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## ABSTRACT

Salmon populations in the North Pacific have been subject to major changes in environment and fishing pressure since the early 1980s, including a climate regime shift in 1988-89, the closure of the high-seas fisheries in 1993, and a subsequent climatic event in 1998. In the present work, we evaluate whether any of these three events has triggered changes in the life-history traits of chum salmon (*Oncorhynchus keta*) from the Namdae River, on the eastern coast of South Korea, using data collected on females and males from 1984 to 2008. We find that the 1988-89 regime shift had the most pervasive effects on female and male maturation schedules and growth. We also demonstrate sex-specific responses: whereas growth showed similar patterns of variation in both sexes, age and length at maturation behaved differently in males and females. Our findings contribute to growing evidence that abrupt transitions in climatic conditions can trigger detectable changes in life-history traits. They also strengthen the observation that biological records of salmon populations of the North Pacific carry a stronger signal for the effects of the 1988-89 regime shift than for the effects of the subsequent environmental changes.

Keywords: Korean chum salmon, Namdae River, growth, maturation, regime shift, fishing moratorium

Highlights

- Regime shift in 1988-1989 had pervasive effects on chum salmon life history.

- Patterns of life-history change were often different for males and females, especially for maturation.
- Body growth is associated with climatic variables and food availability/competition.

## INTRODUCTION

Temporal trends in life-history traits have been described in a number of fish species, including Pacific salmon *Oncorhynchus* spp. (Ricker, 1981, 1995; Bigler et al., 1996; Morita and Fukuwaka, 2007), Atlantic cod *Gadus morhua* (Jørgensen, 1990), and European plaice *Pleuronectes platessa* (Rijnsdorp, 1993). As in many other species, temporal changes in Pacific salmon have been reported for size and age at maturation, growth, fecundity, and egg size (Bigler et al., 1996; Kaeriyama, 1998; Walker et al., 1998; Azumaya and Ishida, 2000; Kaev, 2000). However, in contrast with most other fish species in which both size and age at maturation show fairly consistent declining trends (Trippel, 1995), Pacific salmon have shown fluctuating trends, with both increases and decreases over longer periods (Ricker, 1995; Bigler et al., 1996). Moreover, the periods of decreasing size at maturation have frequently been accompanied by an increase, rather than a decrease, in age at maturation (Bigler et al., 1996; Morita and Fukuwaka, 2007). Finally, while fisheries-induced evolution appears a likely contributor to the detected changes in life-history traits in numerous freshwater and marine fish populations (e.g., Kuparinen and Merilä, 2007; Law, 2007; Fenberg and Roy, 2008; Hutchings and Fraser, 2008), its role in triggering the observed changes in Pacific salmon is less obvious (Healey, 1982; Bigler et al., 1996; Hard et al., 2008; but see Ricker, 1981). To date, environmentally induced phenotypic plasticity is considered by many as the most parsimonious hypothesis for the patterns observed in Pacific salmon (Ishida et al., 1993; Ishida et al., 1995; Pyper and Peterman, 1999; Wertheimer et al., 2004).

Evidence supporting the importance of the environment in driving maturation trends in Pacific salmon comes mostly from the response of salmon populations to recent changes in oceanographic regimes (Hare and Mantua, 2000; King, 2005; Lees et al., 2006; Overland et al., 2008). Despite ongoing controversy, it is commonly assumed that since the mid-twentieth century, the North Pacific has experienced regimes shifts in 1976-77, in the winter of 1988-89 (Beamish et al., 1999; Hare and Mantua, 2000; King, 2005), and in 1998 (McFarlane et al., 2000; King, 2005; Overland et al., 2008). Each of these shifts coincided with significant changes in biological indicators (McFarlane et al., 2000; Chittenden et al., 2009). For example, major changes in migratory behaviour, marine survival, recruitment, growth, and age and size at maturation have been observed in the late 1970s and late 1980s (Beamish and Bouillion, 1993; Beamish et al., 1995; Helle and Hoffman, 1995; Francis et al., 1998; Walker et al., 1998; Hare and Mantua, 2000; Ruggerone et al., 2007; Chittenden et al., 2009) and were associated with detected changes in abiotic factors including sea surface temperature (SST), salinity, and climate indices (Hinch et al., 1995; Ishida et al., 1995; Pyper and Peterman, 1999; Morita et al., 2001; Ishida et al., 2002).

