 2009). A warm ocean current (the Tsushima current) flows northward along the west coast of northeastern Japan, and a cold ocean current (the Oyashio Current) flows southward along the east coast. Body size and age at the maturation of chum salmon overlap broadly among rivers, but the average values show geographic and temporal trends (Supporting Information 2).

The modern hatchery programme for chum salmon, in which fry are released after being fed pellets for 1 to 2 months in rearing ponds, has prevailed since the late 1980s in Japan (Seki, 2005). Before that, most fry were released without having been fed; the advent of feeding was a dramatic innovation in fry-rearing techniques (Kaeriyama, 1999). Additional techniques such as management procedures for fertilized eggs and improvements to the architecture of fry-rearing ponds have also been developed over time, but the details of their implementation are strongly dependent on decisions made by the local staff of each hatchery at the time (Nogawa, 2010). This means that the precise procedures used to rear fry in the hatcheries have differed across rivers and years. Moreover, the number of hatchery releases (i.e. hatchery intensity) increased until the 1980s, irrespective of geographic region (Supporting Information 3). Subsequently, annual trends of the number of fry released have differed among regions. Rearing ponds are filled with groundwater, and sometimes river water is supplemented to sustain the volume of pond water. The growth environment in hatcheries is ideally suited to the demands of chum salmon fry, irrespective of geographic location, and the homogeneous hatchery environment may obscure any geographic trends in fry growth conditions. All hatchery chum salmon originate from natural broodstocks (i.e. eggs are obtained

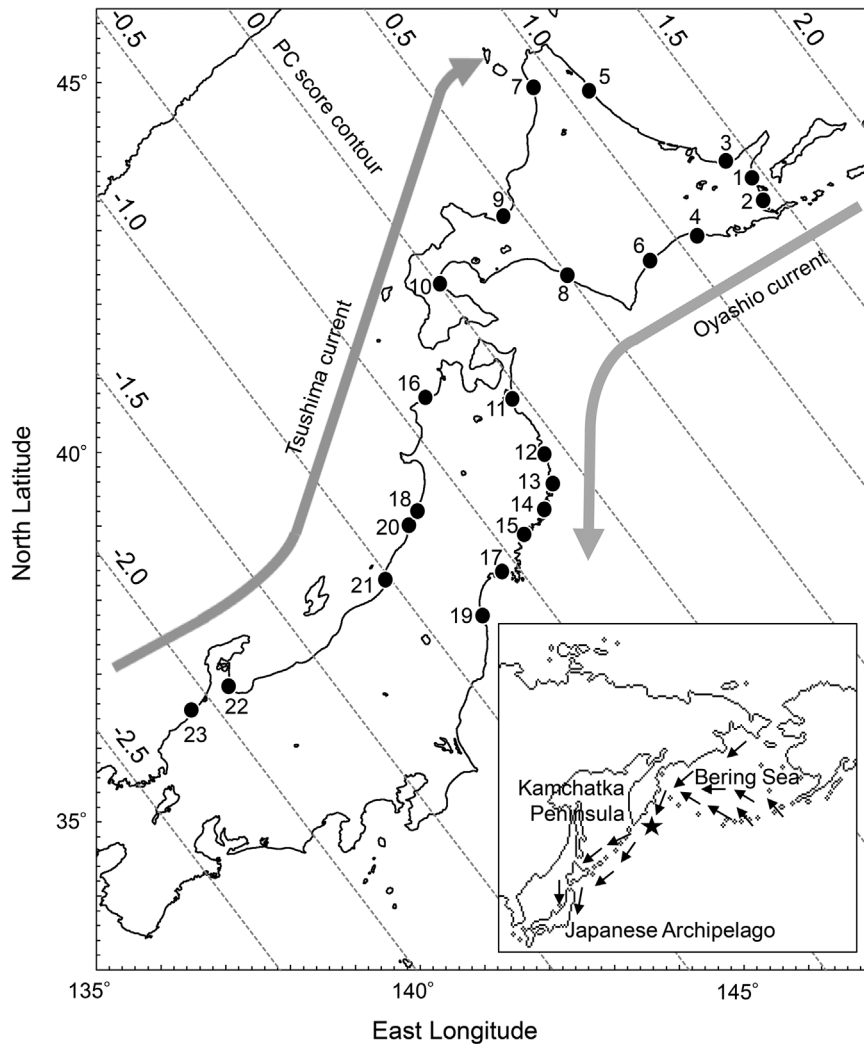


FIGURE 1 Locations of the mouths of the surveyed rivers. The rivers' names, latitudinal and longitudinal coordinates, and principal component (PC) scores summarizing geographic locations are shown in Supporting information 5. Dotted lines are isopleth lines (contours) for PC scores. Grey arrows indicate directions of ocean currents (Tsushima and Oyashio currents). Inset shows the location of the Bering Sea (feeding area) and Japanese Archipelago (spawning area). Black arrows indicate the broad direction of spawning migration routes of Japanese chum salmon (Yonemori, 1975). Japanese chum salmon are assumed to return to their natal rivers via the base point (star symbol: 50°N, 160°E)

from adults returning to the rivers). In Japan, the season for artificial fertilization tends to start earlier at high latitudes because of the early run timings, whereas the season for fry release tends to be later in the more northeasterly rivers owing to the late arrival of spring migration timings at high latitudes (Supporting Information 4). As a result, fry-rearing periods tend to be longer in more northeasterly rivers (Supporting Information 4).

2.2 | Monitoring of reproductive traits

In this study, 23 rivers between 36° and 45° north latitude and 136° and 146° east longitude were chosen for analysis (Figure 1). In these rivers, reproductive traits were analysed in mature females (up to 100 individuals) caught at weirs during the peak season of hatchery broodstock collection from 1994 to 2010. Unfortunately, the location of the natural spawning grounds in each river is unknown, so the physical environmental conditions related to the spawning grounds were not considered in this study. Chum salmon returning to rivers along the western and eastern coasts of Japan are exposed to the effects of the warm Tsushima and cold Oyashio currents, respectively (Figure 1).

