

ORIGINAL ARTICLE

Increase in maturation size after the closure of a high seas gillnet fishery on hatchery-reared chum salmon *Oncorhynchus keta*

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Keywords

fishery-induced evolution, gillnet selectivity, high seas fishery, maturation threshold, ocean growth, phenotypic plasticity.

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Received: 5 November 2007

Accepted: 6 February 2008

First published online 18 March 2008

doi:10.1111/j.1752-4571.2008.00029.x

Abstract

Gillnet fisheries are strongly size-selective and seem to produce changes in size at maturity for exploited fishes. After World War II, large-scale gillnet fisheries targeted Pacific salmon (*Oncorhynchus* spp.) in the high seas area of the North Pacific and the Bering Sea, but these fisheries were closed in 1993. To assess the effects of this high seas gillnet fishery (and its closing) on size at maturity, we examined long-term trends in size at 50% probability of maturing (L_{50}) for chum salmon (*O. keta*) from three populations in Hokkaido, Japan. The L_{50} trends were statistically different among rivers, but showed similar temporal patterns with decreases in the 1970s and early 1980s and increases after the 1985 brood year. While fishery-induced evolution seemed largely responsible for this temporal change in L_{50} during the fishing period, natural selection and phenotypic plasticity induced by environmental changes could contribute to the increases in L_{50} after the relaxation of fishing pressure.

Introduction

Fisheries can cause evolutionary changes toward smaller body sizes and younger ages at maturity (reviewed by Law 2000). This can occur through at least two different mechanisms. One mechanism is an increase in total mortality as a result of adding fishing mortality to natural mortality. This increased total mortality can select for earlier maturity, and therefore a smaller size at maturity (Reznick and Ghalambor 2005). A second mechanism is size-selective mortality that occurs because various fishing methods can be biased toward the capture of certain phenotypes (Stokes et al. 1993). The prevalence of fishery-induced evolutionary change, as a result of some combination of these mechanisms, has been revealed through decreases in fish size or age at maturity during periods vulnerable to fisheries (e.g., Ricker 1981, 1995; Rijnsdorp 1993; Trippel 1995; Olsen et al. 2004).

If a decrease in size or age at maturity is the result of fishery-induced evolution, an increase size or age at maturity would be expected owing to natural selection after the relaxation of fishing pressure, such as would

result from fisheries closures or moratoria. For example, recent studies of pike (*Esox lucius* L.) show that natural selection and fishery selection often act in opposite directions, which causes somatic growth to increase after the relaxation of fishing pressure (Carlson et al. 2007; Edeline et al. 2007). However, increases or recoveries of maturation size after fishery closures or moratoria have rarely been reported (*cf.*, Olsen et al. 2004). Thus, we examined whether the maturation size of chum salmon [*Oncorhynchus keta* (Walbaum)] increased after the closure of a high seas fishery.

Japanese high seas fisheries targeting Pacific salmon (*Oncorhynchus* spp.) were conducted in the central North Pacific and the Bering Sea. Chum salmon caught in the Bering Sea fishery area appeared to originate from Russia and Japan (Ishida et al. 1989). These high seas salmon fisheries developed in the 1950–1970s, decreased in the 1980s, and were closed in 1993 because of enforcement of the Convention for the Conservation of Anadromous Stocks in the North Pacific. This act prohibits salmon harvesting in international waters of the North Pacific and adjacent seas, with the exception of research

activities. High seas salmon fishermen used gill nets with ≥ 121 -mm mesh sizes (Harris 1989). Gillnet fisheries are size-selective and can provide a strong selective force for the evolution of life history traits (Handford et al. 1977; Ricker 1981).

Over the last few decades, the size at maturity of chum salmon has decreased in many populations (reviewed by Bigler et al. 1996). These trends are often interpreted as plastic responses of somatic growth rates resulting from environmental changes or density dependence (Ishida et al. 1993; Helle and Hoffman 1998; Kaeriyama 1998). For example, ocean somatic growth of chum salmon decreased in the 1970s and 1980s, when chum salmon abundance in the North Pacific Ocean increased (Fukuwaka et al. 2007). Under such variable conditions, organisms might be selected for particular plastic responses to specific environmental conditions, i.e., different 'reaction norms' (Stearns 1992; Chapter 6). Of most interest, here is the probability of maturity at a given size and age, the so-called probabilistic maturation reaction norm (PMRN). Recent work has shown how these PMRNs can be used to deduce evolutionary change while controlling for plastic variation in growth rates (Heino et al. 2002; Dieckmann and Heino 2007). We applied this method to recent changes in maturation size in Japanese chum salmon, as the change might be the result of adaptive evolution (Morita et al. 2005). Note that size at maturity (average body size of mature individuals) and PMRN (usually the reaction norm midpoint at the 50% maturation probability) are different measures and could show opposite trends (Morita and Fukuwaka 2007).

Thus, the objectives of this study were to describe temporal changes in maturation sizes for chum salmon before and after the closure of the high seas gillnet fishery. We specifically use the PMRN method to compare these changes to temporal changes in fishery-induced selection and natural selection. However, temporal changes in the PMRN will not necessarily provide a reliable indicator of genetic change, because PMRNs can change plastically with somatic growth (Morita and Fukuwaka 2006, 2007; Law 2007). One way to lessen this problem might be to compare observed changes to those expected based on natural selection (Swain et al. 2007). To this end, we compared the observed PMRNs to estimates of optimal maturation thresholds, with and without fishing mortality.