Much of the evidence for environmentally induced temporal changes in Pacific salmon comes from Japanese and North American time series of chum (*O. keta*) and pink (*O. gorbuscha*) salmon (Helle and Hoffman, 1995, 1998; Beamish et al., 1999; Pyper and Peterman, 1999; McFarlane et al., 2000; Morita et al., 2001; Beamish et al., 2004; Fukuwaka et al., 2007; Kaeriyama et al., 2007a; Ruggerone et al., 2007). Seo et al. (2006; 2009) suggested that comparable changes have also occurred in chum salmon from the Namdae River, on the eastern coast of South Korea. In particular, significant changes in female size at maturation, age at maturation, and scale growth were found to coincide with the 1988-89 regime shift and with the changes in SST, Aleutian Low Pressure Index, and zooplankton densities observed in Korean waters around this period (Kang et al., 2000; Zhang et al., 2000).

To date, the hypothesis that the recent changes in Pacific salmon life-history traits are responses to fishing has mostly been ignored (but seeFukuwaka and Morita, 2008). Chum salmon have been fished both in the high seas and along the coast, which is expected to result in contrasting demographic and evolutionary consequences. Fishing salmon that are returning to spawn changes their abundance, but not their age distribution, whereas high-seas fisheries also shift the age distribution towards dominance of younger fish. Therefore, high-seas fisheries evolutionarily favour early-maturing fish, while coastal fisheries do not have a similar evolutionary impact. Therefore, the 1993 closure of all salmon fisheries in international waters of the North Pacific Ocean and Bering Sea, and the resulting ending of large-scale pelagic high-seas driftnet fishing (Fukuwaka et al., 2007) sets the stage for a more rigorous treatment of the hypothesis that (changes in) fishing pressures contribute to changes in Pacific salmon life histories: the prediction is that the closure of the high-seas fisheries could have resulted in an increased mean age of spawning salmon (Hard et al., 2008). While coastal fisheries have continued after 1993 (Irvine et al., 2009), they are not predicted to have comparable consequences.

Here we extend the analysis by Seo et al. (2006) by examining an additional 10 years of data from the Namdae River, so as to cover the years from 1984 to 2008, and by complementing the data on females with data on males. This allows testing for the existence of a biological response to the 1988-1989 and 1998 climatic anomalies, and it also allows addressing the question of whether changes in life-history traits coincide with the 1993 fishing moratorium. The aims of the present contribution are therefore to test whether (i) the 1988-1989 and the 1998 climatic anomalies can be detected, assuming that climatic events indeed happened, (ii) the 1993 closure of the high-seas fisheries can be detected, even though fishing pressure might have remained high on the coast, (iii) the changes in life-history traits observed during 1984-2008 reflect changes in environmental factors, and (iv) female and male chum salmon show similar temporal patterns in their growth and maturation.

## MATERIAL AND METHODS

### Chum salmon

Chum salmon is a semelparous salmonid distributed over most of the North Pacific Ocean. Available literature indicates that Korean and western Japanese populations of chum salmon follow similar migration routes: after a short stay in coastal areas during their first spring, they migrate to the Okhotsk Sea between early summer and late autumn, continue further to the western North Pacific during their first winter, and finally move to and remain in the Bering Sea and the subarctic North Pacific until their spawning migration (Urawa et al., 2001; Seo et al., 2006). The diet of oceanic chum salmon consists occasionally of fish and squids (Davis et al., 2000), but mostly of zooplankton (Higgs et al., 1995; Tadokoro et al., 1996) and larger crustaceans when populations of pink salmon are large (Tadokoro et al., 1996). Growth occurs essentially from May to November (Salo, 1991; Ishida et al., 1998; Seo et al., 2006). Maturing individuals typically return to their natal river to reproduce in the fall of their third to fifth year, depending on the growth conditions they have experienced (Groot and Margolis, 1991; Seeb et al., 2004; Quinn, 2005).