Sampling was conducted as part of a monitoring survey by national or prefectural governments and research institutes. A geographic cline of artificial propagation peaks over this period extended temporally from mid-October to late November (Supporting Information 4). Because egg size and number basically depend on body size, the fork length of each female was measured. The age of each female determined by scale analysis ranged 2–7, but was mostly 3–5 years old. Raw gonads were removed and weighed (to the nearest 0.1 g) shortly after the fish were caught. Egg size was determined by weighing a certain amount from the gonad (approximately 300 eggs), counting the exact number of eggs, and calculating the average egg weight for each female. The total number of eggs was either fully counted or estimated by dividing the whole gonad weight by the average egg weight. Okamoto et al. (2015) confirmed that the egg size obtained by this simple method is almost the same as the 5%-formalin-fixed egg weight, which has been widely used as an index of egg size (Fleming & Ng, 1987). The datasets contained some incorrect values caused by typographic errors or errors in the measurement of females after spawning. To eliminate these outliers, a regression analysis was conducted by setting \log_e (fork length) as an explanatory variable and \log_e (value of reproductive trait) as a dependent variable; females with absolute val-

TABLE 1 Differences in Akaike's information criterion (Δ AIC) from the lowest AIC models for gonad weight, number of eggs and egg size (egg weight). Shaded cells indicate the lowest AIC models or models for which Δ AIC < 2

Model	Δ AIC		
	Gonad weight	Number of eggs	Egg size
year + PC score + age + year \times PC score + year \times age + PC score \times age + year \times PC score \times age	0.0	0.0	0.0
year + PC score + age + year \times PC score + year \times age + PC score \times age	0.1	2.9	11.9
year + PC score + age + year \times PC score + year \times age	16.1	14.7	11.5
year + PC score + age + year \times PC score + PC score \times age	0.2	4.7	10.9
year + PC score + age + year \times age + PC score \times age	35.7	54.1	17.5
year + PC score + age + year \times PC score	15.5	16.6	10.7
year + PC score + age + year \times age	49.1	63.9	17.0
year + PC score + age + PC score \times age	34.5	57.9	19.0
year + PC score + age	48.0	68.2	18.6

ues of standardized residuals larger than three were not used in the analysis.

2.3 | Data analyses

Geographic coordinates were taken at the mouth of each studied river, as measured on the online map released by the Geospatial Information Authority of Japan (<https://www.gsi.go.jp/>). As the Japanese Archipelago expands towards the northeast direction, the north latitude and east longitude are highly correlated (Pearson's $r = 0.752$, $p < 0.001$). These geographic coordinates were then unified by principal component analysis. The first principal component explained 87.6% of the total variance and increased with increasing north latitude and east longitude (Figure 1). The principal component scores (PC scores) were used in the analyses as indices of the geographic locations.

To test whether geographic clines of reproductive traits showed temporal trends, we applied linear mixed models (multiple regression analyses) with river identity as the random effect, as follows:

$$\begin{aligned} &\text{Reproductive traits (gonad weight, number of eggs, egg size)} \\ &= \text{year} + \text{PC score (geographic location)} + \text{age} + \text{year} \times \text{PC score} \\ &+ \text{year} \times \text{age} + \text{PC score} \times \text{age} + \text{year} \times \text{PC score} \times \text{age} + \text{river}. \end{aligned} \quad (1)$$

The interaction term between year and PC score (year \times PC score) was used to test whether salmon show temporal trends in geographic clines of their reproductive traits which could reflect the effects of global warming and domestication selection through hatchery programmes. Age (a continuous variable) represents the length of time spent in the ocean and is known to have a strong impact on reproductive traits. Interaction terms between age and year (age \times year) and age and PC score (age \times PC score) were used to test whether age influences temporal trends in reproductive traits and whether age influ-

ences geographic clines of reproductive traits, respectively. Because this study focused on annual changes in geographic clines, the second-order interaction term (year \times PC score \times age) was interpreted as a difference in annual changes of geographic clines among ages. The form of the model was chosen by comparing the Akaike's information criterion (AIC) of models with varying numbers of parameters and selecting the model with the lowest AIC (Table 1).

The reproductive trait values were standardized by female fork length, with consideration of non-linear relationships between fish length and reproductive traits as follows (Beacham, 2010):

$$E_s = E_0(L_m/L_0)^a \quad (2)$$

where E_s and E_0 are, respectively, the standardized and actual measured values of reproductive traits for each female. L_m is the mean fork length of all females used in the analyses, and L_0 is the actual measured fork length of each female. a is the slope of the regression line: $\log E_0 = a \log L_0 + c$.

The number of females for each river and each year used in the study, and the geographic coordinates of each river, are shown in Supporting Information 5. All explanatory variables were standardized by mean centring. The alpha level was set at 0.05. All datasets were analysed by using SPSS version 24 (IBM Corp., Armonk, NY, USA).

3 | RESULTS

Several significant interaction terms were detected. The results are summarized by focusing separately on the interaction terms for each reproductive trait.

3.1 | Gonad weight

The regression lines for the geographic clines of gonad weight differed significantly among ages (PC score \times age: $F = 14.81$, $p < 0.001$; Table 2).

TABLE 2 Results of linear mixed models for testing temporal changes in the geographic clines of chum salmon reproductive traits. The models include a random effect of river identity. Principal component (PC) scores indicate the geographic locations of each river mouth

Effect	Coefficient	$df_{\text{numerator}}$	$df_{\text{denominator}}$	F	P
(a) Gonad weight					
Constant	708.7	1	21.00	9559	<0.001
Year	1.185	1	2.987×10^4	60.87	<0.001
PC score	19.46	1	20.98	6.913	0.016
Age	-1.744	1	2.988×10^4	2.687	0.101
Year \times PC score	0.882	1	2.989×10^4	36.90	<0.001
Year \times Age	-0.274	1	2.988×10^4	1.495	0.221
PC score \times Age	-4.122	1	2.989×10^4	14.81	<0.001
Year \times PC score \times Age	-0.253	1	2.988×10^4	1.296	0.255
(b) Number of eggs					
Constant	2956	1	21.00	5458	<0.001
Year	10.11	1	2.989×10^4	224.8	<0.001
PC score	-40.30	1	20.98	0.973	0.335
Age	-66.38	1	2.988×10^4	197.3	<0.001
Year \times PC score	4.600	1	2.989×10^4	50.84	<0.001
Year \times Age	0.203	1	2.987×10^4	0.042	0.838
PC score \times Age	-11.82	1	2.989×10^4	6.174	0.013
Year \times PC score \times Age	1.026	1	2.988×10^4	1.081	0.298
(c) Egg size					
Constant	242.9	1	21.02	6429	<0.001
Year	-0.469	1	2.989×10^4	119.2	<0.001
PC score	10.21	1	21.01	10.91	0.003
Age	5.054	1	2.988×10^4	281.9	<0.001
Year \times PC score	-0.138	1	2.989×10^4	11.35	0.001
Year \times Age	-0.133	1	2.987×10^4	4.410	0.036
PC score \times Age	-0.009	1	2.989×10^4	0.001	0.978
Year \times PC score \times Age	-0.248	1	2.987×10^4	15.57	<0.001

However, the patterns of the temporal trends in the geographic clines were coherent among ages. The significant interaction term between year and PC score suggests that the positive slope of the regression lines for geographic clines became steeper over the years (year \times PC score: $F = 36.90$, $p < 0.001$; Table 2; Figure 2). Gonads were larger in more northeasterly locations, and the annual increase of gonad weight became greater in more northeasterly locations, regardless of age (Figure 2).

