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The effect of climate change on the growth of Japanese chum salmon (*Oncorhynchus keta*) using a bioenergetics model coupled with a three-dimensional lower trophic ecosystem model (NEMURO)

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Abstract

From the 1970s to 1990s, a reduction in the body size of Japanese chum salmon (*Oncorhynchus keta*) was observed. To investigate this body size reduction in the North Pacific, we developed a bioenergetics model for chum salmon coupled with the results from a lower trophic ecosystem model embedded into a three-dimensional global model. In the bioenergetics model, respiration and consumption terms are assumed to be functions of water temperature and prey zooplankton density, which are the determining factors of the reduction of body size. The model reproduced the body size of the 1972 and 1991 year classes of chum salmon. The reproduced body size of the 1972 year class was larger than that of 1991 year class, and this result agrees with observations from the Bering Sea. Our model also reproduced the body size trend from l970 to 2000. The prey density, especially in the eastern North Pacific, had a greater influence on the change of body size than did the SST. This suggests that the size reduction of Japanese chum salmon in the 1990s was partly affected by changes in prey zooplankton density. In the context of the global warming scenario, we discuss changes in the migration route of chum salmon and predict that the population of Japanese chum salmon experience significant declines over this century.

Keywords: bioenergetics model, Japanese chum salmon, size reduction, NEMURO, global warming

1. Introduction

Chum salmon *Oncorhynchus keta* are distributed widely in the Northern Pacific and can be divided into North American and Asian groups. The latter can be divided further into Russian and Japanese groups, which show different migration routes (Neave et al., 1980). The stock of the Japanese group is maintained by artificial release (Kaeriyama, 1999, Hiroi, 1998). Hiroi (1998) and Ishida et al. (1993) pointed out the decrease of body size of Japanses chum salmon in 1970s and 1980s. According to Azumaya and Ishida (2004) and Urawa (2000), in spring the released chum salmon in Hokkaido spend three month at the coast of the Okhotsk Sea, stay in the Okhotsk Sea until late fall, then migrate toward the western North Pacific (WNP), and by the next summer migrate into the Bering Sea (BS). In the BS, they prey mainly on zooplankton and increase their weight. In the fall they move into the Gulf of Alaska in the eastern North Pacific (ENP) to spend the winter. They repeat the BS/ENP migration 3-4 times, meaning for 3-4 years, and then when they are ready to mature in the summer of their fourth/fifth year they return to their home rivers in Hokkaido, Japan.

Kaeriyama (1998), Kaeriyama et al. (2004), and Azumaya and Ishida (2000) pointed out that mature salmon are mainly 4 years old (i.e., an ocean age of 3 years), and differences in growth (wet weight and growth rate) can be observed in fish older than 2 years in the Bering Sea. They suggested that the differences in body weight might arise from variability in prey density, the density effect, and water temperature. Morita et al. (2001) analyzed the correlation between salmon growth and the physical environment and described the positive correlation between the water temperature anomaly and the body weight anomaly.

The back-calculated growth rates of juvenile Hokkaido chum salmon obtained from their scales showed that their growth in the Okhotsk Sea increased in the 1990s (Fig. 1). These growth anomalies were strongly positively correlated with sea surface temperature (SST) in the Okhotsk Sea during summer and fall, but SST was negatively correlated with the area covered by sea ice during winter (Kaeriyama et al., 2007). Zooplankton biomass in the Okhotsk Sea has been decreasing since the 1980s (Shuntov and Dulepova, 1996). Therefore, the increase in growth of Hokkaido chum salmon during the 1990s appears to have been affected by the increase in SST and not directly by the decrease in zooplankton biomass in the Okhotsk Sea (Kaeriyama et al., 2007). Sea ice concentrations also have been decreasing during the last 100 years as air temperatures along the Okhotsk Sea coast of Hokkaido have increased (Aota, 1999). Aota (1999) suggested that this phenomenon could be a symptom of global warming. Therefore, increases in the growth of Hokkaido chum salmon in the Okhotsk Sea since

the 1990s might also be related to effects of global warming.

Return rates of chum salmon released from south Korea and Iwate Prefecture, which is located at the northern part of Honshu island, Japan, have decreased since the 1990s, whereas those of Hokkaido chum salmon have increased since the 1976 regime shift (Fig. 2a). In Hokkaido, the chum salmon populations from Nemuro City and the Okhotsk Sea coasts have had return rates that were markedly higher than those of other populations (Fig. 2b). Korean and Iwate chum salmon are distributed in the southern waters, which are influenced by the Tsushima Warm Current during the spring offshore-migration period. Declines in their return rates did not coincide with years of climate regime shifts (1976, 1988, and 1998). These results suggest that global warming can be expected to have positive effects on Hokkaido chum salmon populations in the Okhotsk Sea, but negative effects on Korean and Iwate populations in the Tsushima Warm Current.

In this study, we examined the causes of the observed growth difference of adult chum salmon using a bioenergetics model coupled with the output from the 3-D NEMURO model (NEMURO coupled with three dimensional physical global model, Aita et al., 2007). We also discuss the effect of water temperature increase on chum salmon survival in the near future.

