



Why age and size at maturity have changed in Pacific salmon

Kentaro Morita*, Masa-aki Fukuwaka

Hokkaido National Fisheries Research Institute, Fisheries Research Agency, 116 Katsurakoi, Kushiro 085-0802, Japan

ABSTRACT: Over the last few decades, the size at which Pacific salmon *Oncorhynchus* spp. attains maturity has decreased in many populations, whereas the age at maturity has increased. Both fisheries-induced evolution and environmentally-induced phenotypic plasticity could contribute to the changing age and size at maturity of Pacific salmon. We evaluated the potential for genetic changes in the maturation schedule of Japanese chum salmon using the probabilistic maturation reaction norm (PMRN) method. We found that the recent decrease in size at maturity, and increase in age at maturity, of Japanese chum salmon can be largely attributed to a phenotypic response to a reduced growth rate, but that fisheries-induced evolution should not be ruled out. Recent claims concerning fisheries-induced evolution of the maturation schedule are based on the decline in the age-specific body size at which the probability of maturing is 50%, a feature of PMRNs. However, the PMRN could change with changing environmental conditions. Therefore, a genetic change cannot be diagnosed only by the PMRN method.

KEY WORDS: Life history · Phenotypic plasticity · Conditional strategy · Thresholds

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INTRODUCTION

Over the last few decades, the size at which Pacific salmon *Oncorhynchus* spp. attains maturity has decreased in many populations, whereas the age at maturity has increased (reviewed by Bigler et al. 1996). These patterns are well recognized in chum salmon *O. keta* (Ishida et al. 1993, Helle & Hoffman 1995, Kaev 1999), sockeye salmon *O. nerka* (Pyper et al. 1999, Holt & Peterman 2004) and pink salmon *O. gorbuscha* (Azumaya & Ishida 2000, Wertheimer et al. 2004). The size at maturity of endemic Asian masu salmon *O. masou* has also decreased (Tago 2002). In Japanese chum salmon, the average size at maturity of each age has decreased by ~5 cm, and the average age at maturity has increased by ~0.5 yr since the 1960s (Fig. 1a,b).

Genetic change associated with commercial fishing has been suggested as being a contributory factor to the observed decline in size at maturity (Ricker 1981, 1995). Ricker (1981, 1995) suggested that the gillnet fishery targeting maturing pink salmon removed large-sized fish at maturity that had grown fast,

because almost all pink salmon mature at the same age, i.e. 2 yr. From 1952 to 1992, many Pacific salmon were caught in the high seas far from their spawning sites by the Japanese fishery using gillnets (Fig. 1c, Morita et al. 2006), which are highly size-selective (Ishida 1969). In addition, losses from gillnetting in the high seas, i.e. mortality caused by high-sea fishing with gillnets but not included in catch statistics, is substantial at ~25 to 50% (Ricker 1976). In such a situation, a fish that matured at a smaller size than the fishable size could take refuge from the high-seas fishery. Therefore, artificial selection toward a small size at maturity could occur for Pacific salmon. In contrast, Welch & Morris (1994) suggested that artificial selection for slower-growing fish cannot be the primary cause of the long-term decline in the size of pink salmon observed since the 1950s because their size at maturity in the early 1930s was similar to what it is today. Additionally, although it may explain the decline in size at maturity, it does not seem to address the increase in age at maturity (Healey 1986).