3.2 | Number of eggs

The regression lines for geographic clines of the number of eggs differed significantly among ages, but the patterns of the temporal trends in the geographic clines were coherent among ages, as was the case for gonad weight (PC score \times age: $F = 6.174$, $p = 0.013$; Table 2).

The significant interaction term between year and PC score suggests that the negative slope of the regression lines for geographic clines of the number of eggs became less steep over the years (year \times PC score: $F = 50.84$, $p < 0.001$; Table 2; Figure 3). The annual increase in egg number was more prominent in northeasterly locations (Figure 3).

3.3 | Egg size

The temporal trends in the geographic clines of egg size differed among ages (year \times PC score \times age: $F = 15.57$, $p < 0.001$; Table 2; Figure 4). The regression lines had positive slopes regardless of year or age, and the temporal trends became clearer with increasing age. The annual decrease in egg size in more northeasterly locations was prominent in 5-year-olds (Figure 4).

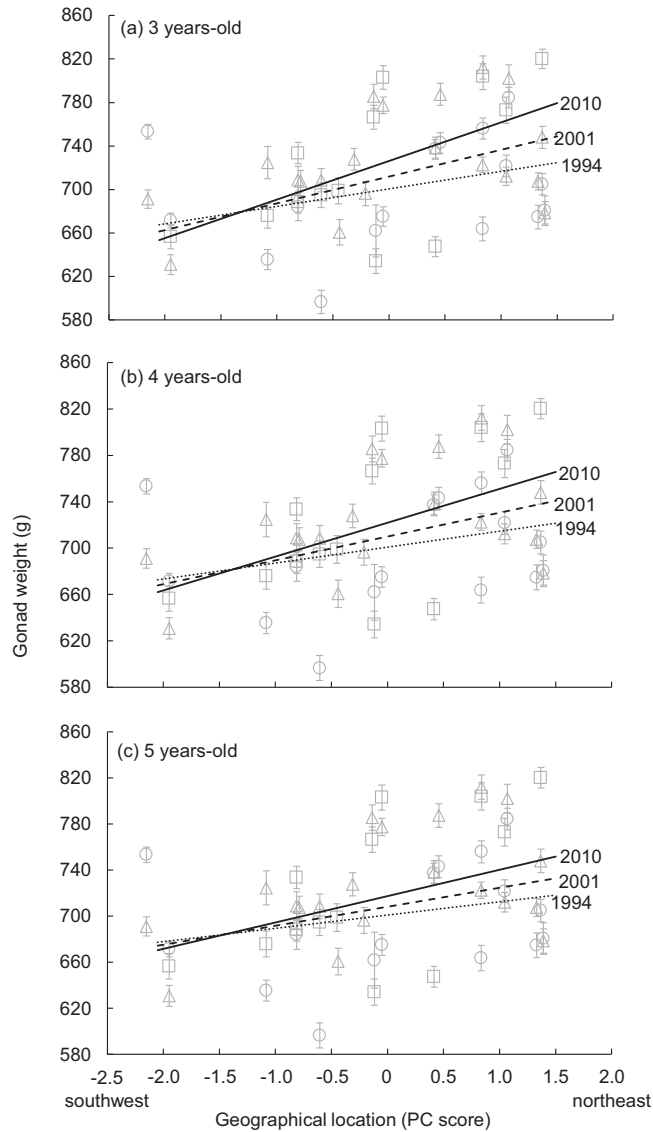


FIGURE 2 Temporal changes in geographic clines of gonad weight for each age (a: 3 years old; b: 4 years old; c: 5 years old). Values of reproductive traits were standardized by female body size (fork length). The regression lines for each surveyed year shift sequentially from 1994 to 2010. To simplify the graphs, only lines for the first (1994) and last (2010) surveyed years, and an intervening year (2001), are shown. Dotted lines and circles, dashed lines and triangles and solid lines and squares indicate 1994, 2001 and 2010, respectively. Estimated regression lines are (a) 1994: $y = 16.11x + 699.9$; 2001: $y = 24.61x + 710.7$; 2010: $y = 35.53x + 724.6$; (b) 1994: $y = 13.79x + 700.1$; 2001: $y = 20.50x + 709.0$; 2010: $y = 29.12x + 720.4$; (c) 1994: $y = 11.51x + 700.4$; 2001: $y = 16.47x + 707.3$; 2010: $y = 22.84x + 716.3$. Symbols and error bars show means and SEs of each river for each year

4 | DISCUSSION

In this study, we successfully demonstrated that geographic clines of chum salmon life-history traits show temporal trends. We speculate that these temporal trends might be caused by multiple interacting