2. Method

The bioenergetics fish model we used follows Rudstam (1988), Ware (1978), Beauchamp et al. (1989) and Trudel et al. (2004). Kamezawa et al. (2007) modified the bioenergetics model for chum salmon. The model includes temperature-dependent and food concentration-dependent terms. Aita et al. (2007) calculated time-dependent features of water temperature and lower trophic compartments using an ecological-physical coupled global 3-D model, and they used NEMURO (Kishi et al., 2007) as an ecological model. Our bioenergetics model used output data from Aita et al. (2007) that was generated by 3-D NEMURO.

In our discussion of the global warming scenario, we used Kawamiya et al.'s (2005) SST (Sea Surface Temperature) data, which predicted physical fields under the SRES A2 scenario. As the predicted SST has bias due to the technical reason, the predicted anomaly of SST was added to the present SST (http://goos.kishou.go.jp).

2.1 Migration

Figure 3 shows a schematic view of the three oceanic spatial domains and the numbers of life stages based on Urawa (2000). The stages are shown in Table 1 after

Kamezawa et al., (2007). In our model, chum salmon migrate among the boxes shown in Fig.3 according to stage transitions shown in Table 1 instantaneously.

2.2 Bioenergetics model

The following equation describes individual fish growth of chum salmon:

$$\frac{dW}{dt} = [C - (R + S + F + E)] \cdot \frac{CAL_z}{CAL_f} \cdot W \qquad 1$$

where C is consumption (g prey·g fish^{-1}·d^{-1}), E is excretion or losses of nitrogenous excretory wastes (g prey·g fish^{-1}·d^{-1}), F is egestion or losses due to feces (g prey·g fish^{-1}·d^{-1}), R is respiration or losses through metabolism (g prey·g fish^{-1}·d^{-1}), S is specific dynamic action or losses due to energy costs of digesting food (g prey·g fish^{-1}·d^{-1}), and CAL_z / CAL_f is the conversion rate between prey and fish. The individual processes are described below. Consumption and respiration are nonlinear functions of fish weight and water temperature. In addition to the physiological parameters, the model requires information about the caloric content of herring (this is seasonal) and prey, diet composition, typical prey densities, and water temperature.

Consumption   C

Consumption is estimated as the proportion of maximum daily ration for chum salmon at a particular mass and temperature. The maximum daily consumption rate (g of prey per g body mass of salmon per day) is estimated using an allometric function of mass from *ad libitum* feeding experiments conducted at the optimum temperature.

The basic form of the consumption function is:

$$C = C_{MAX} \cdot \rho \cdot f_c(T) \qquad (2)$$

$$C_{MAX} = ac \cdot W^{bc} \qquad (3)$$

$$\rho = \frac{v_i}{K_i + PD \cdot v_i} \qquad (4)$$

where C_{max} is the maximum specific consumption rate (g prey·g fish^{-1}·d^{-1}), $f_C(T)$ is a temperature-dependence function for consumption, T is water temperature (ºC), W is salmon mass (g wet weight), and C_{MAX} is the consumption rate (g·g^{-1}·d^{-1}) of an individual predator i, the values of which were determined following Beauchamp et al. (1989) (Table 2). PD is the density of prey (g weight m^{-3}) and v_i is the vulnerability at

stage i, which was determined to be 1 for all stages. K_i is the half saturation constant (g prey m^{-3}), which was determined to be 0.55 referring that of Pacific saury by Ito et al. (2004) (Table 2). a_c is the intercept of the mass-dependence function for a 1 g fish at the optimum water temperature and b_c is the coefficient of the mass dependence.

Thornton and Lessem's (1978) description of temperature dependence is essentially the product of two sigmoid curves – one fit to the increasing portion of the temperature-dependence function (*gcta*) and the other to the decreasing portion (*gctb*).

$$f_c(T) = gcta \cdot gctb \qquad 5$$

where

$$tt5 = \frac{1}{te2 - te1} \qquad 6$$

$$t5 = tt5 \cdot alog\left[0.98 \cdot \frac{1.0 - xk1}{0.02 \cdot xk1}\right] \qquad 7$$

$$t4 = e^{[t5 \cdot T - te1]} \qquad 8$$

$$tt7 = \frac{1}{te4 - te3} \qquad 9$$

$$t7 = tt7 \cdot alog\left[0.98 \cdot \frac{1.0 - xk4}{0.02 \cdot xk4}\right] \qquad 10$$

$$t6 = e^{[t7 \cdot te4 - T]} \qquad 11$$

$$gcta = \frac{xk1 \cdot t4}{1.0 + xk1 \cdot t4 - 1.0} \qquad 12$$

$$gctb = \frac{xk4 \cdot t6}{1.0 + xk4 \cdot t6 - 1.0} \qquad 13 \quad ,$$

and where *te1* is the lower temperature at which the temperature dependence is a small fraction, *xk1*, of the maximum rate and *te2* is the water temperature corresponding to *xk2* of the maximum consumption rate in increasing portion of the curve. For the decreasing portion of the curve, *te3* is the water temperature ($\geq$ *te2*) at which dependence is *xk3* of the maximum, and *te4* is the temperature at which dependence is some reduced fraction *xk4* of the maximum rate. Welch et al. (1995) showed that salmon in the ENP occur where SST is below 10.4°C in spring and between 8°C and 12°C in summer. Nagasawa (2000) reported that salmon are distributed between 3.9°C and 5.0°C in the WNP and between 5.2°C and 6.7°C in the central Pacific. Consequently, we chose the parameter values shown in Table 2 to use in our model.