*Email: moritak@affrc.go.jp

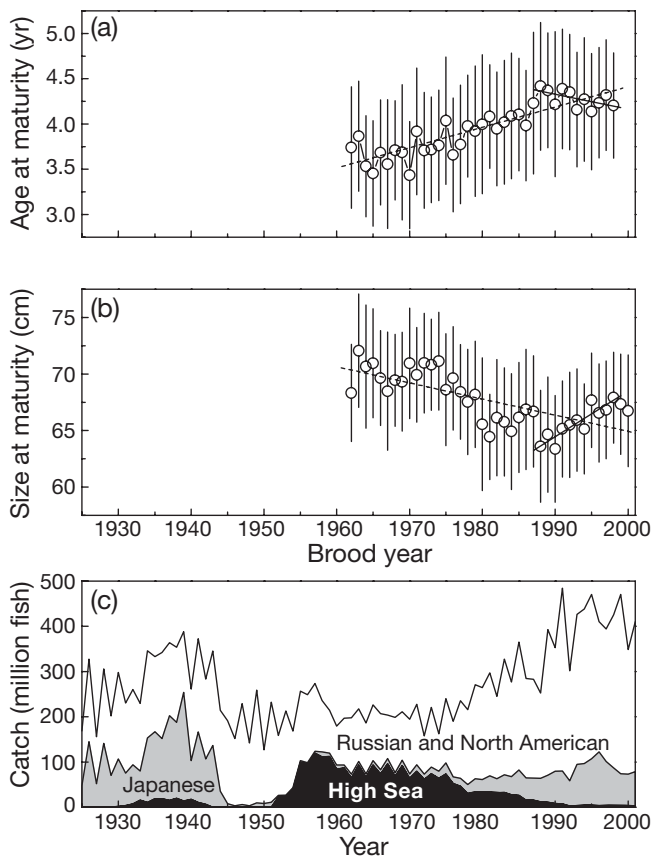


Fig. 1. (a) Long-term changes in average age at maturity of chum salmon *Oncorhynchus keta*: dashed line, 1962 to 1998, $r = 0.87$, $p < 0.001$; solid line, 1988 to 1998, $r = -0.57$, $p = 0.07$. (b) Long-term changes in average size at maturity of Age 4 yr chum salmon: dashed line, 1962 to 2000, $r = -0.70$, $p < 0.001$; solid line, 1988 to 1998, $r = 0.90$, $p < 0.001$. Biological data are averages from 3 major rivers in northern Japan (Ishikari, Tokachi and Nishibetsu) monitored by the National Salmon Resources Center, Fisheries Research Agency. Error bars are SD. (c) Catch trends of Pacific salmon *Oncorhynchus* spp. showing the Japanese, Russian and North American fisheries and Japanese high-seas fishery (Eggers et al. 2003)

The genetic changes associated with fishing become known as fisheries-induced evolution (Conover et al. 2005, Reznick & Ghilambor 2005). High fishing mortality and size-selective fishing are two of the most important causes of fisheries-induced evolution. Theoretical studies showed that selection for early maturation (i.e. decreased age and size at maturity) is more likely to occur, but selection for delayed maturation is also possible depending on the pattern of artificial selection (Law & Grey 1989, Heino 1998, Ernande et al. 2004). Fisheries-induced evolution has been suggested to account for some of the observed trends in age and size at maturity (e.g. North Sea plaice *Pleuronectes platessa*, Grift et al. 2003; Atlantic cod *Gadus morhua*, Olsen et al. 2004, 2005).

This essay comprises (1) a brief literature review of the environmental causes of the decline in size at maturity of Pacific salmon, (2) an evaluation of the potential for genetic changes in the maturation schedule of Japanese chum salmon, using the probabilistic maturation reaction norm (PMRN) method, and (3) a critical review of the application of the PMRN method to the study of fisheries-induced evolution.

ENVIRONMENTAL CAUSES OF THE DECLINE IN SIZE AT MATURITY

Environmentally-induced phenotypic plasticity contributes to the changing age and size at maturity of Pacific salmon (Ishida et al. 1993, 1995, Welch & Morris 1994, Cox & Hinch 1997, Pyper & Peterman 1999, Wertheimer et al. 2004). Most studies suggest relationships among temperature, population size, and body size at maturity. For example, the growth of Pacific salmon is density-dependent, and the number of individuals of this genus more than doubled during the last quarter of the 20th century. This increase in population size may have led to a decrease in per-capita food availability and, thus, a decrease in the size at maturity (Bigler et al. 1996). Ishida et al. (1993, 1995) found that increases in abundance and decreases in sea-surface temperature were significantly associated with the reduced body length of chum salmon in the North Pacific. Interestingly, these trends appear to have reversed during the 1988 to 1998 brood years (Fig. 1; Kaeriyama & Katsuyama 2001, Eggers et al. 2003, Kaev & Romasenko 2003), and size at maturity has been increasing with decreasing population size since the late 1990s (Kaeriyama & Katsuyama 2001). Pyper & Peterman (1999) reported that increases in abundance and sea-surface temperature were significantly associated with reduced adult body length in sockeye salmon in British Columbia and Alaska. However, the evidence supporting environmentally-induced phenotypic plasticity is based on correlation, and not causation.