To date, most returning chum salmon in Korea originate from hatcheries established as part of artificial enhancement programs. This is true also for the salmon returning to the Namdae River, which has been heavily supplemented with hatchery-raised fish since the establishment of the Yangyang Inland Fisheries Research Institute in 1984. In this river, hatchery individuals are released from the stream drainage in February and March at a length of approximately 50 mm and a weight of 0.6-1.2 g (Seong, 1998), and migrate to coastal areas within one month (Kang et al., 2007).

## Data collection

In the Namdae River, chum salmon are caught during their spawning migration and used for *in vitro* fertilization. Fish are harvested with river-blocking nets deployed 1.5 km away from the mouth of the river, from late September to early December. Each year from 1984 to 2008, between 10 and 1,100 returning individuals were sampled for data collection (except in 1995, 1999, 2000, 2002 and 2004, when either no data could be collected for financial reasons or the data were lost to a flood that damaged the hatchery facilities). Differences in sample size across years primarily reflect variation in sampling intensity, rather than in the number of returning fish (catches ranged from 2,570 to 27,721 individuals). At times, small numbers of sampled individuals resulted from limited resources available for monitoring the Namdae River chum population. Data included weight, fork length, and scale samples collected from an area between the dorsal and the anal fin, two to three rows above the lateral line.

Scale reading was performed under a profile projector. On each scale, annuli were counted for age determination, and the distances from the focus to the check, to each annulus, and to the edge of the scale were measured to the nearest micrometre and used for growth-rate estimation (Fukuwaka and Kaeriyama, 1997). The aforementioned check forms at the time of transition to open waters, and the distance between the focus of the scale and the check therefore corresponds to growth in the river and in brackish waters. We generally assumed scale resorption to be negligible (Helle and Hoffman, 1998), but discarded scales with obvious signs of resorption. For each individual, the best-preserved scale was chosen for the final measurement and all values were collected by the same well-trained scientist. However, scales collected between 2000 and 2004 were available only for age determination (subsequent measurements of growth increments could not be performed, as the biological material was lost to a flood that damaged the hatchery facilities). Actual age was expressed using the "year-olds" method (Seo et al., 2006), according to which an individual's age is equivalent to the number of annuli on its scale plus 1. Hence, an individual released in year $y$ that returns in year $y + 2$ displays two annuli and therefore is considered of age 3.

Among females, only 19 fish were caught at age 2. Therefore, these individuals (ca. 0.6% of the 3,379 females) were omitted from the analysis. This was further justified by the observation that females returning at age 2 are usually not fully mature. Among males, the 72 individuals caught at age 5 (ca. 3.1% of the 2,336 males) were also omitted. Data are summarized in Table A1, Appendix A.

## Growth estimations

Since growth is commonly reported in units of body length, we applied back-calculation procedures (Francis, 1990) to estimate body length-at-age from scale length-at-age.

Based on preliminary analyses (Appendix B), we chose the biological intercept (BI) method (Campana, 1990) and calculated body length-at-age according to

$$L_t = L_c + \frac{S_t - S_c}{S_c - S_0}\left(L_c - L_0\right), \tag{1}$$

where $L_t$ and $S_t$ are the body length and scale length at age $t$ respectively, $L_c$ and $S_c$ are the body length and scale length at capture, and $L_0$ and $S_0$ are the body length and scale length at the onset of proportionality between scale and body growth, i.e., when body and scales start growing systematically and at a proportional rate. As independent data for estimating the latter two parameters were not available for chum salmon from the Namdae River, we followed Morita et al. (2005) and used $L_0$ = 4 cm and $S_0$ = 0.114 mm.

Annual growth at any given age $t$ was calculated by subtracting the back-calculated length at age $t$ from the back-calculated length achieved at the turn of the next growth year, i.e., at age $t+1$ (e.g., growth at age 2 is calculated as growth from age 2 to 3: $\Delta L_2 = L_3 - L_2$). Since annual growth from age 3 onwards remained largely constant in both females and males (Results), growth rates at age 3 and beyond were merged within each sex, so as to increase sample sizes for the subsequent analyses.