Materials and methods

Hatchery chum salmon populations

We examined chum salmon populations in the Chitose River (a tributary of the Ishikari River), the Nishibetsu River, and the Tokachi River, all in Hokkaido, Japan. The

Chitose River is located in central Hokkaido and discharges into the Sea of Japan, near where a salmon hatchery was built in 1888. The Nishibetsu River is located in eastern Hokkaido and discharges into the Nemuro Strait between the Sea of Okhotsk and the Pacific Ocean, near a salmon hatchery built in 1890. The Tokachi River is located in eastern Hokkaido and discharges into the Pacific Ocean, near a salmon hatchery built in 1899. Chum salmon populations in these three rivers/hatcheries are genetically isolated from each other (Okazaki 1982). Little information is available on natural spawning populations in these three rivers, although a small number of carcasses ($< 100^{-1}$), potentially from naturally spawning adults, have been observed in the upper reaches of the Chitose River (Ito et al. 2005). Regardless, we consider our study populations to be of hatchery origin, as is the case for nearly all Japanese chum salmon (Hiroi 1998).

After release from hatcheries to rivers, Japanese chum salmon migrate widely in the North Pacific and adjacent waters (Fig. 1). The oceanic migration of chum salmon is a feeding migration, with individuals feeding on zooplankton such as jellyfish, ctenophores, and crustaceans (Quinn 2005). Japanese chum salmon are distributed in the Sea of Okhotsk during their first summer of ocean life, but move to the Bering Sea for their second and sub-

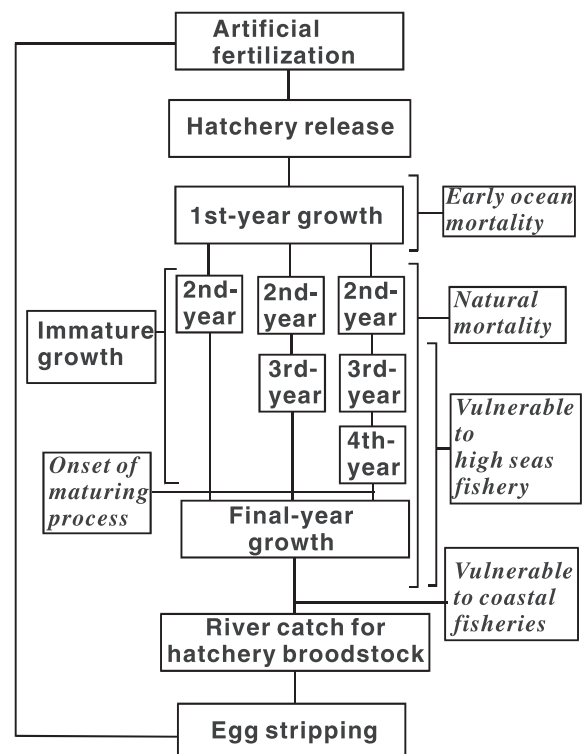


Figure 1 Schematic diagram of the life history of hatchery-reared chum salmon.

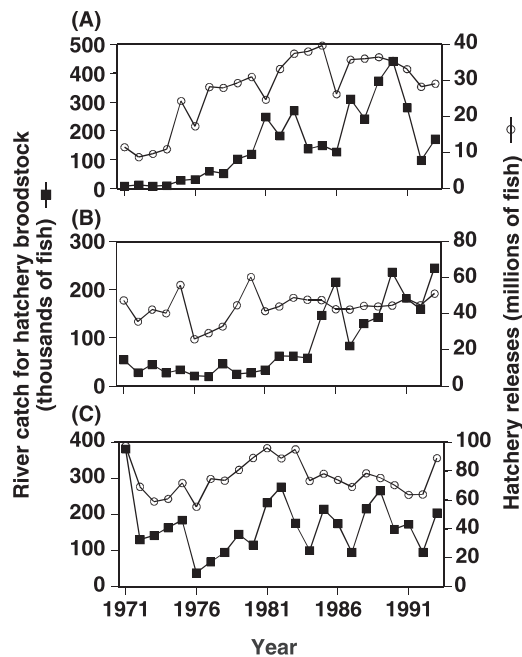


Figure 2 Numbers of hatchery broodstock caught in rivers and releases of chum salmon in the Chitose River (A), Nishibetsu River (B), and Tokachi River (C), 1971–1993.

sequent summers (Urawa et al. 2001). Somatic growth rates are highest during the summer (Ishida et al. 1998), and annual natural mortality coefficients (i.e., the instantaneous mortality rate caused by sources other than fisheries) range from 0.156 to 0.316 year⁻¹ during offshore stages (Parker 1962; Ricker 1964, 1976). In the Bering Sea, immature and maturing chum salmon were vulnerable to the high seas fishery, which was size-selective (more details are provided below). In chum salmon, onset of the maturation process should occur at 3–5 years of age at or before the spring preceding the final year of ocean life (T. A. Onuma, H. Katsumata, K. Makino, M. Fukuwaka, P. Swanson and A. Urano, unpublished manuscript). During spawning migrations toward natal rivers, maturing chum salmon were vulnerable to coastal fisheries that primarily used trap nets. We assume that the coastal trap nets were not size-selective because the mesh sizes (≤ 105 mm in Hokkaido) were too small for maturing chum salmon to escape.