ASSESSING FISHERIES-INDUCED EVOLUTION USING THE PMRN METHOD

Recent claims concerning fisheries-induced evolution of the maturation schedule are based on the decline in the age-specific body size at which the probability of maturing is 50%, a feature of PMRNs (e.g. Grift et al. 2003, Olsen et al. 2004, 2005). The PMRN method is based on the logistic regression:

$$\text{logit}(p) = \log\left(\frac{p}{1-p}\right) = c_{0,a} + c_{1,a}I$$

where p is the probability of maturing, l is body size, $c_{0,a}$ is a constant for each age a , and $c_{1,a}$ is a coefficient for l for each age. Assuming that a fitted logistic regression is a cumulative distribution function, the body size at 50% probability of maturing indicates an average size threshold for maturity that can be calculated as $-c_{0,a} \times c_{1,a}^{-1}$, with a variance of $\pi^2/3c_{1,a}^2$ (Metcalf et al. 2003). Because it is usually difficult to identify newly matured fish (i.e. first-time spawning fish) for iteroparous species, a statistical method to estimate PMRNs when age at first maturity is unknown has been proposed (Grift et al. 2003, Barot et al. 2004). Usually, the variance in the size threshold for maturity is not negligible, indicating that genetic variance or factors other than body size affect maturation.

Morita et al. (2005) estimated the PMRN using data on chum salmon ascending the Shari River, eastern Hokkaido, Japan, during the breeding season of 1992 to 1997 (Fig. 2). Because Pacific salmon are semelparous species, the maturity ogive is the same as the PMRN, i.e. we need not use the method of Barot et al. (2004). The probability of maturing increased with fork length, but the reaction norm midpoint at 50% maturation probability (i.e. average threshold size at maturity) decreased with increasing age (Fig. 2). Note that the observed average size at maturity is markedly different from the reaction norm midpoint at 50% maturation probability. The average size at maturity increased with age, but this does not mean that older fish need a larger body size to mature.

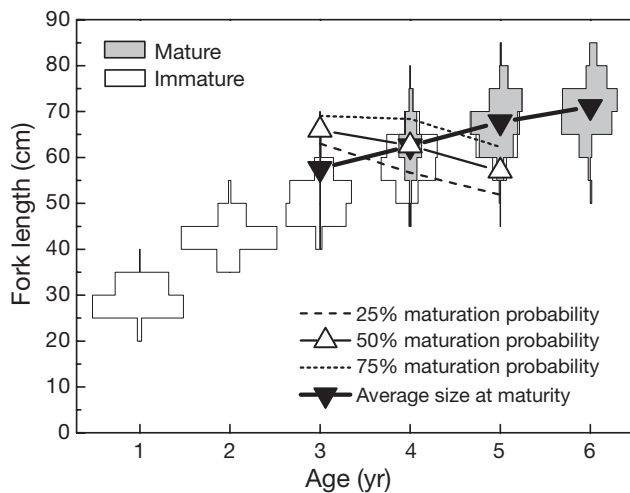


Fig. 2. *Oncorhynchus keta*. Probabilistic maturation reaction norm (PMRN) of chum salmon (Morita et al. 2005). Data include 3 cohorts, the 1989 to 1991 brood years, and pooled sexes. Left and right histograms for each age correspond to females and males, respectively. There is no significant difference in the PMRN between sexes; however, size at each age differed significantly between sexes. Details of data and their treatment are described elsewhere (Morita et al. 2005)

Morita et al. (2005) simulated the potential modification of average age and size at maturity of chum salmon in response to changing growth rate using a size-structured model with constant age- and size-specific maturation rates (i.e. time-invariant PMRNs, as in Fig. 2). The results suggested that the decrease in size at maturity and increase in age at maturity over the last 4 decades could result from a reduced growth rate alone, without any change in the PMRN (Fig. 3). However, to our knowledge, no studies have reported the long-term trends in the PMRN in Pacific salmon, because it is generally difficult to estimate size-frequency distribution of immature *Oncorhynchus* spp.

CAN PMRNs DIAGNOSE GENETIC CHANGES?