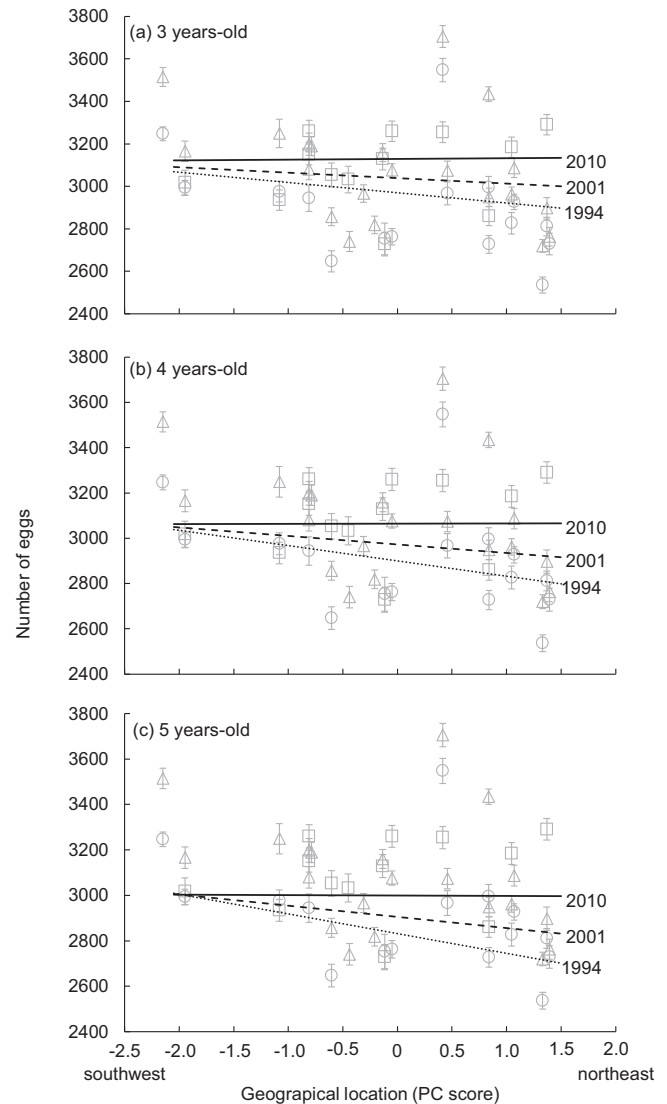


FIGURE 3 Temporal changes in geographic clines of the number of eggs for each age (a: 3 years old; b: 4 years old; c: 5 years old). Values of reproductive traits were standardized by female body size (fork length). The regression lines for each surveyed year shift sequentially from 1994 to 2010. To simplify the graphs, only lines for the first (1994) and last (2010) surveyed years, and an intervening year (2001), are shown. Dotted lines and circles, dashed lines and triangles and solid lines and squares indicate 1994, 2001 and 2010, respectively. Estimated regression lines are (a) 1994: $y = -48.29x + 2972$; 2001: $y = -25.50x + 3041$; 2010: $y = 3.800x + 3129$; (b) 1994: $y = -67.70x + 2904$; 2001: $y = -37.66x + 2974$; 2010: $y = 0.970x + 3065$; (c) 1994: $y = -86.73x + 2836$; 2001: $y = -49.57x + 2908$; 2010: $y = -1.804x + 3000$. Symbols and error bars show means and SEs of each river for each year

anthropogenic impacts, including climate change and domestication selection (Thuiller, 2007). Japan is located at the southern limit of the chum salmon range, and the effects of climate change are generally easily detectable at such distribution range margins (e.g. Jump et al., 2006). Additionally, the proliferation of modern Japanese hatchery programmes over several decades may have exposed Japanese chum

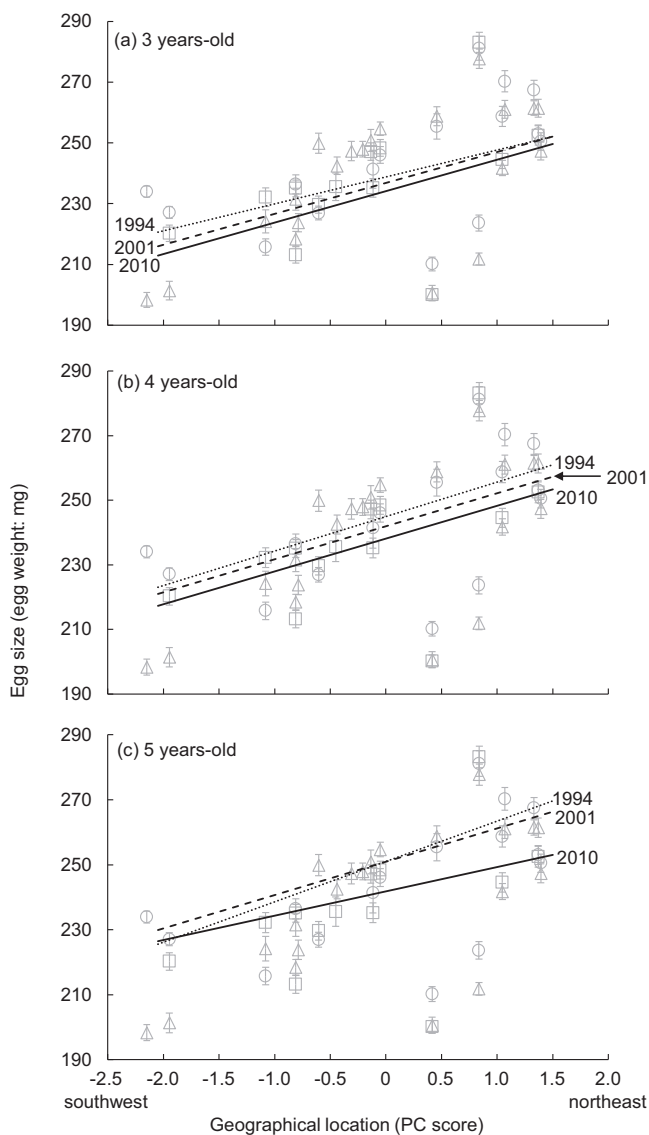


FIGURE 4 Temporal changes in geographic clines of egg size (egg weight: mg) for each age (a: 3 years old; b: 4 years old; c: 5 years old). Values of reproductive traits were standardized by female body size (fork length). The regression lines for each surveyed year shift sequentially from 1994 to 2010. To simplify the graphs, only lines for the first (1994) and last (2010) surveyed years, and an intervening year (2001), are shown. Dotted lines and circles, dashed lines and triangles and solid lines and squares indicate 1994, 2001 and 2010, respectively. Estimated regression lines are (a) 1994: $y = 8.881x + 238.4$; 2001: $y = 10.19x + 236.3$; 2010: $y = 10.35x + 233.7$; (b) 1994: $y = 10.68x + 244.4$; 2001: $y = 10.23x + 241.4$; 2010: $y = 10.17x + 237.6$; (c) 1994: $y = 12.44x + 250.4$; 2001: $y = 10.27x + 250.4$; 2010: $y = 7.487x + 241.4$. Symbols and error bars show means and SEs of each river for each year

salmon to intense domestication selection (Kitada, 2013). This may allow easy detection of our hypothesized patterns caused by domestication selection. The relationships between geographic location and reproductive traits varied greatly around the regression lines, but this may have been because salmon reproductive traits are also affected

by site-specific factors in addition to latitude and longitude, such as the size of incubation gravels in natural rivers (Quinn et al., 1995). Moreover, the number of fry released and the specific fry-rearing techniques adopted by the staff of each hatchery could also be regarded as site-specific factors, although the general procedures used by hatchery programmes (i.e. fry are obtained through artificial fertilization, and then are reared and fed in hatcheries until they reach an appropriate size for seaward migration) have remained constant among Japanese hatcheries since the advent of feeding (Kaeriyama, 1999; Nogawa, 2010).