After entering their natal river, most fish were collected in a fish weir set to capture hatchery broodstock. The numbers of adult chum salmon caught for hatchery broodstock in the Chitose and Nishibetsu Rivers increased from the 1970s to the 1990s, showing a similar temporal trend to that for the total catch of Asian chum salmon. Catches in the Tokachi River were relatively stable over this period [Fig. 2; Hokkaido Salmon Hatchery (HSH)

(1972–1997a); National Salmon Resources Center (NSRC) 1998–2004a]. Because they are semelparous, adult chum salmon were killed before egg or sperm stripping. Stripped eggs were artificially fertilized with sperm and incubated in a salmon hatchery. Juveniles were reared with dry pellet feed and released from the hatchery to the river in the spring of the subsequent year at *ca.* 5 cm fork length. The number of juveniles released into the Chitose River was stable from the late 1970s to the 1990s, and releases into the Nishibetsu and Tokachi Rivers were stable from the 1970s to the 1990s (Fig. 2). This stability was largely because of fixed hatchery carrying capacities, determined by the size and number of fish at release and the amount of available water (Websters 2001). Adult salmon caught in rivers exceeding hatchery capacity were not used for breeding. Although artificial selection or domestication selection is certainly possible in hatcheries (McLean et al. 2005; reviewed by Waples 1991, 1999; Reisenbichler and Rubin 1999), such information is not available for our study populations.

High seas salmon fisheries in the North Pacific included two main types. The mothership fishery involved approximately 40 catcher boats that delivered salmon to a factory ship (i.e., the mothership), which then produced canned, salted, and frozen salmon. In contrast, land-based fisheries involved individual fishing boats that delivered salmon to a base port for processing. In the Bering Sea and central North Pacific, the mothership fishery operated from 1952 to 1989 and then changed to a land-based fishery from 1990 to 1993. In the western North Pacific, a land-based fishery predominated from 1952 to 1993. The best fishing season for chum salmon in the mothership fishery was in July (Peterson 1974). During the summer, Japanese populations accounted for a high proportion of chum salmon in the Bering Sea (Ishida et al. 1989; Seeb et al. 2004). Chum salmon catches from the high seas fisheries in the central North Pacific and the Bering Sea accounted for 0.5–33% of total Asian chum salmon catches, including the high seas fishery in the western North Pacific and the coastal and riverine catches, during 1969–1991 (Fig. 3; Eggers et al. 2003). In the 1960s and 1970s, chum salmon catches in the central North Pacific and the Bering Sea were larger than before. While catches in the central North Pacific and the Bering Sea decreased after 1979, catches in other areas, mainly coastal fisheries, increased rapidly in the 1980s.

Estimation of threshold size for maturation

To estimate mean threshold size for maturation of chum salmon, we estimated fork length at 50% maturity, L_{50} , from adult chum salmon returning to the three rivers. We examined only females because fecundity selection

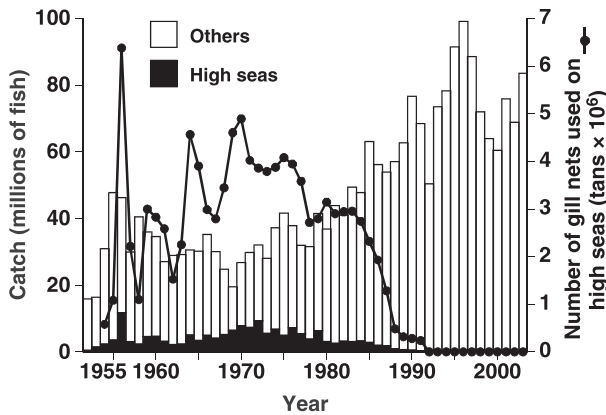


Figure 3 Chum salmon catches in Asia (bars) and number of gill nets used in the high seas area (line) from 1952 to 2003. The solid bar indicates the catch in the high seas area east of 170°E. The open bar indicates catches along the Asian coasts, in rivers, and in offshore areas west of 170°E. The number of gill nets used during 1952 and 1953 was not available. One tan (panel) of gill net is ca. 50 m in length and ca. 7 m in height.

acted on female optimal maturation threshold. Returning females were caught in rivers from 1976 to 1997, mainly using fish weirs. In total, 6911 females were sampled; each individual fork length (cm) was measured, and a scale was collected from the region between the dorsal and anal fins and near the lateral line. Fish age was determined by counting the number of annuli on a scale.

We estimated $L50$ using back-calculated fork lengths at immature and maturing ages because the timing of the onset of maturity is nearly coincident with the timing of annulus formation (winter to spring) (Fukuwaka 1998; Campbell et al. 2003; T. A. Onuma, H. Katsumata, K. Makino, M. Fukuwaka, P. Swanson and A. Urano, unpublished manuscript). Scale radii, from the center of focus to every annulus and to the edge of the scale, were measured to the nearest micrometer along the longest axis of the scale using a video micrometer system. The biological intercept method was used to estimate fork length at each ocean age (Campana 1990). In the biological intercept back-calculation, we used a 4-cm fork length and a 114 μm scale radius as the base points (Fukuwaka and Kaeriyama 1994).

To estimate $L50$, we used the PMRN method with a generalized linear model (GLM) with maturity as a binary dependent variable (i.e., mature or immature), back-calculated fork length and age as continuous independent variables, and brood year as a categorical independent variable (Heino et al. 2002). In this estimation, we assumed a quasibinomial distribution of error, allowing a larger variance than the nominal variance of a binomial distribution because of the overdispersion of maturity

variables (McCullagh and Nelder 1989; R Development Core Team 2007). We used the statistical package R version 2.5.1 (The R Foundation for Statistical Computing) for the estimations (R Development Core Team 2007). The model equation was

$$\text{logit}(\text{maturity}) = \alpha_b + \beta_1(\text{fork length}) + \beta_2(\text{age}), \quad (1)$$

where α_b was the intercept for brood year b , and β_1 and β_2 were slopes (Heino et al. 2002). Age-specific $L50$ was calculated as

$$L50_{b,\text{age}} = -\frac{[\alpha_b + \beta_2(\text{age})]}{\beta_1}. \quad (2)$$

Confidence limits for $L50$ were estimated using the delta method from the covariance matrix of parameters.