Respiration and metabolism   R

The respiration rate is the amount of energy used for routine metabolism and it depends on body weight, ambient temperature, and activity (swimming speed) (Trudel et al., 2004; Ware, 1978). The equations below illustrate how R is calculated.

$$R = Rs + Ra \cdot 5.258 \qquad\qquad 14$$

$$Rs = ars \cdot W^{br} \cdot \exp \quad cr \cdot T \qquad 15$$

$$Ra = ara \cdot W^{dr} \cdot U^{er} \qquad\qquad 16$$

$$U = au \cdot W^{bu} \qquad\qquad 17$$

$$\left(\frac{13560\,joules}{gO_2} \cdot \frac{1cal}{4.18\,joules} \right) \div \left(\frac{2580\,joules}{g\,zoop} \cdot \frac{1cal}{4.18\,joules} \right) = 5.258\;g\;\;zoop/gO_2$$

where

Rs   standard metabolism

ars   Oxygen consumption rate at 0°C per 1 g wet weight which depends on temperature

Ra   metabolism when the fish moves

ara   Oxygen consumption rate at 0°C per 1 g wet weight which depends on activity

U   swimming speed

5.258   conversion rate from $g\,0_2\,g\,fish^{-1}\,day^{-1}$ to $g\,prey\,g\,fish^{-1}\,day^{-1}$ (Megrey et al., 2002)

zoop :zooplankton biomass

br, cr, dr, er, au, bu: constants defined in Table 2.

Specific dynamic action (SDA) = losses due to energy costs of digesting food, egestion (F), and excretion(E)

These three terms can be calculated as follows,

$$SDA = S \cdot (C - F) \qquad\qquad 19$$

$$F = a_F \cdot C \qquad\qquad 20$$

$$E = a_E \cdot (C - F) \qquad\qquad 21$$

SDA is the proportion of assimilated energy lost to specific dynamic action, *C* is the specific consumption rate (g·g^{-1}·d^{-1}), and *F* is the specific egestion rate (g·g^{-1}·d^{-1}). Egestion (*F*, fecal waste) and excretion (*E*, nitrogenous waste) can be computed as a constant proportion of consumption.

S, a_F, a_E constant

These values used in our model were taken from Ito et al. (2004), in which they were determined for Pacific saury. Although the ecology and physiology of chum salmon differ from those of saury, these values are supported to be useful to the other species in the Northern Pacific (Megrey et al., 2007a,b; Rose at al., 2007), thus we used the same values.

2.3 NEMURO ecosystem model

The prey density and water temperature values in our bioenergetics model were obtained from Aita et al. (2007), who calculated a 3-D physical-ecological coupled model (3-D NEMURO) for the northern Pacific from 1948 to 2002. We used the daily averaged output for the upper 20 m of the water column and also averaged spatially within each box. In the Gulf of Alaska, chum salmon prefer jelly fish rather than copepods (Kaeriyama et al., 2004), and we assumed predatory zooplankton (PZ) to be prey: in NEMURO, ZP includes jerry fish, salps, and/or krill (Kishi et al., 2007). NEMURO describes zooplankton density as nitrogen density (mol N l^{-1}) and we converted it into wet weight following Megrey et al., 2002)

$$\frac{14\mu \, g\mathrm{N}}{\mu \, \mathrm{moleN}} \cdot \frac{1.0\mathrm{e}^{-6}g}{\mu \, g} \cdot \frac{1g\mathrm{dry \, weight}}{0.07\mathrm{Ndry \, weight}} \cdot \frac{1g\mathrm{wet \, weight}}{0.2\mathrm{dry \, weight}} \cdot \frac{1.0\mathrm{e}^{3}\mathrm{litters}}{\mathrm{m}^{3}} \qquad 22$$

However, the converted value is smaller than the observed value (Kamezawa et al. 2007). Kamezawa et al. (2007) converted ZP from NEMURO based on WOA (World Ocean Atlas) 2003 and NPAFC (North Pacific Anandromous Fish Commission) 2004 as follows:

$$\frac{\mathrm{observational \, zooplankton \, value}}{\mathrm{ZP \, value \, Aita \, et \, al. \, 2007}} = 1.937 \qquad 23$$

$$\mathrm{ZP} = \mathrm{ZP} \times 1.937$$

24

In our global warming scenario, we used predicted water temperature taken from Kawamiya et al. (2005), who simulated physical fields according to the IPCC IS92a global warming scenario. We used the outputs from Kawamiya et al. (2005) to simulating responses of Japanese chum salmon to global warming.