Our hypotheses readily explain the causes of the geographic clines of chum salmon reproductive traits. Increasing gonad mass, that is increasing gonadal investment in more northeasterly locations, may be due to lower migration costs caused by shortened migration distance. Previous studies of salmon migration have focused on the distances travelled after river entry (Beacham & Murray, 1993; Kinnison et al., 2001; B. Jonsson & N. Jonsson, 2006). Our findings newly suggest that oceanic migration distances are also negatively correlated with gonadal investment. In addition, the opposite directions and different temperatures of ocean currents on the western (Tsushima current: warm and northward-flowing) and eastern (Oyashio current: cold and southward-flowing) coasts of Japan may reinforce the higher migration costs in western rivers. Although females can increase gonadal investment in more northeasterly locations, they might not be able to increase fecundity, which in fish species is often defined as the number of eggs (Wootton, 1990). Within each year, the number of eggs decreased in more northeasterly locations because egg size, which is in a trade-off relationship with the number of eggs, must increase in northeasterly locations to enable fry to adapt to growth environments in which temperature or freshwater productivity, or both, are low. In chum salmon, egg size influences the size of the newly emerged fry (Beacham & Murray, 1985), and fry size at the time of ocean entry determines the survival rate in the ocean (Urawa et al., 2018). In short, the energy allocation to gonadal investment may turn out to be in the form of increased egg size to increase fry growth or survival, or both, in northeasterly locations. Alternatively, chum salmon may not regulate gonadal investment by fecundity after the start of spawning migration, because salmonid species are likely to determine fecundity before a growth stage such as feeding migration in the ocean (N. Jonsson et al., 1996).

Under captive breeding programmes, hatchery salmon can increase their gonadal investment through domestication selection because they lack the energetic costs of breeding behaviours such as redd construction and breeding competition (Fleming & Gross, 1989). Our results showed that the annual increase in gonad weight was greater in more northeasterly locations, suggesting that the degree of conversion to gonadal investment was larger in these more northeasterly locations. The relaxation effect of artificial propagation programmes on competitive costs should be greater in more northeasterly locations because the size of salmon runs tends to increase in more northeasterly rivers (Saito et al., 2015) and the intensity of breeding competition depends on salmon density (van den Berghe & Gross, 1989). In

contrast, the effect of global warming on gonadal investment may be actualized as a plastic decrease in egg size, because females may principally control energy allocation to the gonad through egg size adjustment. The decrease in egg size with time was more prominent in older females. As older females spend more time in the warming Bering Sea, their egg size may gradually decrease in response to a decrease in condition factor, which is an index of migration energy stockpiling in fish (Chellappa et al., 1995; Morita et al., 2010).

Our hypothesis that salmon are evolving to have more, smaller, eggs, rather than having fewer, larger, eggs, was supported by the changes over years in the northeasterly locations. In nature, salmon fry grow more slowly in the more northerly rivers because of lower food availability (Inoue et al., 2013) and reduced temperatures (Neuheimer & Taggart, 2007). Low temperatures physiologically decrease growth by decreasing the efficiency of food conversion for growth (Brett et al., 1969; but see Seibel & Drazen, 2007). Therefore, salmonids are likely to have fewer, larger eggs in these unproductive conditions to compensate for the high mortality cost in early life (Hutchings, 1991; Tamate & Maekawa, 2000). However, increasing water temperatures through global warming is ameliorating these growth environments. In addition, with domestication selection through captive rearing, having more, smaller eggs might be adaptive, because there is no risk of food shortage in early life. Even small fry, therefore, have higher survival rates in rearing environments than in natural streams (Heath et al., 2003; Hagen et al., 2019). In particular, a favourable change in the growth environment from natural streams to captive rearing – especially an improvement in food availability – will be more pronounced in northeasterly locations because of the homogeneous hatchery facilities. The rearing period of chum salmon fry in hatcheries tends to be longer in more northeasterly locations owing to the earlier spawning season and the later stocking season (Supporting Information 4). Therefore, hatchery-reared fry in more northeasterly locations can gain growth advantages over those in the southwest, and this, in turn, may facilitate their having more eggs of smaller size. Given these possibilities, the temporal trend of having more eggs of smaller size may be more pronounced in northeasterly locations. In contrast, the southwesterly rivers in this study were near the southern limit of the chum salmon range. In these rivers, increasing water temperatures may lead to conditions too warm for chum salmon. Under high-temperature conditions, salmon evolve to have larger eggs and decreased fecundity (B. Jonsson & N. Jonsson, 2009). In southwesterly locations, this selection through global warming may counteract the temporal trend towards numerous small eggs through domestication selection. Overall, the temporal trends of the geographic clines in fecundity and egg size of chum salmon are accountable by considering selection through both global warming and domestication.

For the sustainable use of biological resources, sustaining diverse populations with different life-history traits adapted to changing regional environments through natural and sexual selection is necessary (Saccheri & Hanski, 2006; Schindler et al., 2010). Adaptations to each regional environment sometimes appear as geographic clines, as this study demonstrates, but we cannot deny the possibility that the current clines are the outcome of temporal changes due to adaptation

to anthropogenic impacts. Today, in the so-called Anthropocene, we should consider several co-occurring anthropogenic impacts on natural and sexual selection when evaluating the life-history traits of organisms (Edeline et al., 2007).

For salmon fisheries, the temporal trends of life-history traits through fisheries-induced evolution remain a problem for sustaining populations (Hard et al., 2008; Kuparinen & Festa-Bianchet, 2017). Our findings suggest that salmon populations have geographically adapted reproductive traits that include adaptation to global warming. However, domestication selection may disturb their adaptation in some locations. In fact, O'Sullivan et al. (2020) demonstrated that hatchery-reared Atlantic salmon *Salmo salar* stocked into natural environments had fewer offspring than wild conspecifics; this decreased the entire population's productivity. For the sustainable use of salmon resources, maintaining geographically adapted life-history traits, such as reproductive traits, during adaptation to climate change is essential. Therefore, the conservation of wild populations formed by natural selection is preferable to the stocking of hatchery-reared fry.