The estimates of body length-at-age obtained using the biological intercept method were in accordance with values from the literature (Fukuwaka et al., 2007; Kaeriyama et al., 2007b). We therefore report only results obtained based on body length data in the main text. Since exploratory analyses showed some discrepancies between these results and those obtained based on scale length, in Appendix B we elaborate on the challenges inherent to using back-calculation methods and provide results from the analyses based on scale length.

## Abundance estimations

Following Ishida et al. (2002) and Fukuwaka et al. (2007), our index of salmon abundance consisted of the Japanese catch-per-unit effort (CPUE) data for the central North Pacific; we extracted the values from Nagasawa et al. (2005) for the Bering Sea. CPUE was calculated as the number of fish caught per 30 tans of research gillnet (one tan is 50 m long). Because chum salmon and pink salmon overlap in their distribution (Azumaya and Ishida, 2000), CPUE data for both species were used such that both inter- and intra-specific density-dependent effects could be accounted for.

## Environmental data

Environmental data included estimates of the Pacific Decadal Oscillation index (PDO), the Aleutian Low Pressure Index (ALPI), SST, and zooplankton biomass. Those estimates covered the years 1980 to 2008. PDO and ALPI are, together with the Southern Oscillation Index and the North Pacific Index, the most commonly cited indices of climatic and oceanographic conditions for the Pacific Ocean (Benson and Trites, 2002). ALPI became positive in 1977 after a prolonged negative phase, and remained positive until 1988 (e.g., Beamish et al., 1997; Mantua et al., 1997; Benson and Trites, 2002). Summer PDO was positive before 1998 and became slightly negative subsequently (Overland et al., 2008), while SST displayed major changes both in 1997 (Napp and Hunt, 2001) and in 1998 (Minobe, 2002).

We used the average PDO from June to September of each year $y$ (as in Fukuwaka et al., 2007) and the average ALPI from December of year $y - 1$ to March of year $y$ (as in

McFarlane et al., 2000) as climate indices for year *y*. Summer PDO was favoured over winter PDO, as the latter has shown no detectable shift since 1977 (Overland et al., 2008). PDO data were obtained from Mantua (http://jisao.washington.edu/pdo/PDO.latest) and ALPI estimates from DFO (http://www.pac.dfo-mpo.gc.ca/science/species-especes/climatology-ie/cori-irco/alpi/index-eng.htm). Following Seo et al. (2006), the SST and zooplankton biomass data we used were recorded in two major habitats utilized by chum salmon during ocean growth, i.e., in the Okhotsk Sea (first year) and in the Bering Sea (second to last year). August to November SST in the Okhotsk Sea (48-58°N and 145-155°E) and June to November SST in the Bering Sea (52-58°N and 180-160°W) were taken as provided by the NOAA-CIRES Climate Diagnostics Center (http://www.cdc.noaa.gov/Timeseries). Summer zooplankton biomass for the eastern Bering Sea was extracted from Sugimoto and Tadokoro (1997); data from the western Bering Sea were not available to us. Furthermore, data on zooplankton biomass in the Okhotsk Sea during our study period were found to be too scarce to be useful.

## Statistical analyses

We hypothesized that our time series would display up to three abrupt changes: two associated with the 1988-89 and the 1998 regimes shifts, and one with the 1993 high-seas fishing moratorium. We assumed that each event represented the end of a period and treated 1988, 1993, and 1998 as the last years of those periods. Unfortunately, the available data did not allow for the simultaneous detection of multiple consecutive changes in life-history traits, because the inter-annual variability was too high relative to the length of the available time series and to the effect size of the tested events (Andersen et al., 2008). These data did not allow for the detection of not pre-defined break points either. We therefore treated each event separately, by fitting three different threshold models to the data: the first model had its break point in 1988, the second in 1993, and the third in 1998.