The PMRN method quantifies the maturation schedule after accounting for the variation in body size at a given age. Therefore, the PMRN may be insensitive to phenotypic plasticity in growth because it assumes that body size is sufficient to determine maturation at a given age. If the variation in the threshold size at maturity, $\sigma^2 = \pi^2/3c_{1,a}^2$, is attributable to genetic variance (i.e. the heritability of the threshold size at maturity is high), the method would be useful for assessing genetic changes in the maturation schedule. To understand genetic changes in the PMRN, knowledge of the heritability of the threshold size at maturity is critical (cf. Wesselingh & de Jong 1995, Wesselingh &

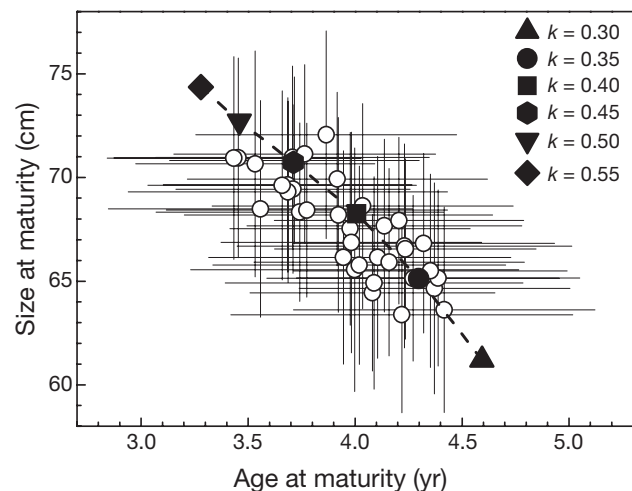


Fig. 3. *Oncorhynchus keta*. Simulated and observed covariation in average age at maturity and average size at maturity of Age 4 yr chum salmon. Filled symbols indicate simulated changes in response to changing growth rate k using a size-structured model (Morita et al. 2005) with an invariable probabilistic maturation reaction norm as in Fig. 2. Open circles are observed data as in Fig. 1a,b. Error bars are SD

Klinkhamer 1996). However, a comprehensive understanding of the sources of variation in the threshold size at maturity (genetic or environmental variance) is still lacking in fishes.

Spatial variation in threshold size may reflect variable environmental conditions provided by different habitats, or different genotypes adapting to different habitats. For example, the threshold size at maturity of male parr differs according to habitat in Atlantic salmon *Salmo salar* (Aubin-Horth & Dodson 2004, Baum et al. 2004, Aubin-Horth et al. 2006). Baum et al. (2004) and Aubin-Horth et al. (2006) showed that the threshold size at maturity decreased with altitude and distance from the mouth of the river, respectively. In addition to genotype, temperature, food availability, condition factors and growth history affect the maturation probability independent of body size at a given age (Bromage et al. 1992, Silverstein et al. 1998, Henderson & Morgan 2002, Dhillon & Fox 2004, Morgan 2004, Baum et al. 2005, Watanabe & Yatsu 2006, Morita & Fukuwaka 2006).

Morita et al. (2000) compared the maturation schedule of white-spotted charr *Salvelinus leucomaenis* in below-dam river sections accessible to the migrant form with above-dam river sections inaccessible to the migrant form. Because above-dam river sections are populated by only the resident form (i.e. precocious fish), it is hypothesized that above-dam fish will mature at earlier ages and smaller sizes. We reanalyzed these data (Morita et al. 2000, Morita & Yamamoto 2001) using a PMRN method (Fig. 4). Age 1+ yr males above the dam had a smaller threshold size at maturity than did those below. Because a significant difference was observed in PMRNs between above- and below-dam sections (likelihood ratio test $G^2_2 = 31.2$, $p < 0.001$), one may suppose that fish have evolved rapidly following isolation by dams. However, the PMRN for below-dam fish changed plastically when they were transplanted to an above-waterfall section about 16 mo before maturation ($G^2_2 = 36.3$, $p < 0.001$), and no significant difference between the sections was detected when fishes from both sections were transplanted to a common above-waterfall section ($G^2_2 = 0.425$, $p = 0.809$). Therefore, the observed difference in the PMRN for these populations could be largely attributable to differences in environmental conditions (Morita et al. 2000).