When immature fork lengths are back-calculated from scales of mature fish, the estimated $L50$ can be biased by mortality suffered during immature ages (Morita et al. 2005). Thus, to correct the bias because of natural and fishing mortality, the maturity variable was weighted by estimating the number of fish alive at a specific age per number of samples, assuming that the exploitation rate of coastal fisheries was constant and uniform:

$$W_{r,b,a,m} = \frac{C_{r,y=b+m}A_{r,y=b+m,m}/N_{r,b,a,m}}{\exp[-(m-a)M] \prod_{y=b+a}^{b+m} [1 - H_y S(l_{y-b})]}, \quad (3)$$

where

$$H_y = 1 - \exp(-qE_y),$$

$$S(l_a) = \exp\left[-\frac{(l_a/12.1 - R_1)^2}{2\sigma_1^2}\right] + \omega \exp\left[-\frac{(l_a/12.1 - R_2)^2}{2\sigma_2^2}\right],$$

$$l_a = \frac{FL_a + FL_{a+1}}{2},$$

$W_{r,b,a,m}$ was weighted for fish age at maturity m for brood year b at river r and back-calculated age a . $C_{r,y}$ was the number of fish caught in river r in year y ; $A_{r,y,m}$ was the proportion of fish of age at maturity m caught in year y and river r ; $N_{r,b,a,m}$ was the number of samples of age at maturity m for brood year b at river r and back-calculated age a ; M was the natural mortality coefficient for ocean life; H_y was the encounter rate of fish to gill nets; q was the catchability coefficient; E_y was fishing effort in tans (or panels) of gill nets for year y ; $S(l)$ was a binormal selection function of 121-mm mesh gillnets for fork length l ; R_1 , R_2 , σ_1 , σ_2 , ω were parameters in the binormal gillnet selection function (Millar and Fryer 1999); and FL_a was the back-calculated fork length for age a .

To calculate the weight at maturity variable, river catches, and age compositions for female chum

salmon during returning years were obtained from HSH (1972–1997a, 1996–1997b) and NSRC (1998–2004a, 1998–2004b). The number of tans of gill nets used east of 170°E by the high seas fishery was obtained from the International North Pacific Fisheries Commission (INPFC 1958–1996). For gill net selection parameters, we used $R_1 = 5.36$, $R_2 = 32.2$, $\sigma_1 = 0.496$, $\sigma_2 = 4.88$, and $\omega = 28700$ (M. Fukuwaka, T. Azumaya, N. Davis and T. Nagasawa, unpublished manuscript).

To confirm that estimated temporal changes of $L50$ were not artifacts because of estimation biases with assumed mortalities, we examined some cases with realistic ranges of natural mortality and fishing mortality. We used three values of M (i.e., 0.1, 0.2, and 0.3) and brood year-specific M values calculated from the river catch-at-age data. The abundance of chum salmon was largely affected by the coastal environment during early ocean life (Fukuwaka and Suzuki 2002; Mueter et al. 2002). However, natural ocean mortality could not be rejected as a determinant of chum salmon abundance. Thus, in addition to three constant values of M , we calculated brood year-specific M values, assuming that freshwater and early coastal survival was uniform and the exploitation rates of the coastal fisheries were the ratio of the coastal catch to the sum of the coastal and river catches in each region of Hokkaido.

For cases of different fishing mortalities, we used three values of q : 5.0×10^{-8} , 7.5×10^{-8} , and 1.0×10^{-7} . The mean estimate of q for the period from 1954 to 1991 was 4.71×10^{-8} (range 1.81×10^{-8} to 1.35×10^{-7}), assuming that all catches in the high seas fishery were reported, no non-catch losses occurred, fishing gear selected only maturing fish, and all maturing fish were caught along the Asian coast and in rivers. However, the values may be underestimates because violations of the high seas fishery regulation were observed (Fredin et al. 1977) and estimates of non-catch fishing mortality by gill nets were less than 50% for immature fish and approximately 25% for maturing fish (Ricker 1976).

Tests for differences among rivers and temporal trends

To test for differences among rivers or temporal trends in $L50$ values, we used GLM and ANOVA. To test for differences among river populations, we used the significance of the interaction terms with rivers included in the model:

$$\text{logit}(\text{maturity}) = \alpha_{br} + \beta_{1,r}(\text{fork length}) + \beta_{2,r}(\text{age}). \quad (4)$$

To test for temporal trends in $L50$ before and after the closure of the high seas fishery, we assessed significant differences in the slopes for brood years as continuous variables between the period before the 1985 brood year

and the period since the 1985 brood year (i.e., the significance of the interaction term brood \times period) in the model:

$$\text{logit}(\text{maturity}) = \alpha_{rp} + \beta_{1,r}(\text{fork length}) + \beta_{2,r}(\text{age}) + \beta_{3,rp}(\text{brood}), \quad (5)$$

where subscript p indicates either the period before the 1985 brood year or since the 1985 brood year. In these tests, we used a quasibinomial GLM (McCullagh and Nelder 1989; R Development Core Team 2007). The significances of the main effects and interaction effects were tested using F -statistics because the likelihood ratio test could not be used in the quasibinomial GLM. The rate of $L50$ change in haldanes was estimated in standard deviations per generation using coefficients in the equation (5) (Hendry and Kinnison 1999):

$$\begin{aligned} h &= \frac{x_2/\text{SD}_{\text{pooled}} - x_1/\text{SD}_{\text{pooled}}}{g} \\ &= \frac{\text{change rate of } L50}{\text{SD of } L50} (\text{generation length}), \\ &= \frac{-\beta_{3,rp}/\beta_{1,r}}{\sqrt{\pi^2/(3\beta_{1,r}^2)}} (\text{generation length}), \end{aligned}$$

where x_2 and x_1 were the mean trait values at two different times, $\text{SD}_{\text{pooled}}$ was the pooled standard deviation, and g was the number of generation (years divided by generation length). Generation length was the average age at maturity for parents by river and by period, which was calculated from the age composition and the number of broodstocks used in the hatcheries.