We used threshold models (Seber and Wild, 1979), which allow for the simultaneous estimation and comparison of multiple independent regression slopes within a single time series. This is achieved by defining time variables that incrementally increase over each of the segments of a time series. For example, in our first threshold model, the first time variable increases from –4 to 0 from 1984 to 1988 and then remains constant at 0, whereas the second time variable remains at 0 from 1984 to 1988 and then increases by 1 in each subsequent year. In order to quantify possible shifts in trait values between the end and the beginning of two subsequent periods, we allowed for period-specific intercepts by treating period as a factor (when the intercepts are identical, the two line segments are connected). Our choice of statistical method was justified by the fact that we made a priori assumptions about the occurrence of detectable shifts in our time series in 1989, 1993 and 1998. Alternative methods that do not require such assumptions have been proposed and successfully applied elsewhere (e.g., Rodionov, 2004; Rodionov and Overland, 2005).

We compared the three threshold models to three alternative models: a null model assuming no change in life-history traits over time (constant), a second model assuming a linear (monotonic) change, and a third model assuming a smooth but possibly non-monotonic change (realized through a second-order polynomial). Hence we systematically compared six models.

The comparative approach outlined above was applied for age and length at spawning and for growth. However, depending on the response variable, different classes of models were used. Specifically, temporal trends in age at spawning were quantified using an ordered logistic regression model (McCullagh, 1980). Linear trends in body length at spawning were quantified using a linear mixed-effect model (LME, Pinheiro and Bates, 2000), in which cohort was a random term, included to account for the effects of common birth year on growth history. Because length at spawning increased approximately linearly with age at spawning (Results), age at spawning was treated as a covariate (regression variable). Through visual inspection of the data, temporal patterns in body length were found to be comparable across age at spawning classes in females, but not in males. Hence, we estimated interaction effects between age at spawning and time in males. Similar LME models were also used to analyze the growth data. For all analyses of growth rates, age at spawning was treated as a covariate, ocean age was treated as a factor, and cohort and individuals were included as nested random effects. Including individual identity as a random effect was necessary to account for repeated measurements within individuals. Effects of ocean age and age at spawning on male and female growth rates were tested simultaneously by quantifying interaction effects between these terms. Given that growth varied significantly with ocean age and with age at spawning (Results), we systematically included both terms in our analyses of temporal variation in growth rates. Since chum salmon grow in a different environment in their first ocean year than in subsequent years (see section ‘Chum salmon’), temporal patterns in growth rates were likely to vary between ocean-age groups. Accordingly, time and age were tested in interaction.

LME models were also used to estimate environmental effects on growth rates. In these models, cohort and individuals were represented by nested random effects, and densities of chum salmon and pink salmon, SST, zooplankton density, summer PDO, and ALPI as covariates. Growth in individuals of age 1 was regressed on environmental conditions encountered in the Okhotsk Sea, while conditions in the Bering Sea were used for subsequent age classes. For those latter analyses, we assumed the response of growth rates to environmental factors to be comparable in all ocean-age groups and across age-at-spawning classes. Accordingly, both terms entered the models for their additive effects on growth only. Because zooplankton estimates for the Bering Sea were unavailable for four years of our study period, we used the data for which all zooplankton estimates were available to fit a model including zooplankton as predictor (“Limited data set”, Table 3), and data from all years to fit a model excluding zooplankton (“Full data set”, Table 3). Because evidence from coho salmon (*O. kisutch*) suggests that climatic effects occur in the oceanic phase of the salmon life cycle rather than in the freshwater phase (Bradford, 1999), growth in freshwater was ignored in all growth-rate analyses. That is, for these analyses distances between the scale’s focus and check were not included.

All computations were performed in R (R Development Core Team, 2008). Model selection was based on the information-theoretic approach (Burnham and Anderson, 2002), and the Akaike Information Criterion (AIC) was chosen as the selection criterion. All LME models were fit using the function lme in the R library nlme. Since the numbers of females of age 5 and of males of age 2 were low, all analyses were repeated using datasets including only females and males of age 3 and 4.