ACKNOWLEDGEMENTS

We thank all the dedicated staff of the fish hatcheries for salmon sampling. We also thank Thomas P. Quinn for his helpful comments on an early draft of this manuscript; Kazumasa Ohkuma, Kengo Suzuki, Shunpei Sato and Tsutomu Ohnuki for their support in this study; and the Hokkaido National Fisheries Research Institute staff for their cooperation with our investigation. This study was partly supported by the Research Council of Norway project "Global trout: investigating environmental change through more-than-human world systems" project no 287438.

CONFLICT OF INTEREST

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

K.H. and K.M. wrote the manuscript, and K.H. and Y.O. analysed the data. K.M. supervised this study. All authors contributed critically to the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.pc866t1pr> (Hasegawa et al., 2021)

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1002/2688-8319.12107>

ORCID

Koh Hasegawa  <https://orcid.org/0000-0001-6827-8322>

Kentaro Morita  <https://orcid.org/0000-0002-7803-2438>

REFERENCES

Armbruster, P., Bradshaw, W. E., Ruegg, K., & Holzapfel, C. M. (2001). Geographic variation and the evolution of reproductive allocation in the

- pitcher-plant mosquito, *Wyeomyia smithii*. *Evolution; International Journal of Organic Evolution*, 55, 439–444. <https://doi.org/10.1111/j.0014-3820.2001.tb01306.x>
- Beacham, T. D. (2003). Comment on “Rapid evolution of egg size in captive salmon” (II). *Science*, 302, 59. <https://doi.org/10.1126/science.1086625>
- Beacham, T. D. (2010). Revisiting trends in the evolution of egg size in hatchery-enhanced populations of Chinook salmon from British Columbia. *Transactions of the American Fisheries Society*, 139, 579–585. <https://doi.org/10.1577/T09-093.1>
- Beacham, T. D., & Murray, C. B. (1985). Effect of female size, egg size, and water temperature on developmental biology of chum salmon (*Oncorhynchus keta*) from the Nitinat River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, 42, 1755–1765. <https://doi.org/10.1139/f85-220>
- Beacham, T. D., & Murray, C. B. (1993). Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). *Journal of Fish Biology*, 42, 485–508. <https://doi.org/10.1111/j.1095-8649.1993.tb00354.x>
- Beck, H. E., Zimmermann, N. E., McVicar, T. R., Vergopolan, N., Berg, A., & Wood, E. F. (2018). Present and future Köppen-Geiger climate classification maps at 1-km resolution. *Scientific Data*, 5, 180214. <https://doi.org/10.1038/sdata.2018.214>
- Brakefield, P. M., & de Jong, P. W. (2011). A steep cline in ladybird melanism has decayed over 25 years: A genetic response to climate change? *Heredity*, 107, 574–578. <https://doi.org/10.1038/hdy.2011.49>
- Brett, J. R., Shelbourn, J. E., & Shoop, C. T. (1969). Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *Journal Fisheries Research Board of Canada*, 26, 2363–2394. <https://doi.org/10.1139/f69-230>
- Chellappa, S., Huntingford, F. A., Strang, R. H. C., & Thomson, R. Y. (1995). Condition factor and hepatosomatic index as estimates of energy status in male three-spined stickleback. *Journal of Fish Biology*, 47, 775–787. <https://doi.org/10.1111/j.1095-8649.1995.tb06002.x>
- Christie, M. R., Marine, M. L., French, R. A., & Blouin, M. S. (2012). Genetic adaptation to captivity can occur in a single generation. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 238–242. <https://doi.org/10.1073/pnas.1111073109>
- Edeline, E., Carlson, S. M., Stige, L. C., Winfield, I. J., Fletcher, J. M., James, J. B., Haugen, T. O., Vøllestad, L. A., & Stenseth, N. C. (2007). Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 15799–15804. <https://doi.org/10.1073/pnas.0705908104>
- Einum, S., & Fleming, I. A. (1999). Maternal effects of egg size in brown trout (*Salmo trutta*): Norms of reaction to environmental quality. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 266, 2095–2100. <https://doi.org/10.1098/rspb.1999.0893>
- Einum, S., Kinnison, M. T., & Hendry, A. P. (2003). Evolution of egg size and number. In A. P. Hendry & S. C. Stearns (Eds.), *Evolution illuminated salmon and their relatives* (pp. 126–153). Oxford University Press.
- Fleming, I. A., & Ng, S. (1987). Evaluation of techniques for fixing, preserving, and measuring salmon eggs. *Canadian Journal of Fisheries and Aquatic Sciences*, 44, 1957–1962. <https://doi.org/10.1139/f87-240>