2.4 Time steps for the bioenergetics model

Urawa (2000) suggested that the inter-annual variations in wet weight of chum salmon can be observed after they migrate into the WNP from the Okhotsk Sea. In our analysis, we excluded the juvenile period spent in the Okhotsk Sea and begin the

simulation at age 404 days when the fish are in the WNP. The time step used was 3600 sec and zooplankton density and water temperature were taken from Aita et al. (2007).

2.5 Global warming scenario

Welch et al. (1998) suggested that the geographic distribution of sockeye salmon in the BS will shrink if the atmospheric CO_2 base doubles based on the present relationship between the CPUE (Catch Per Unit Effort) and SST. We introduce a similar procedure for chum salmon. The survival of chum salmon released into the Hokkaido River is well correlated with the water temperature of the Okhotsk Sea while the fish remain there (Kaeriyama et al., 2007). In addition, the optimal temperature for chum salmon in the BS can be estimated based on the relationship between CPUE and SST (Ueno and Ishida, 1996), and Fukuwaka et al. (2007) estimated the optimal temperature for the salmon's time spent in the NWP during winter. Based on the above literature, we propose the following criteria for the survival of chum salmon of Hokkaido stock;

Growth, Feeding : 8–12   : 1st year in the Okhotsk Sea (July–October)
Wintering: 4–6   : 1st year in WNP (November–June)
Growth, Feeding: 8–12   : 2nd year in the Bering Sea (July–October)
Wintering: 4–6   : 2nd year in the Gulf of Alaska (November–June)

3. Results and discussion

Figure 4 shows the time series of the simulated body weight of chum salmon for the 1972 year class (a) and the 1991 year class (b) together with observed body weight (Kamezawa et al., 2007). Figure 4-(c) shows the difference in wet weight between the 1972 and 1991 year classes for the control case (thin line), for the constant prey with time-dependent temperature case (bold line), and for the constant temperature with time-dependent prey case (dashed line). The time derivative of growth in summer (April to November) is larger than that in winter (December to March) in each case, because the growth rate becomes high due to high temperature in this area. And the difference in growth between these two year classes was caused by differences in prey density in the ENP during winter to spring (from February to July) of ocean age 3 and 4 fish. Figure 5 shows the time-dependent features of body weight of chum salmon in the BS in summer from 1971 to 1999, **a) observed and b) simulated results.** Simulated results describe the observed features well: 1) Ocean age 1 does not exhibit interannual variation; 2) from ocean ages 2 to 4, interannual variation of body weight is evident; and 3) the data show a log trend of decrease from 1970s through the 1990s and an increase in the late 1990s. The correlation coefficients between the observed and the

simulated results are -0.19, 0.45, 0.43 an 0.65 for ocean age of 1, 2, 3 and 4, respectively (significant). The inter-annual variations in body weight were caused mainly by differences in prey density, which were brought about by interannual variation in climate change, like PDO (Pacific Decadal Oscilation)   According to Aita et al., (2007), PDO brought about decadal zooplankton/phytoplankton density anomaly. The present model does not include feedback from feeding pressure by salmon to the lower trophic ecosystem, however, we should include top-down effects in future. Consequently we can conclude that inter-annual climate change brought about the change of prey density in the Gulf of Alaska, and the inter-annual body weight anomaly of chum salmon was caused. This means that without a competition among species, we can explain the time dependent change of body size of chum salmon to some extent.

We pointed out that the prey density plays important role in the wet weight of chum salmon described above, however, as pointed in section 2.5, sea surface temperature must also play an important role in the distribution area. The Intergovernmental Panel on Climate Change (IPCC) concluded in its Fourth Assessment Report of 2007 that global warming caused by human activity is indeed taking place. What impact will global warming have on salmon? We predicted the situation for chum salmon in 2050 and 2095 based on the IPCC SRES-A1B scenario using their optimal temperature. The hatched portions of Figures 6 and 7 represent the areas in which chum salmon can survive based on the estimated SST increase. The survival conditions are described in section 2.5. Our model predicts that (1) in the North Pacific, the habitat in eastern waters (i.e., the Gulf of Alaska) decreases significantly, and chum salmon distribution area moves northward and increases in parts of the Arctic Ocean during summer; the carrying capacity of chum salmon would decrease specifically in the subarctic area. (2) Hokkaido chum salmon could lose their migration route to the Sea of Okhotsk by 2050, and the population experience significant declines over this century. (3) In the BS, the carrying capacity of chum salmon would significantly decrease by 2050, it encounters strict density-dependence effects, and the population would lose its distribution area by 2100.