# RESULTS

## Age at spawning

The best model for explaining temporal variation in female age at spawning was the threshold model with a break point in 1993 (Fig. 1, Table 1). Age at spawning increased from 1984 to 1993 (ordered logistic regression: ${}_{a} = 0.15 \pm 0.017$ yr$^{-1}$, $p < 0.001$) and decreased subsequently ( ${}_{b} = \ 0.07 \pm 0.017$ yr$^{-1}$, $p < 0.001$), after a slight shift upwards between the two periods ( ${}_{p} = 0.52 \pm 0.19$, $p = 0.009$). In males, the selection procedure strongly favoured the model describing changes in age at spawning in response to the 1988-1989 regime shift (Fig. 1, Table 1). Age at spawning decreased prior to 1989 ( ${}_{a} = \ 0.3 \pm 0.044$ yr$^{-1}$, $p < 0.001$) and increased subsequently ( ${}_{b} = 0.06 \pm 0.008$ yr$^{-1}$, $p < 0.001$), after a significant shift upwards ( ${}_{p} = 1.42 \pm 0.12$, $p < 0.001$). Note that the coefficients relate to responses measured in logits (log-odds).

## Length at spawning

### *Change in length at spawning with age at spawning*

Individuals spawning later were larger: body length at spawning (Fig. 2) significantly increased with age at spawning in females (LME model: $= 4.25 \pm 0.12$ cm/yr, $p < 0.001$) and in males ( $= 6.8 \pm 0.16$ cm/yr, $p < 0.001$).

### *Temporal variation in length at spawning*

The best model for temporal variation in body length at spawning in both females and males was a threshold model with a break point in 1988 (Table 1). In females, body length decreased prior to the regime shift ( ${}_{a} = \ 0.58 \pm 0.13$ cm/yr, $p < 0.001$) and then stabilized at a lower level ( $_{b} = 0.03 \pm 0.03$ cm/yr, $p = 0.29$; $_{p} =$ $1.71 \pm 0.31$ cm, $p < 0.001$; Fig. 2). In males, body length at spawning increased from 1984 to 1988 in individuals of age 2 ( $_{a} = 2.92 \pm 0.61$ cm/yr, $p < 0.001$), but the slope gradually decreased ( $_{a\ age} =$ $1.15 \pm 0.21$ cm/yr, $p < 0.001$) such that the trend was negative in older males (Fig. 2). From 1989 onwards, length at spawning had a slight tendency to increase ( $_{b} = 0.35 \pm 0.12$ cm/yr, $p = 0.004$). This was true for all ages ($\beta_{b\times age} = -0.06 \pm 0.04$ cm/yr, $p = 0.096$). Differences in body length at spawning around 1988 were negative in two years old males ( $_{p} =$ $3.17 \pm 1.56$ cm, $p = 0.042$) and increasingly positive in older males ($\beta_{p\times age} = 1.07 \pm 0.53$ cm, $p = 0.044$).

All results pertaining to body length at spawning remained similar when datasets were restricted to individuals of age 3 and 4.

## Growth

### *Changes in growth with ocean age and age at spawning*

Growth rates decreased with spawning age (LME model, females: $=$ $0.85 \pm 0.08$ cm/yr, $p < 0.001$; males: $=$ $1.06 \pm 0.09$ cm/yr, $p < 0.001$), and with ocean age within each spawning-age group (females: $F_{2,8334} = 3303$, $p < 0.001$; males: $F_{1,4240} = 1351$, $p < 0.001$). Furthermore, the significant negative interaction term between ocean age and age at spawning in females ($F_{2.8334} = 102$, $p < 0.001$) and in males ($F_{2,4240} = 22$, $p < 0.001$) suggested that the decrease in growth with each subsequent year at sea was steeper the later individuals spawned (Fig. 3).

### Temporal variation in growth

The best models for temporal variation in female and male body growth was, once again, the threshold model with a break point in 1988 (Figs. C.1 and C.2, Appendix C, Table 1). In both females and males, growth before and after the regime shift generally decreased over time and across all ocean ages, except for ocean age 1 after 1988 (Table 2). The decrease was more pronounced later in life than at early ocean ages. Growth rates right after the regime shift were either higher than before or stayed unchanged (Table 2).