- Fleming, I. A., & Gross, M. R. (1989). Evolution of adult female life history and morphology in a Pacific salmon (coho: *Oncorhynchus kisutch*). *Evolution; International Journal of Organic Evolution*, 43, 141–157. <https://doi.org/10.2307/2409170>
- Fleming, I. A., & Gross, M. R. (1990). Latitudinal clines: A trade-off between egg number and size in Pacific salmon. *Ecology*, 71, 1–11. <https://doi.org/10.2307/1940241>
- Fleming, I. A., Einum, S., Jonsson, B., & Jonsson, N. (2003). Comment on “Rapid evolution of egg size in captive salmon” (II). *Science*, 302, 59. <https://doi.org/10.1126/science.1084695>
- Forsman, A., & Shine, R. (1995). Parallel geographic variation in body shape and reproductive life-history within the Australian scincid lizard *Lampropholis delicata*. *Functional Ecology*, 9, 818–828. <https://doi.org/10.2307/2389979>
- Garant, D. (2020). Natural and human-induced environmental changes and their effects on adaptive potential of wild animal populations. *Evolutionary Applications*, 13, 1117–1127. <https://doi.org/10.1111/eva.12928>
- Gardner, J. L., Heinsohn, R., & Joseph, L. (2009). Shifting latitudinal clines in avian body size correlate with global warming in Australian passerines. *Proceedings of the Royal Society B*, 276, 3845–3852. <https://doi.org/10.1098/rspb.2009.1011>
- Gollman, B., & Gollman, G. (1996). Geographic variation of larval traits in the Australian frog *Geocrinia victoriana*. *Herpetologica*, 52, 181–187.
- Groot, G. (1991). *Pacific salmon life histories*. UBC Press.
- Hagen, I. J., Jensen, A. J., Bolstad, G. H., Diserud, O. H., Hindar, K., Lo, H., & Karlsson, S. (2019). Supplementary stocking selects for domesticated genotypes. *Nature Communications*, 10, 1–8. <https://doi.org/10.1038/s41467-018-08021-z>
- Hard, J. J., Gross, M. R., Heino, M., Hilborn, R., Kope, R. G., Law, R., & Reynolds, J. D. (2008). Evolutionary consequences of fishing and their implications for salmon. *Evolutionary Applications*, 1, 388–408. <https://doi.org/10.1111/j.1752-4571.2008.00020.x>
- Hasegawa, K., Okamoto, Y., & Morita, K. (2021). Data from: Japanese chum salmon reproductive traits. Dryad, Digital Repository. <https://doi.org/10.5061/dryad.pc866t1pr>
- 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>
- Hendry, A. P., Dittman, A. H., & Hardy, R. W. (2000). Proximate composition, reproductive development, and a test for trade-offs in captive sockeye salmon. *Transactions of the American Fisheries Society*, 129, 1082–1095. [https://doi.org/10.1577/1548-8659\(2000\)129%3C1082:PCRDAA%3E2.0.CO;2](https://doi.org/10.1577/1548-8659(2000)129%3C1082:PCRDAA%3E2.0.CO;2)
- Hutchings, J. A. (1991). Fitness consequences of variation in egg size and food abundance in brook trout *Salvelinus fontinalis*. *Evolution; International Journal of Organic Evolution*, 45, 1162–1168. <https://doi.org/10.1111/j.1558-5646.1991.tb04382.x>
- Inoue, M., Sakamoto, S., & Kikuchi, S. (2013). Terrestrial prey inputs to streams bordered by deciduous broadleaved forests, conifer plantations and clear-cut sites in southwestern Japan: Effects on the abundance of red-spotted masu salmon. *Ecology of Freshwater Fish*, 22, 335–347. <https://doi.org/10.1111/eff.12029>
- Johnston, T. A., & Leggett, W. C. (2002). Maternal and environmental gradients in the egg size of an iteroparous fish. *Ecology*, 83, 1777–1791. [https://doi.org/10.1890/0012-9658\(2002\)083\[1777:MAEGIT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1777:MAEGIT]2.0.CO;2)
- Jonsson, B., & Jonsson, N. (2006). Life-history effects of migratory costs in anadromous brown trout. *Journal of Fish Biology*, 69, 860–869. <https://doi.org/10.1111/j.1095-8649.2006.01160.x>
- Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, 75, 2381–2447. <https://doi.org/10.1111/j.1095-8649.2009.02380.x>
- Jonsson, N., Jonsson, B., & Fleming, I. A. (1996). Does early growth cause a phenotypically plastic response in egg production of Atlantic salmon? *Functional Ecology*, 10, 89–96. <https://doi.org/10.2307/2390266>
- Jump, A. S., Hunt, J. M., & Penuelas, J. (2006). Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology*, 12, 2163–2174. <https://doi.org/10.1111/j.1365-2486.2006.01250.x>
- Kaeriyama, M. (1999). Hatchery programmes and stock management of salmonid populations in Japan. In B. R. Howell, E. Moksness, &