Morita & Fukuwaka (2006) examined the relationships among body size, previous growth history and maturation probability in chum salmon. Previous growth history was more closely linked to maturation probability than was body size, and the annual growth increment of the previous year was the most important factor affecting whether a fish matured during the subsequent season. This finding is consistent with

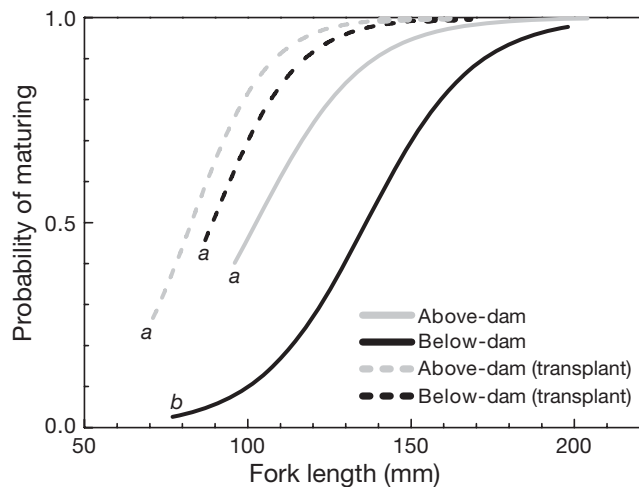


Fig. 4. *Salvelinus leucomaenis*. Fitted logistic regression of the probability of parr maturation based on fork length of Age 1+ yr male white-spotted charr above and below dams (data from Morita et al. 2000), and for fishes from each section transplanted to a common above-waterfall section about 16 mo before maturation (data from Morita & Yamamoto 2001). Regressions plotted for the range of fork lengths used. Different letters denote statistically significant differences based on likelihood-ratio tests

endocrinological studies of salmonid maturation in which somatic growth during the fall and winter affected the onset of maturation in the next autumn (Campbell et al. 2006). Thorpe (1986) argued that body size is a measure of past performance; in contrast, growth rate is a measure of current performance and thus provides a better basis for developmental decisions than body size alone. Thus, the PMRN could change with changing growth patterns. Morita & Fukuwaka (2006) showed that the relationship between body size and maturation could probably be plastically modified by growth history because individuals of similar body size (at the same age) can have different growth histories.

Therefore, genetic change cannot be diagnosed only by the PMRN method. When interpreting the trends of the PMRN, it is necessary to quantify how the age-specific body size at 50% probability of maturing is altered in response to changing temperature and food availability before invoking evolution. Even when age-specific growth rates show no change between years, food availability may show an increasing trend coincident with increasing age-specific maturation rates (i.e. declining trends in age and size at maturity) because energy allocation toward somatic growth versus reproduction should decrease. It is still unclear how the PMRN is altered in response to changing environment; this merits further study (e.g. Grift et al. 2007).

CONCLUDING REMARKS

The age and size at maturity of fishes, including salmonids, are flexible and depend on a variety of environmental conditions. The PMRN may also covary with changing environments. While it is important to detect evidence of the effects of fisheries-induced evolution on age and size at maturity, it is equally important to address the relative contribution of fisheries-induced evolution and environmentally induced phenotypic plasticity to the observed changes in age and size at maturity. For example, the recent decrease in size at maturity and increase in age at maturity of Japanese chum salmon can be largely attributed to a phenotypic response to a reduced growth rate, but fisheries-induced evolution should not be ruled out.