4. Future works

In the bioenergetics model, we assumed the date of migration to be determined by calendar date, but this assumption does not consider the ecological demands of the fish. We should include in the model the relationship between growth and migration date. We did not include the density effect of salmon either. Tadokoro et al. (1996) pointed out that there is bimodal competition for prey between chum salmon and pink

salmon, and this effect also must be included in the next step. In our global warming scenario, we used averaged water temperature in the top 20 m of the water column, but salmon might opt for deeper depths when swimming and migrating and only use shallower depths when feeding. This kind of change of ecological behavior is not considered in our discussions. Moreover, chum salmon might adapt to warmer temperatures. Consequently, this paper analyzed environmental effects on chum salmon growth and only suggests possible outcomes for the future.

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Figure captions

Fig. 1. Annual change in growth at the first year of Ishikari River chum salmon in the Okhotsk Sea (Kaeriyama et al., 2007).

Fig. 2. Temporal changes in return rate of a) Hokkaido, Iwate, and Korean chum salmon populations and of b) local populations in Hokkaido.

Fig. 3. Schematic view of the three oceanic spatial domains and the numbers of life stages simulated in the model. The three oceanographic domains correspond to the western North Pacific (WNP), the Bering Sea (BS), and the eastern North Pacific (ENP).

Fig. 4. Simulated wet weight (line) and observed wet weight (squares) for a) the 1972 year class and b) the 1991 year class. c) The difference in wet weight between the 1972 and 1991 year classes for the control case (thin line), for the constant prey with time-dependent temperature case (bold line), and for the constant temperature with time-dependent prey case (dashed line).

Fig. 5. Time-dependent feature of body size in the Bering Sea in summer from 1971 to 1999. a) observed (based on data base of FRA, Japan) and b) simulated results.

Fig. 6. The impact of global warming on the ocean distribution of chum salmon based on the ICPP SRES-A1B scenario. Hatched portion represents the area where chum salmon can survive.

Fig. 7. The impact of global warming on the ocean distribution of chum salmon based on the ICPP SRES-A1B scenario near Hokkaido, Japan.

Table captions

Table 1. Life stages of the chum salmon bioenergetics model.