- T. Svåsand (Eds.), *Stock enhancement and sea ranching* (pp. 153–167). Blackwell.
- Kinnison, M. T., Unwin, M. J., Hendry, A. P., & Quinn, T. P. (2001). Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. *Evolution; International Journal of Organic Evolution*, 55, 1656–1667. <https://doi.org/10.1111/j.0014-3820.2001.tb00685.x>
- Kitada, S. (2013). Japanese chum salmon stock enhancement: Current perspective and future challenges. *Fisheries Science*, 80, 237–249. <https://doi.org/10.1007/s12562-013-0692-8>
- Kuparinen, A., & Festa-Bianchet, M. (2017). Harvest-induced evolution: Insights from aquatic and terrestrial systems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160036. <https://doi.org/10.1098/rstb.2016.0036>
- Lowe, E. C., Wilder, S. M., & Hochuli, D. F. (2014). Urbanization at multiple scales is associated with larger size and higher fecundity of an Orb-weaving spider. *PLoS ONE*, 9, e105480. <https://doi.org/10.1371/journal.pone.0105480>
- Martin, T. E., Bassar, R. D., Bassar, S. K., Fontaine, J. J., Lloyd, P., Mathewson, H. A., Niklison, A. M., & Chalfoun, A. (2006). Life-history and ecological correlates of geographic variation in egg and clutch mass among passerine species. *Evolution; International Journal of Organic Evolution*, 60, 390–398. <https://doi.org/10.1554/05-429.1>
- Mayr, E. (1956). Geographical character gradients and climatic adaptation. *Evolution; International Journal of Organic Evolution*, 10, 105–108. <https://doi.org/10.1111/j.1558-5646.1956.tb02836.x>
- McGurk, M. D. (2000). Comparison of fecundity-length-latitude relationships between nonanadromous (kokanee) and anadromous sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Zoology*, 78, 1791–1805. <https://doi.org/10.1139/cjz-78-10-1791>
- McNeil, W. J. (1980). Legal aspects of salmon ranching in the Pacific. In J. E. Thorpe (Ed.), *Salmon ranching* (pp. 383–394). Academic Press.
- Morita, K., Tamate, T., Sugimoto, Y., Tago, Y., Watanabe, T., Konaka, H., Sato, M., Miyauchi, Y., Ohkuma, K., & Nagasawa, T. (2009). Latitudinal variation in egg size and number in anadromous masu salmon *Oncorhynchus masou*. *Journal of Fish Biology*, 74, 699–705. <https://doi.org/10.1111/j.1095-8649.2008.02150.x>
- Morita, K., Fukuwaka, M., Tanimata, N., & Yamamura, O. (2010). Size-dependent thermal preferences in a pelagic fish. *Oikos*, 119, 1265–1272. <https://doi.org/10.1111/j.1600-0706.2009.18125.x>
- Naish, K. A., Taylor, 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](https://doi.org/10.1016/S0065-2881(07)53002-6)
- Neuheimer, A. B., & Taggart, C. T. (2007). The growing degree-day and fish size-at-age: The overlooked metric. *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 375–385. <https://doi.org/10.1139/F07-003>
- Nogawa, H. (2010). Development of artificial salmon propagation in Japan – A foreword-. *Journal of Fisheries Technology*, 3, 1–8. (in Japanese with English abstract)
- Okamoto, Y., Morita, K., & Ohkuma, K. (2015). Egg weight and diameter conversion equations and preliminary results for geographic variation in egg size in *Oncorhynchus* spp. *Nippon Suisan Gakkaishi*, 81, 465–467 (in Japanese) <https://doi.org/10.2331/suisan.81.465>
- Okazaki, T. (1982). Geographical distribution of allelic variations of enzymes in chum salmon *Oncorhynchus keta*, river populations of Japan and the effects of transportation. *Bulletin of the Japanese Society of Scientific Fisheries*, 48, 1525–1535.
- O'Sullivan, R. J., Aykanat, T., Johnston, S. E., Rogan, G., Poole, R., Prodöhl, P. A., de Eyto, E., Primmer, C. R., McGinnity, P., & Reed, T. E. (2020). Captive-bred Atlantic salmon released into the wild have fewer offspring than wild-bred fish and decrease population productivity. *Proceedings of the Royal Society B*, 287, 1671. <https://doi.org/10.1098/rspb.2020.1671>
- Pigeon, G., Festa-Bianchet, M., Coltman, D. W., & Pelletier, F. (2016). Intense selective hunting leads to artificial evolution in horn size. *Evolutionary Applications*, 9, 521–530. <https://doi.org/10.1111/eva.12358>
- Quinn, T. P., Hendry, A. P., & Wetzel, L. A. (1995). The influence of life history trade-offs and the size of incubation gravels on egg size variation in sockeye salmon (*Oncorhynchus nerka*). *Oikos*, 74, 425–438. <https://doi.org/10.2307/3545987>
- Quinn, T. P., Vøllestad, L. A., Peterson, J., & Gallucci, V. (2004). Influences of fresh water and marine growth on the egg size – egg number tradeoff in coho and chinook salmon. *Transactions of the American Fisheries Society*, 133, 55–65. <https://doi.org/10.1577/T03-032>
- Richter, A., & Kolmes, S. A. (2005). Maximum temperature limits for Chinook, coho, and chum salmon, and steelhead trout in the Pacific Northwest. *Reviews in Fisheries Science*, 13, 23–49. <https://doi.org/10.1080/10641260590885861>
- Rivrud, I. M., Sonkoly, K., Lehoczki, R., Csányi, S., Storvik, G. O., & Mysterud, A. (2013). Hunter selection and long-term trend (1881–2008) of red deer trophy sizes in Hungary. *Journal of Applied Ecology*, 50, 168–180. <https://doi.org/10.1111/1365-2664.12004>
- Saccheri, I., & Hanski, I. (2006). Natural selection and population dynamics. *Trends in Ecology and Evolution*, 21, 341–347. <https://doi.org/10.1016/j.tree.2006.03.018>
- Saito, T., Okamoto, Y., & Sasaki, K. (2015). Biological characteristics of chum salmon in Japan. *Bulletin of Fisheries Research Agency*, 39, 85–120 (in Japanese with English abstract)
- Schaefer, D., & Domroes, M. (2009). Recent climate change in Japan – Spatial and temporal characteristics of trends of temperature. *Climate of the Past*, 5, 13–19. <https://doi.org/10.5194/cp-5-13-2009>
- Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, 465, 609–613. <https://doi.org/10.1038/nature09060>
- Seibel, B. A., & Drazen, J. C. (2007). The rate of metabolism in marine animals: Environmental constraints, ecological demands and energetic opportunities. *Philosophical Transactions of the Royal Society B*, 362, 2061–2078. <https://doi.org/10.1098/rstb.2007.2101>
- Seki, J. (2005). Study of characteristic of feeding habitat of juvenile chum salmon and their food environment in the Pacific coastal waters, central part of Hokkaido. *Bulletin of the National Salmon Resources Center*, 7, 1–104 (in Japanese with English abstract).
- Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, 1, 401–406. <https://doi.org/10.1038/nclimate1259>
- Tamate, T., & Maekawa, K. (2000). Interpopulation variation in reproductive traits of female masu salmon, *Oncorhynchus masou*. *Oikos*, 90, 209–218. <https://doi.org/10.1034/j.1600-0706.2000.900201.x>
- Tamate, T., & Maekawa, K. (2006). Latitudinal variation in sexual size dimorphism of sea-run masu salmon, *Oncorhynchus masou*. *Evolution*, 60, 196–201. <https://doi.org/10.1111/j.0014-3820.2006.tb01094.x>
- Taylor, E. B. (1991). A review of local adaptation in Salmonidac, with particular reference to Pacific and Atlantic salmon. *Aquaculture*, 98, 185–207. [https://doi.org/10.1016/0044-8486\(91\)90383-I](https://doi.org/10.1016/0044-8486(91)90383-I)
- Thuiller, W. (2007). Climate change and the ecologist. *Nature*, 448, 550–552. <https://doi.org/10.1038/448550a>
- Todd, C. D., Hughes, S. L., Marshall, C. T., MacLean, J. C., Lonergan, M. E., & Biuw, E. M. (2008). Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. *Global Change Biology*, 14, 958–970. <https://doi.org/10.1111/j.1365-2486.2007.01522.x>

- 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). American Fisheries Society.
- Urawa, S., Sato, S., Takahashi, M., & Saito, T. (2012). Status of hatchery-origin chum salmon in the Bering Sea deduced from otolith mark recoveries. *North Pacific Anadromous Fish Commission Technical Report*, 8, 52–53.
- Van Den Berghe, E. P., & Gross, M. R. (1989). Natural selection resulting from female breeding competition in a Pacific salmon (Coho: *Oncorhynchus kisutch*). *Evolution; International Journal of Organic Evolution*, 43, 125–140. <https://doi.org/10.1111/j.1558-5646.1989.tb04212.x>
- Wootton, R. J. (1990). *Ecology of teleost fishes*. Chapman and Hall.
- Yonemori, T. (1975). A trial analysis of the results obtained from tagging on chum salmon originating from Hokkaido. *International North Pacific Fisheries Commission*, 32, 130–161

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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