### Environmental variation in growth

After accounting for effects of age at spawning and ocean age, two effects emerged for both sexes and regardless of whether all years or only years with zooplankton estimates were used: body growth systematically increased with summer PDO and decreased with density of chum salmon. When we considered only the years with zooplankton estimates, female body growth increased also with increasing zooplankton densities and decreased with ALPI, whereas for the entire data set, a positive correlation with SST emerged (Table 3). In males, the patterns were broadly similar to those observed in females. However, body growth in males increased with increasing SST in both data sets, and there was no indication of an effect of pink-salmon density (Table 3).

Environmental effects on growth in the Okhotsk Sea (age 1) were limited to ALPI. ALPI had a significant, positive effect on growth in females ( $= 0.17 \pm 0.06$ cm per unit of change in ALPI, $p = 0.003$) and a marginal effect on growth in males ( $= 0.12 \pm 0.07$ cm per unit of change in ALPI, $p = 0.08$).

All results pertaining to body growth remained similar when datasets were restricted to individuals of age 3 and 4.

## DISCUSSION

Our analyses of age at maturation, size at maturation, and growth in male and female chum salmon from the Namdae River indicate that the 1988-1989 regime shift had the strongest effects on both sexes. Our results thereby contribute to a growing body of evidence that abrupt transitions in climatic conditions can cause noticeable changes in life-history traits. Since the Namdae River chum population represents a significant fraction of the Korean chum population as a whole, our results also serve to strengthen existing indications that the biological evidence for the 1988-1989 regime shift in Korean chum salmon populations is stronger than that for the subsequent environmental changes.

### Maturation schedule and growth

Our results agree with earlier observations of a decrease in female body size at spawning during the second half of the 1980s and a concomitant increase in age at spawning. Existing observations come from chum salmon from the Namdae River (Seo et al., 2006), as well as from other populations of chum salmon (e.g., Bigler et al., 1996; Helle and Hoffman, 1998; Fukuwaka et al., 2007; Morita and Fukuwaka, 2007). In males, the pre-1989 decrease in age at spawning and in body length at spawning (for older age groups), and the post-1989 increase in these two traits are also in agreement with earlier results (Kaeriyama and Katsuyama, 2001; Seo et al., 2006; Fukuwaka et al., 2007; Morita and Fukuwaka, 2007). Yet, these maturation trends were different between males and females as the decrease in body size at spawning observed in females was accompanied by an increase, rather than a decrease, in age at spawning.

Overall, female and male body growth in the Bering Sea decreased over time, although the trend was shallow after 1989 and even occasionally reversed. This observation corroborates existing results by Azumaya and Ishida (2000) and Morita et al. (2001). It further matches temporal patterns in zooplankton biomass in the North Pacific, which decreased to the lowest level on record in 1989 and remained low at least until 1997 (Lees et al., 2006), and also coincides with the increase in chum salmon population size during the last quarter of the 20th century (Kaeriyama and Katsuyama, 2001). Because growth was found to be density-dependent in our study population, this increase in population size and the concurrent reduction in food availability could explain the observed decrease in growth (e.g., Ishida et al., 1993; Azumaya and Ishida, 2000; Wertheimer et al., 2004).

The observed maturation trends partly corroborate the assumption that decrease in growth alone can trigger a decrease in size at spawning and a concomitant increase in age at spawning (Morita et al., 2005). However, variation in growth does not fully capture the maturation trends observed in females after 1993 and in males prior to 1989. Changes in size-dependent mortality or maturation tendency may serve as possible auxiliary explanations, but little data is available to corroborate or challenge this assumption.

The detected differences between male and female chum salmon with regard to temporal trends in maturation and growth, suggest that males and females follow different maturation reaction norms (Stearns and Crandall, 1984), implying a type of life-history dimorphism that has already been documented for some other fish species (Heino and Dieckmann, 2008). While natural and sexual selection pressures shaping reproductive traits of the Namdae River chum salmon are difficult to characterize, as most returning fish are of hatchery origin, the detected dimorphism must relate to sex-specific impacts of body size on the reproductive success of spawning males and females.