Direction of selection

To examine the effect of fishery-induced selection on observed $L50$, we compared the direction of selection and response to selection. The direction of selection on a brood year-specific $L50$ was the sign of the difference between the brood year-specific optimal maturation threshold and the observed $L50$:

$$\text{Direction of selection} = \text{sign}(Lm_{b,3} - L50_{b,3}),$$

where Lm was the optimal maturation threshold. The response to selection was the sign of the difference between the observed $L50$ and the $L50$ 4 years later:

$$\text{Response to selection} = \text{sign}(L50_{b+4,3} - L50_{b,3}),$$

because most female chum salmon mature when 4 years old (ocean age 3 corresponded to 4 years old at maturity). We used the Ives–Gibbons correlation coefficient for testing between these dichotomous variables, which

ranges from -1 to 1 (Zar 1999). The significance of the coefficient was tested using a binomial test with a null hypothesis $H_0: P = 0.5$. When the direction corresponds to the response perfectly, the correlation coefficient is 1 , and the test rejects the null hypothesis. When the direction corresponds to the response in half of the cases, the correlation coefficient is 0 , and the test does not reject the null hypothesis. However, when the direction conflicts with the response perfectly, the correlation coefficient is -1 , and the test rejects the null hypothesis.

To predict optimal maturation thresholds, we used the integral projection model for the life history of hatchery-reared chum salmon (Appendix A). We estimated the optimal brood year-specific intercept for the maturation function α_b with fixed values of β_1 and β_2 by maximizing the net reproductive rate, R_0 , because density dependence acted at hatchery capacity. To examine the effect of fishing selection on $L50$, we estimated optimal maturation thresholds under two alternative assumptions: presence and absence of fishing mortality. While temporal changes in optimal maturation threshold with fishing mortality reflected offshore mortality, including natural and fishing mortalities, values of optimal maturation threshold without fishing reflected the effect of somatic growth because R_0 was determined by mortality and fecundity.

Results

Estimated $L50$ increased after the 1985 brood year, while it had decreased before the 1985 brood year (Fig. 4). In the late 1980s, the fishing effort by the high seas fishery decreased sharply (Fig. 3). Although we only used mature fish caught in rivers that had experienced size-selective fishing mortality on the high seas to estimate $L50$, the temporal correspondence was not an artifact of the $L50$ estimation because our calculations were weighted using fishing effort and similar temporal trends were observed for $L50$ values with different values of q . In examining cases with different values of q or M , $L50$ did differ among cases but changed similarly through time. The maturity function and estimated $L50$ values also differed among river populations ($P < 0.001$ for interaction terms of α_{br} and $\beta_{1,r}$, but $P = 0.101$ for the interaction term of $\beta_{2,r}$ in GLM equation (4) in the case of $q = 7.5 \times 10^{-8}$ and $M = 0.2$). However, a similar temporal trend in $L50$, that is, decreasing before the 1985 brood year and increasing after the 1985 brood year, was observed ($P < 0.001$ for the interaction term of $\beta_{3,rp}$ in GLM equation (5), the same sign of $\beta_{3,rp}$ among river populations in both periods, plus before the 1985 brood year and minus after the 1985 brood year). The rate of phenotypic change in $L50$ estimated from GLM coefficients was -0.214 haldanes (generation length = 3.57 years) for the Chitose River,

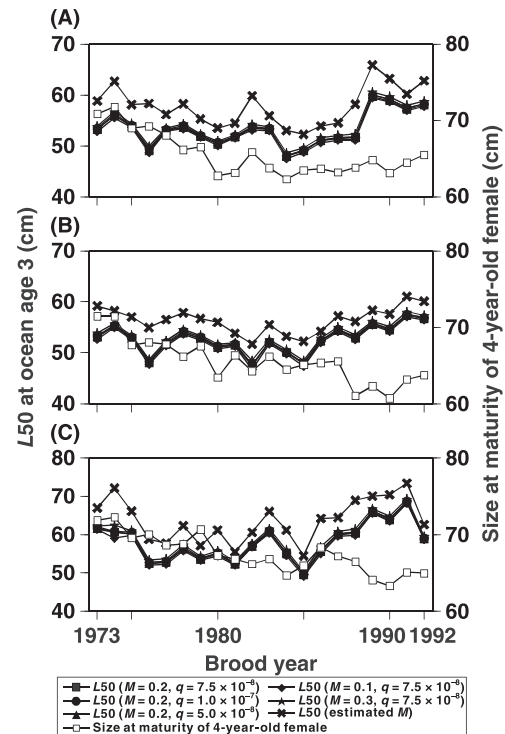


Figure 4 Estimated $L50$ for female chum salmon at ocean age 3 (i.e., 4 years old) under assumptions of M and q values (see 'Materials and methods') and size at maturity (i.e., average fork length of mature individuals) for 4 year-olds from the 1973 to 1992 cohorts from the Chitose River (A), Nishibetsu River (B), and Tokachi River (C) populations. Not all results from possible combinations of different values of M and q are shown because estimates of other combinations were similar to values presented in this figure.