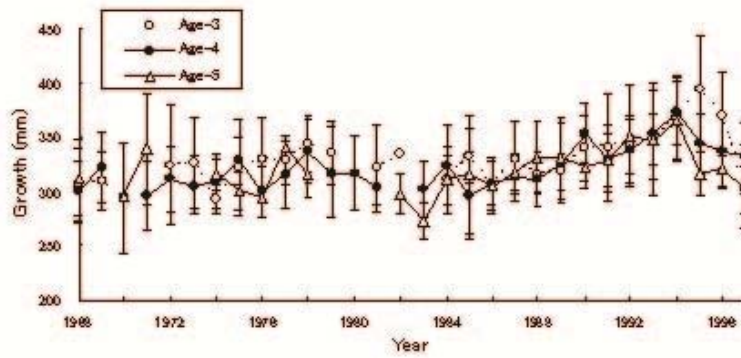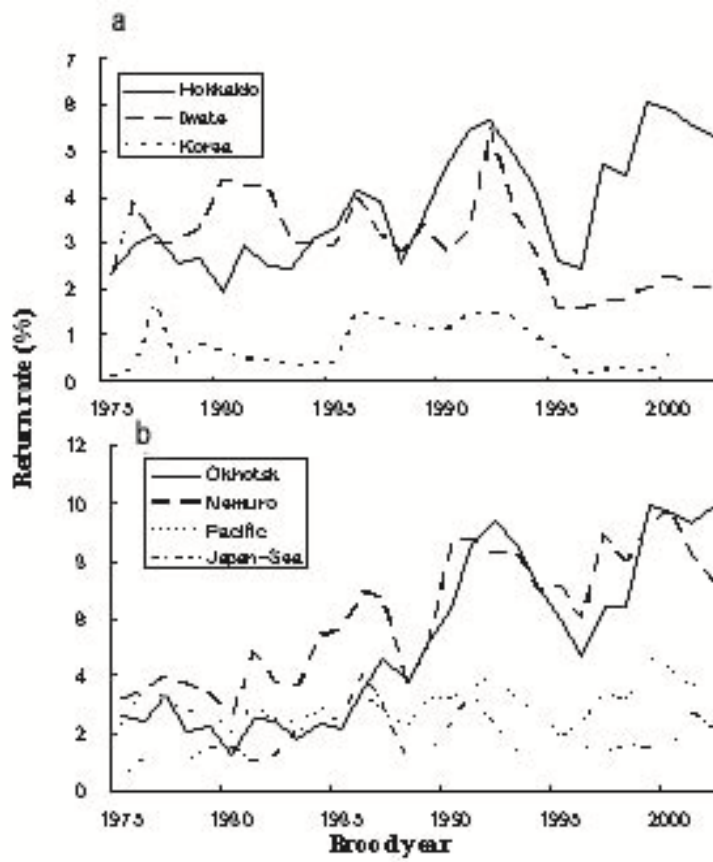Table 2. Summary of parameter values used in the chum salmon bioenergetics model.
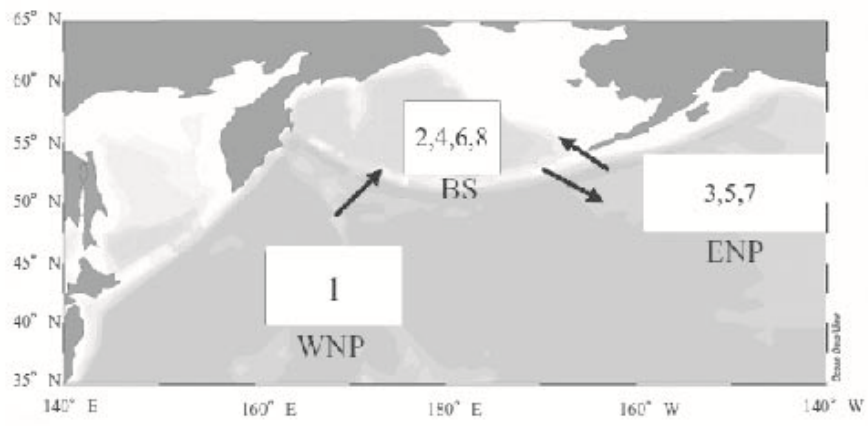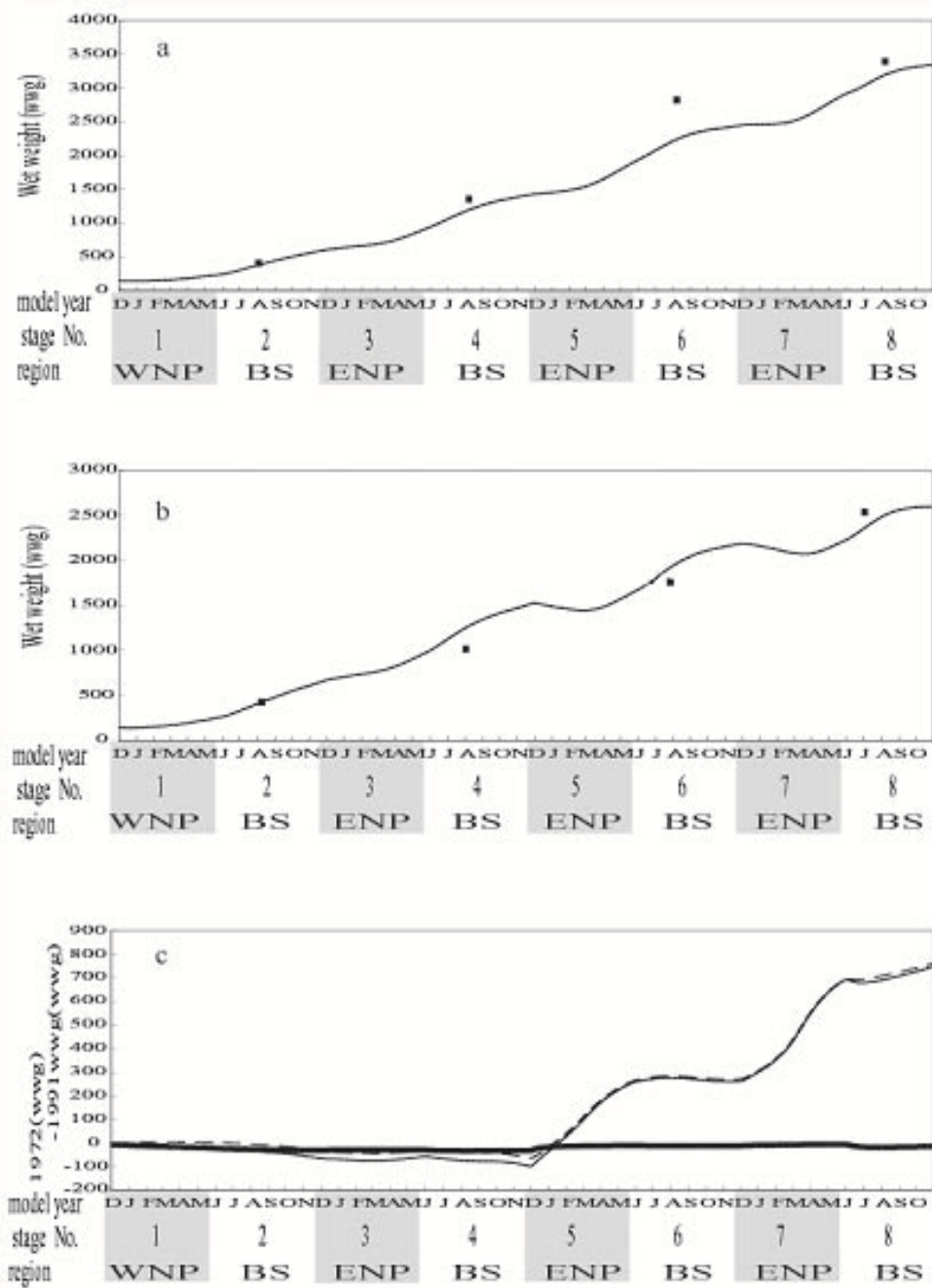
Fig.1