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LITERATURE CITED

- Aubin-Horth N, Dodson JJ (2004) Influence of individual body size and variable thresholds on the incidence of a sneaker male reproductive tactic in Atlantic salmon. *Evolution* 58:136–144
- Aubin-Horth N, Bourque JF, Daigle G, Hedger R, Dodson JJ (2006) Longitudinal gradients in threshold sizes for alternative male life history tactics in a population of Atlantic salmon (*Salmo salar*). *Can J Fish Aquat Sci* 63:2067–2075
- Azumaya T, Ishida Y (2000) Density interactions between pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) and their possible effects on distribution and growth in the North Pacific Ocean and Bering Sea. *N Pac Anadromous Fish Comm Bull* 2:165–174
- Barot S, Heino M, O'Brien L, Dieckmann U (2004) Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. *Evol Ecol Res* 6:659–678
- Baum D, Laughton R, Armstrong JD, Metcalfe NB (2004) Altitudinal variation in the relationship between growth and maturation rate in salmon parr. *J Anim Ecol* 73:253–260
- Baum D, Laughton R, Armstrong JD, Metcalfe NB (2005) The effect of temperature on growth and early maturation in a wild population of Atlantic salmon parr. *J Fish Biol* 67:1370–1380
- Bigler BS, Welch DW, Helle JH (1996) A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). *Can J Fish Aquat Sci* 53:455–465
- Bromage N, Jones J, Randall C, Thrush M, Davies B, Springate J, Duston J, Barker G (1992) Broodstock management, fecundity, egg quality and the timing of egg production in the rainbow trout (*Oncorhynchus mykiss*). *Aquaculture* 100:141–166
- Campbell B, Dickey J, Beckman B, Young G, Pierce A, Fukada H, Swanson P (2006) Previtellogenic oocyte growth in salmon: relationships among body growth, plasma insulin-like growth factor-1, estradiol-17beta, follicle-stimulating hormone and expression of ovarian genes for insulin-like growth factors, steroidogenic-acute regulatory protein and receptors for gonadotropins, growth hormone and somatolactin. *Biol Reprod* 75:34–44
- Conover DO, Arnott SA, Walsh MR, Munch SB (2005) Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). *Can J Fish Aquat Sci* 62:730–737
- Cox SP, Hinch SG (1997) Changes in size at maturity of Fraser River sockeye salmon (*Oncorhynchus nerka*) (1952–1993) and associations with temperature. *Can J Fish Aquat Sci* 54:1159–1165
- Dhillon RS, Fox MG (2004) Growth-independent effects of temperature on age and size at maturity in Japanese medaka (*Oryzias latipes*). *Copeia* 2004:37–45
- Eggers DM, Irvine J, Fukuwaka M, Karpenko V (2003) Catch trends and status of North Pacific salmon. *N Pac Anadromous Fish Comm Doc* 723, Revision 2
- Ernande B, Dieckmann U, Heino M (2004) Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. *Proc R Soc Lond B* 271:415–423
- Grift RE, Rijnsdorp AD, Barot S, Heino M, Dieckmann U (2003) Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Mar Ecol Prog Ser* 257:247–257
- Grift RE, Heino M, Rijnsdorp AD, Kraak SBM, Dieckmann U (2007) Three-dimensional maturation reaction norms for North Sea plaice. *Mar Ecol Prog Ser* 334:213–224
- Healey MC (1986) Optimal size and age at maturity in Pacific salmon and effects of size-selective fisheries. *Can Spec Publ Fish Aquat Sci* 89:39–52
- Heino M (1998) Management of evolving fish stocks. *Can J Fish Aquat Sci* 55:1971–1982
- Helle JH, Hoffman MS (1995) Size decline and older age at maturity of two chum salmon (*Oncorhynchus keta*) stocks in western North America, 1972–92. *Can Spec Publ Fish Aquat Sci* 121:245–260
- Henderson BA, Morgan GE (2002) Maturation of walleye by age, size and surplus energy. *J Fish Biol* 61:999–1011
- Holt CA, Peterman RM (2004) Long-term trends in age-specific recruitment of sockeye salmon (*Oncorhynchus nerka*) in a changing environment. *Can J Fish Aquat Sci* 61:2455–2470
- Ishida T (1969) The salmon gillnet mesh selectivity curve. *Int N Pac Fish Comm Bull* 26:1–11
- Ishida Y, Ito S, Kaeriyama M, McKinnell S, Nagasawa K (1993) Recent changes in age and size of chum salmon (*Oncorhynchus keta*) in the North Pacific Ocean and possible causes. *Can J Fish Aquat Sci* 50:290–295
- Ishida Y, Welch DW, Ogura M (1995) Potential influence of North Pacific sea-surface temperatures on increased production of chum salmon (*Oncorhynchus keta*) from Japan. *Can Spec Publ Fish Aquat Sci* 121:271–275
- Kaeriyama M, Katsuyama K (2001) Increase in body size with decrease in population size of chum salmon returning to Hokkaido, Japan since the late 1990s. *N Pac Anadromous Fish Comm Newsl* 5:6–7
- Kaev AM (1999) Dynamics of some biological indexes of *Oncorhynchus keta* in connection with the formation of its numbers. *J Ichthyol* 39:642–651
- Kaev AM, Romasenko LV (2003) Some results of studying chum salmon in Ilyushin and Sernovodka rivers on the Kunashir Island (Kuril Islands). *N Pac Anadromous Fish Comm Doc* 670. Sakhalin Research Institute of Fisheries and Oceanography, Yuzhno-Sakhalinsk
- Law R, Grey DR (1989) Evolution of yields from populations with age-specific cropping. *Evol Ecol* 3:349–359
- Metcalfe JC, Rose KE, Rees M (2003) Evolutionary demo-