-0.170 haldanes (generation length = 3.80 years) for the Nishibetsu River, and -0.089 haldanes (generation length = 4.07 years) for the Tokachi River before the 1985 brood year (12 years), and 0.782 haldanes (generation length = 3.90 years) for the Chitose River, 0.527 haldanes (generation length = 3.93 years) for the Nishibetsu River, and 0.746 haldanes (generation length = 4.36 years) for the Tokachi River after the 1985 brood year (8 years) when $q = 7.5 \times 10^{-8}$ and $M = 0.2$. Size at maturity (i.e., average fork length of mature individuals) for 4-year-old fish decreased throughout the study period that differed from the temporal pattern of $L50$.

The optimal maturation threshold under the assumption of the presence of fishing mortality increased until the mid 1980s, reflecting decreased high seas fishing effort (Fig. 5). Estimated $L50$ values when $q = 7.5 \times 10^{-8}$ and $M = 0.2$ were larger than the optimal maturation threshold until the mid 1980s. After 1985, estimated $L50$ values were often smaller than the optimal maturation threshold. The optimal maturation threshold under the assumption

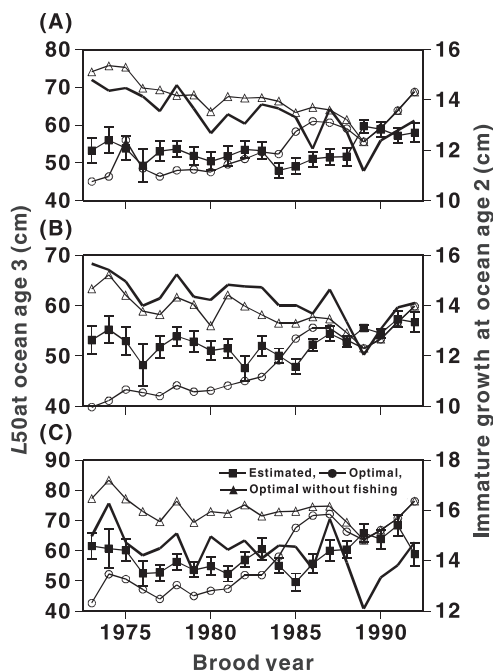


Figure 5 Estimated *L50*, optimal *L50*, optimal *L50* without high seas fishing at ocean age 3 (thin lines), and weighted average of immature growth at ocean age 2 (thick line) under the assumption of $M = 0.2$ and $q = 7.5 \times 10^{-8}$ for 1973–1992 cohorts from the Chitose River (A), Nishibetsu River (B), and Tokachi River (C) populations of female chum salmon. Vertical bar indicates 95% confidence interval of estimated *L50*.

of the absence of fishing mortality decreased until the 1989 brood year but increased after the 1989 brood year, reflecting temporal changes in immature growth. The temporal changes in estimated *L50* at ocean age 3 did not correspond to either the change in optimal maturation threshold without fishing mortality ($r = -0.180$ to -0.005 , $p = 0.448$ to 0.982 , $n = 20$) or to the change in immature growth at ocean age 2 ($r = -0.326$ to -0.125 , $p = 0.161$ to 0.599 , $n = 20$). These indicate that observed *L50* was not only affected by optimal phenotypic plasticity

induced by changes in somatic growth but also by fishing mortality.

In two cases, $q = 7.5 \times 10^{-8}$ or $q = 1.0 \times 10^{-7}$ and $M = 0.2$, the estimated direction of selection corresponded to the observed temporal changes in *L50* (Table 1). In all other cases, the estimated direction of selection did not correspond to the observed response of *L50*.

The predicted optimal maturation threshold was sensitive to assumed natural and fishing mortalities, whereas changes in the estimated *L50* were smaller because of different values of assumed mortalities (Fig. 4). This indicates that the interpretation of temporal changes in *L50* for chum salmon is dependent on the assumptions of natural or fishing mortalities.

Discussion

Here, we showed an increase in the maturation size threshold for chum salmon after the closure of high seas gillnet fishery. That is, chum salmon tended to mature at larger ages and larger sizes. Observed rates of phenotypic change during the recovery (0.527–0.782 haldanes over 8 years, i.e., 1.83–2.05 generations) were similar to previously reported rates of contemporary phenotypic change (Hendry and Kinnison 1999) but were lower than the change in similarly-estimated maturation thresholds for Atlantic cod (*Gadus morhua* L.) during intense fishing (Olsen et al. 2004). A size-structured consumer-resource model that considered reduced food competition and size-selectivity caused by harvesting, predicted multiple alternative ecological and evolutionary stable states (ESSs) for size at maturity (de Roos et al. 2006). In such a case, protracted and high fishing pressure (i.e., 40 years, ca. 25 generations, and a 60% exploitation rate) could cause a shift to a new ESS, which might then prolong the reduced size at maturity, even during a moratorium. The exploitation rate of the high seas salmon fishery on Asian chum salmon was 33% at its maximum, assuming the fishery caught only maturing fish. Although we did not assess alternative ESSs for chum salmon maturation thresholds,

Table 1. Ives–Gibbons correlation coefficients (r_n) and significance levels (P) between the direction of selection and the sign of the response of *L50* estimated under assumptions of M and q values (see ‘Materials and methods’).