Fig.2

Fig.3

Fig.4
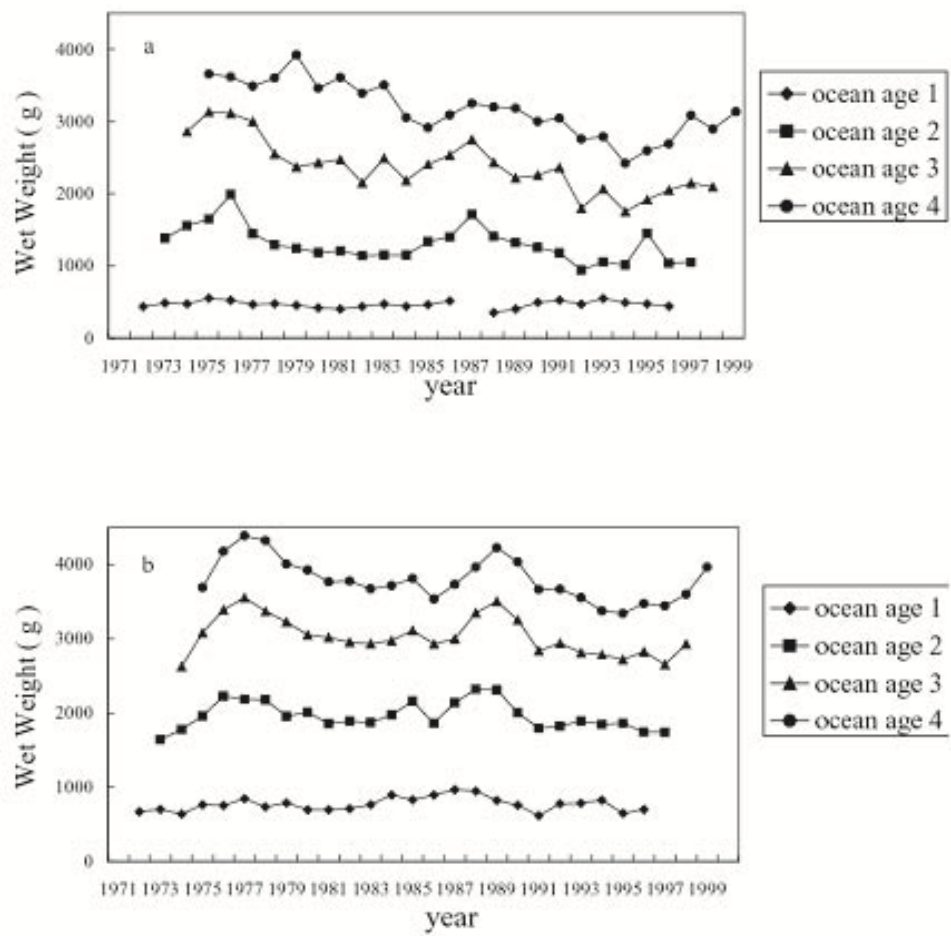
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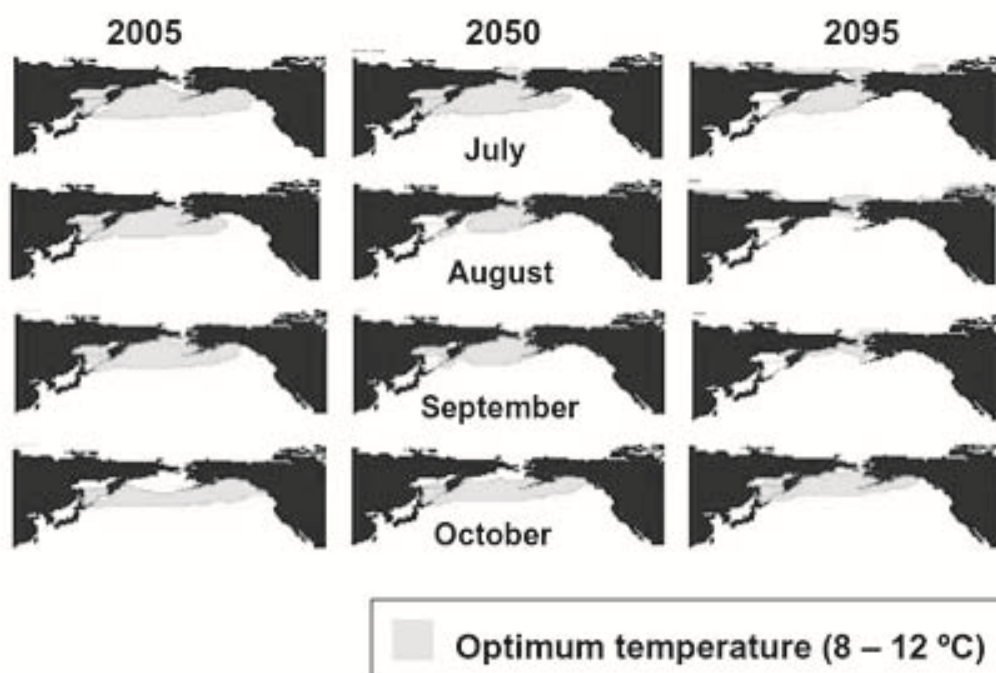
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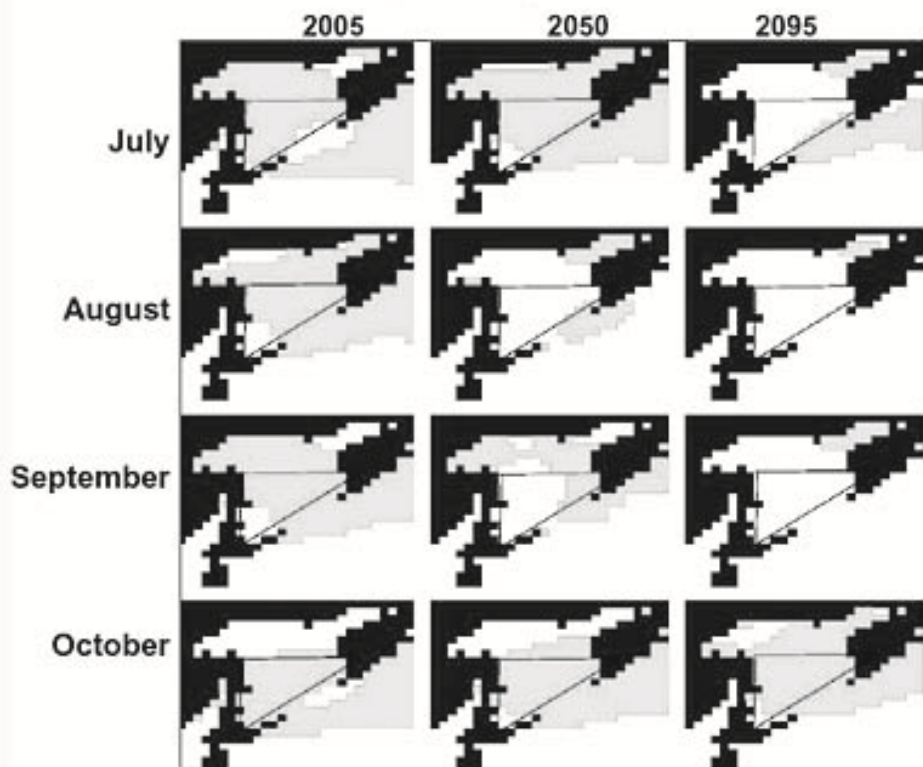
Fig.7