- graphy of monocarpic perennials. *Trends Ecol Evol* 18: 471–480
- Morgan MJ (2004) The relationship between fish condition and the probability of being mature in American plaice (*Hippoglossoides platessoides*). *ICES J Mar Sci* 61:64–70
- Morita K, Fukuwaka M (2006) Does size matter most? The effect of growth history on the probabilistic reaction norm for salmon maturation. *Evolution* 60:1516–1521
- Morita K, Yamamoto S (2001) Contrasts in movement behavior of juvenile white-spotted charr between stocks above and below a dam. *Fish Sci* 67:179–181
- Morita K, Yamamoto S, Hoshino N (2000) Extreme life history change of white-spotted char (*Salvelinus leucomaenis*) after damming. *Can J Fish Aquat Sci* 57:1300–1306
- Morita K, Morita SH, Fukuwaka M, Matsuda H (2005) Rule of age and size at maturity of chum salmon (*Oncorhynchus keta*): implications of recent trends among *Oncorhynchus* spp. *Can J Fish Aquat Sci* 62:2752–2759
- Morita K, Saito T, Miyakoshi Y, Fukuwaka M, Nagasawa T, Kaeriyama M (2006) A review of Pacific salmon hatchery programmes on Hokkaido Island, Japan. *ICES J Mar Sci* 63:1353–1363
- Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, Ernande B, Dieckmann U (2004) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428:932–935
- Olsen EM, Lilly GR, Heino M, Morgan MJ, Brattey J, Dieckmann U (2005) Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 62:811–823
- Pyper BJ, Peterman RM (1999) Relationships among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*), 1967–1977. *Can J Fish Aquat Sci* 56:1716–1720
- Pyper BJ, Peterman RM, Lapointe MF, Walters CJ (1999) Patterns of covariation in length and age at maturity of British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*) stocks. *Can J Fish Aquat Sci* 56:1046–1057
- Reznick DN, Ghalambor CK (2005) Can commercial fishing cause evolution? Answers from guppies (*Poecilia reticulata*). *Can J Fish Aquat Sci* 62:791–801
- Ricker WE (1976) Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. *Can J Fish Aquat Sci* 33:1483–1524
- Ricker WE (1981) Changes in the average size and average age of Pacific salmon. *Can J Fish Aquat Sci* 38:1636–1656
- Ricker WE (1995) Trends in the average size of Pacific salmon in Canadian catches. *Can Spec Publ Fish Aquat Sci* 121: 593–602
- Silverstein JT, Shearer KD, Dickhoff WW, Plisetskaya EM (1998) Effects of growth and fatness on sexual development of chinook salmon (*Oncorhynchus tshawytscha*) parr. *Can J Fish Aquat Sci* 55:2376–2382
- Tago Y (2002) Recent decrease in mean body weight of adult masu salmon caught in the Jinzu River. *Suisanzoshoku* 50: 387–391
- Thorpe JE (1986) Age at first maturity in Atlantic salmon. *Salmo salar*: freshwater period influences and conflicts with smolting. *Can Spec Publ Fish Aquat Sci* 89:7–14
- Watanabe C, Yatsu A (2006) Long-term changes in maturity at age of chub mackerel (*Scomber japonicus*) in relation to population declines in the waters off northeastern Japan. *Fish Res* 78:323–332
- Welch DW, Morris JFT (1994) Evidence for density-dependent marine growth in British Columbia pink salmon populations. *N Pac Anadromous Fish Comm Doc* 97. Department of Fisheries and Oceans, Nanaimo
- Wertheimer AC, Heard WR, Maselko JM, Smoker WW (2004) Relationship of size at return with environmental variation, hatchery production, and productivity of wild pink salmon in Prince William Sound, Alaska: does size matter? *Rev Fish Biol Fish* 14:321–334
- Wesselingh RA, de Jong TJ (1995) Bidirectional selection on threshold size for flowering in *Cynoglossum officinale* (hound's tongue). *Heredity* 74:415–424
- Wesselingh RA, Klinkhamer PGL (1996) Threshold size for vernalization in *Senecio jacobaea*: genetic variation and response to artificial selection. *Funct Ecol* 10:281–288

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