<i>M</i>	<i>q</i>	Chitose River		Nishibetsu River		Tokachi River	
		r_n	<i>P</i>	r_n	<i>P</i>	r_n	<i>P</i>
0.2	5.0×10^{-8}	0.176	0.166	0.778	<0.001	0.000	0.407
0.2	7.5×10^{-8}	0.647	<0.01	0.556	<0.01	0.444	<0.05
0.2	1.0×10^{-7}	0.765	<0.001	0.444	<0.05	0.333	<0.05
0.1	7.5×10^{-8}	-0.059	0.500	0.444	<0.05	0.000	0.407
0.3	7.5×10^{-8}	0.176	0.166	0.111	0.240	0.222	0.119
Estimated	7.5×10^{-8}	0.125	0.227	0.000	0.402	0.000	0.402

the actual duration of this high-intensity fishing does not seem to have been sufficient to have prevented recovery of the maturation threshold after fishing ceased. However, despite the recovery in maturation thresholds, the observed average size at maturity has either remained stable or has decreased (Fig. 4). Such contrasts between phenotypic and genetic responses to environmental change appear common (Merilä et al. 2001; Gienapp et al. 2008), and probably reflect opposing influences of natural selection and the plastic influence of environmental conditions. For chum salmon, it seems that selection favors maturity at larger sizes but ocean conditions are still leading to slower growth, thus resulting in no increase in observed mean body size.

Although our results are consistent with an interpretation of evolutionary responses to the cessation of a size-selective high seas fishery, other explanations must be considered. The coastal trap net fishery is one such possibility, particularly because it had a very high exploitation rate throughout the study period. We suggest that this fishery was not the cause of changes in maturation size thresholds, primarily because the mesh size of the traps (≤ 105 mm in Hokkaido) is too small for mature chum salmon to escape. We further suggest that the overall increases in size-independent mortality owing to this fishery are not driving the observed trends. Harvesting both immature and mature individuals can reduce size and age at maturity, but harvesting only mature individuals can increase size and age at maturity in iteroparous organisms (Law and Grey 1989; Heino 1998; Ernande et al. 2004). Pacific salmon, however, are semelparous and, in this case, there is no theoretical reason to suspect that increasing size-independent mortality for adults alone (Fig. 3) would lead to selection for larger size at maturity. We confirmed this expectation by finding that changes in coastal exploitation rates do not affect optimal maturation threshold values (result not shown).

Another possible explanation for changes in maturation thresholds is hatchery effects. Here, we considered that a stable hatchery capacity leads to fecundity selection as a countering force to fishery-induced selection on maturation thresholds (Ratner and Lande 2001). In a growing population, selection favors younger age at maturity because individuals maturing at younger ages can have a larger contribution to the future population than individuals maturing at older ages (Stearns 1992). If somatic growth rate does not change, selection toward a younger age at maturity leads to a decrease in the maturation threshold. It is therefore worth considering whether production changes in the hatcheries might have shifted from a period of population growth, thus favoring younger age at maturity, to a stable population at carrying capacity, thus favoring older age at maturity. Until 1985, hatchery

releases increased and the maturation threshold decreased in the Chitose River. However, maturation thresholds in the Nishibetsu and Tokachi Rivers also decreased during the same period, whereas hatchery releases there showed no temporal trends. Thus, the decrease in maturation threshold until the mid 1980s may not have been induced by temporal changes in hatchery releases. Although other aspects of domestication or artificial selection on size at maturity may occur in these hatchery populations, any such effects are unknown.

Finally, changes in maturation thresholds might be the result of phenotypic plasticity induced by environmental change. Indeed, the maturation threshold (L_{50}) for chum salmon changes plastically with somatic growth rate, a reaction norm that may be adaptive (Morita et al. 2005; Morita and Fukuwaka 2006). In general, historical trends in PMRNs will never be able to fully exclude the possibility of correlated, but unmeasured, environmental drivers (Law 2007; Morita and Fukuwaka 2007). Additional support for evolutionary responses might therefore be gained by showing that observed changes in maturation thresholds are well-predicted by observed selection (Swain et al. 2007) or by optimality models (present study). Here, we found that temporal changes in L_{50} mostly corresponded to predictions with respect to changes in fishing but not to predictions with respect to changes in immature growth or optimal maturation thresholds without fishing. This correspondence between changes in fishing and changes in both predicted and observed maturation thresholds supports our conclusion that the observed trends are at least partly driven by genetic adaptations to changes in fishing pressure. Swain et al. (2007) reached a similar conclusion based on their analysis of selection on, and phenotypic change in, size at age in Gulf of St Lawrence cod stocks.

Why does the cessation of fishing lead to the recovery of life history parameters in some stocks, such as Japanese chum salmon (this study), but not in others, such as some cod stocks (Olsen et al. 2004)? We suggest that the difference may be related to trophic levels. For Atlantic cod off southern Labrador and eastern Newfoundland, which prey on fish or macroinvertebrates, the maturation threshold has begun to recover after fishing ceased but population sizes remain very low (Olsen et al. 2004, 2005; Frank et al. 2005). Maladaptation of life history traits induced by fisheries was cited as one of the causes for this prolonged depression in abundance (Olsen et al. 2004, 2005; Walsh et al. 2006). A contrasting situation is found in plankton-feeding chum salmon, which are showing recovery in maturation thresholds and have a very high stock abundance (Eggers et al. 2003; Fukuwaka et al. 2007; Morita and Fukuwaka 2007). Similarly, planktivorous Norwegian spring-spawning herring (*Clupea harengus* L.) have shown full recovery of maturation thresholds

and stock condition following the relaxation of fishing (Engelhard and Heino 2004). We suggest that these trophic level differences lead to different genetic and plastic bases for maturation thresholds and therefore different evolutionary responses following changes in fishing pressure. For example, lower trophic levels may be more strongly affected by temporal and spatial fluctuations in primary and secondary productivity (Beamish and Bouillon 1993; Robinson and Ware 1999; Hutchings 2000; Hutchings and Baum 2005). Under these conditions, genetic variation in maturation thresholds might be maintained, thereby allowing more rapid responses to changes in selection.