Stage	Ages(day)	Period	Region
1	404–586	12/1–5/31	W.North Pacific (WNP)
2	587–769	6/1–11/30	Bering Sea (BS)
3	770–951	12/1–5/31	E.North Pasific (ENP)
4	952–1134	6/1–11/30	Bering Sea (BS)
5	1135–1316	12/1–5/31	E.North Pasific (ENP)
6	1317–1499	6/1–11/30	Bering Sea (BS)
7	1500–1681	12/1–5/31	E.North Pasific (ENP)
8	1682–1834	6/1–10/31	Bering Sea (BS)

Table 1

Symbol	Parameter description	Value
Consumption,Cmax		
ac	Intercept for Cmax parameter	0.303
bc	Coefficient for Cmax parameter versus weight	-0.275
xk1	Proportion of Cmax for te1	0.1
xk2	Proportion of Cmax for te2	0.98
xk3	Proportion of Cmax for te3	0.98
xk4	Proportion of Cmax for te4	0.5
te1	Temperature for xk1	3.0
te2	Temperature for xk2	3.9^a 5.0^b
te3	Temperature for xk3	5.0^c 10.0^b 8.0^d
te4	Temperature for xk4	10.4^a 12.0^b
K_i	Half saturation constant	0.55^e
Metabolism,R		
ars	Intercept for standard metabolic rate of 1-g fish at 0°C	0.0799
br	Coefficient standard metabolism versus body weight	0.8
cr	Coefficient standard metabolism versus temperature	0.069
ara	Intercept for swimming cost	eqn(11)
dr	Coefficient for swimmng cost versus body weight	0.44
er	Coefficient for swimmng cost versus swimming speed	2.42
Swimming Speed,U		
au	Intercept, for optimal foraging speed	20.3
bu	Coefficient versus weight	0.132
Egestion and Excreation,F , E and SDA		
af	Propotion of consumed food egested	0.16
ae	Propotion of consumed food excreted	0.1
ss	Coefficient for Specific Dynamic Action	0.175
Cal		
CALf	Caloric equivalent of fish	1323.68
CALz	Caloric equivalent of zooplankton	617.22

[a] value for stage1,3,5,7 chum salmon
[b] value for stage2,4,6,8 chum salmon
[c] value for stage1 chum salmon
[d] value for stage3,5,7 chum salmon
[e] value for stage1–8 chum salmon

Table 2