In summary, fishery-induced evolution seemed largely responsible for the temporal change in the maturation threshold for Japanese chum salmon during the fishing period, whereas natural selection and phenotypic plasticity likely contributed to changes that occurred after the relaxation of fishing. Ocean growth and size at maturity of chum salmon decreased with increased abundance in the 1970s to mid 1990s, which seemed to result from density dependence (Ishida et al. 1993; Bigler et al. 1996). More recently, the sizes of adults caught in rivers and ocean growth have increased significantly, and the chum salmon stock level has remained at a historic high (Helle and Hoffman 1998; Eggers et al. 2003; Fukuwaka et al. 2007; Morita and Fukuwaka 2007). Helle and Hoffman (1998) suggested that the change in association between abundance and growth was caused by a change in ocean carrying capacity for salmon. Changing somatic growth can induce plastic changes in size and age at maturity (Morita et al. 2005; Morita and Fukuwaka 2007). Because of partial genetic control of size at maturity in Pacific salmon (Smoker et al. 1994; Gall and Neira 2004), environmentally induced changes in somatic growth can also induce evolutionary changes in size at maturity through natural selection.

Acknowledgments

We thank A. Hendry for invaluable comments and suggestions to earlier versions of the manuscript and for the invitation to contribute to the Special Issue. We also thank R. Waples for the invitation, and the staff of the National Salmon Resources Center, Fisheries Research Agency, for their careful collection of data and samples.

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Appendix A. Estimation of optimal threshold size at maturation for female chum salmon

To predict the optimal threshold size at maturation by brood year, we used the integral projection model modified for the life history of hatchery reared chum

salmon (Fig. 1) (Ellner and Rees 2006). The number of chum salmon in a fork length class x_j at time $t + 1$ was

$$n(x_j, t + 1) = w \sum_{i=1}^m [P_b(x_j, x_i) + F_b(x_j, x_i)] n(x_i, t),$$

where w was the width of the fork length class, m was the number of fork length classes covering the range of possible fork lengths, P_b was the survival and growth rate from a class x_i to a class x_j for brood year b , and F_b was the production of female juveniles in a class x_j by a female in a class x_i for brood year b . The optimal maturation function was computed by numerical maximization of the net reproductive rate, R_0 , because hatchery capacities limited juvenile releases in early life. R_0 equals the average per capita life time juvenile production of a cohort of newborns.

Survival and growth rate was

$$P_b(x_j, x_i, a) = s_b(x_i)[1 - m(x_i, a)]g_b(x_j, x_i, a),$$

where $s_b(x_i)$ was the annual survival rate at fork length x_i , $m(x_i, a)$ was the maturation rate at fork length x_i and age a , and $g_b(x_j, x_i, a)$ was the transition rate due to immature growth from fork length class x_i to x_j at age a . The survival rate function includes natural mortality and fishing mortality as in equation (3):

$$s_b(x_i) = \exp(-M)[1 - H_{y=b+3}S(x_i)].$$

The production of female juveniles from a female in fork length class x_i was

$$F_b(x_j, x_i) = s_b(x_i)m(x_i, a)(1 - c)hs_c0.5j_b(x_j) \sum mg_b(y, x_i, a)f(y),$$

where c was the exploitation rate of coastal fisheries, h was the hatchery survival from the egg stripping to the release, s_c was the freshwater and coastal survival of released juveniles, $j_b(x_j)$ was the fork length distribution of ocean age 1 fish, $mg_b(y, x_i, a)$ was the transition rate from fork length class x_i to y at age a due to final year growth, and $f(y)$ was the fecundity function at final fork length y . Functions and parameters used in the model are shown in Table A1. We estimated growth parameters by brood year from back-calculated fork lengths weighted by the estimated number of fish alive at a specific age per number of samples shown in the 'Materials and methods'.

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Table A1. Functions and parameters of demographic processes in the life history model for female chum salmon. CH, Chitose River; NI, Nishibetsu River; TO, Tokachi River.

Demographic process	Function or parameters	Calculation method
Ocean natural mortality	$M = 0.1, 0.2, \text{ and } 0.3$	
Catchability coefficient	$q = 0$ (without fishing mortality), $5.0 \times 10^{-8}, 7.5 \times 10^{-8}, \text{ and } 1.0 \times 10^{-7}$ (with fishing mortality)	
Maturation rate	$\text{logit}(m) = \alpha_b + \beta_1 x + \beta_2 a$	GLM with weights using different values of M and q
Immature growth	$x_j - x_i = \alpha_b + \beta_1 x_i + \beta_2 a + e$	ANOVA of back-calculated growth with weights using different values of M and q
Exploitation rate of coastal fisheries	$c = 0.809$ (CH), 0.948 (NI), and 0.931 (TO)	$1 - \text{Geometric mean [upstream migration rate (UMR), 1976–1997]. UMR} = \text{river catch}/(\text{river catch} + \text{coastal catch})$ in the region was obtained from HSH (1977–1997a) and NSRC (1998a)
Hatchery survival	$h = 0.9$	
Freshwater and coastal survival	Number of ocean age 1 fish/ number of released juveniles	VPA using different values of M and q
Fork length distribution of ocean age 1 fish	Mean $x_j + e$	Average of back-calculated fork length with weights using different values of M and q
Final year growth	$y - x_i = \alpha_b + \beta_1 x_i + \beta_2 a + e$	ANOVA of back-calculated growth with weights using different values of M and q
Fecundity	$\text{log}_{10} f = -2.81 + 3.47 \text{ log}_{10} y$ (CH), $\text{log}_{10} f = -1.61 + 2.76 \text{ log}_{10} y$ (NI), and $\text{log}_{10} f = -3.07 + 3.55 \text{ log}_{10} y$ (TO)	Geometric linear regression using the authors' unpublished data