### Challenges associated with detecting changes in life histories

A number of factors may have hindered detecting the biological effects of the 1993 and 1998 events. First, data after 1994 were often sparse, with some or all data missing between 1999 and 2005 (Table 1). This compromised our ability to detect a response to the 1998 shift in particular. Incomplete time series have previously been held accountable for controversial conclusions (Lees et al., 2006). These gaps in a short time series might also have prevented us from identifying a response to the closure of the fisheries, as more comprehensive data on chum salmon from Japan have successfully revealed such a response (Fukuwaka and Morita, 2008).

Second, because of the high inter-annual variability shown by our time series, we could robustly identify at most one change at a time. It could therefore be that the 1988-1989 regime shift overshadowed the influence of the later events, impeding us from detecting them.

Third, responses to changes in climate and in exploitation patterns are likely to unfold over a range of temporal scales in different traits (Waples et al., 2008; Chittenden et al., 2009; Brander, 2010; Drinkwater et al., 2010). Demographic and plastic effects during the ocean phase unfold rapidly, but become observable in mature salmon with a delay of up to several years. Evolutionary effects unfold much slower, at generational time scales.

Fourth, because chum salmon catches started to decline already in the 1980s (Irvine et al., 2009), the demographic effects of the 1993 moratorium on high-seas fishing might have been too weak to be detectable. At the same time, coastal fisheries continued and may even have intensified (Irvine et al., 2009). However, we do not expect this to be important, unless coastal fisheries are strongly size-selective.

Fifth, the nature of the biological responses triggered by abrupt changes in climate and/or exploitation is complex (Lees et al., 2006; Jiao, 2009; Overland et al., 2010). Because the state of returning chum salmon reflects the environment they have encountered throughout their life, manifestations of an abrupt environmental change are gradually increasing with time as fish that have been exposed to the modified condition for longer duration are returning to spawn. Moreover, because chum salmon can show considerable resilience to changes in environmental conditions, abrupt changes in the environment might not be accompanied by similarly abrupt changes in their life-history traits. Hence, detecting such responses and assigning them with reasonable confidence to specific causes is challenging (Brander, 2010; Ottersen et al., 2010; Perry et al., 2010). In particular, climate and exploitation (and changes therein) may affect multiple traits simultaneously, and the resulting effects may differ between life stages (Ruggerone et al., 2007; Crozier et al., 2008; Jiao, 2009) and depending on the complex genetic covariance structures between traits (Etterson and Shaw, 2001). Moreover, when multiple life-stage transitions are delicately tuned to conditions in different environments, effects on early life stages are likely to have long-lasting and unpredictable repercussions in subsequent years (Crozier et al., 2008; Planque et al., 2010).

Finally, although effects of climate and exploitation (and changes therein) are traditionally believed to be additive, evidence suggests that they are predominantly multiplicative and should be treated accordingly (Benson and Trites, 2002; Crozier et al., 2008; Planque et al., 2010).

## Conclusions and outlook

The present work supports earlier studies showing major changes in female age and size at spawning and in female growth around the late 1980s. It thereby adds to a growing body of evidence indicating that climatic changes in the North Pacific during the last quarter of the 20th century had profound effects on numerous populations of Pacific salmon. Since data on temporal variation in life-history traits of chum salmon from the Namdae River are sparse and variable, it remains a challenge to determine whether responses to the closure of the driftnet fishery and to the 1998 regime shift are truly absent or just cannot be detected owing to data limitations. It is also possible that our initial assumption that these two events occurred and were significant is debatable as the evidence for the 1998 regime shift is mixed (e.g., Irvine and Fukuwaka, 2011) and the high-seas driftnet fisheries declined already before their closure in 1993 (Irvine et al., 2009). Our analyses have also highlighted uncertainties in a commonly applied method for back-calculating body length from scale measurements, which we suggest warrants further attention.

Since age and size at spawning are important life-history traits (Roff, 1992; Stearns, 1992), and given the importance of growth for survival and maturation and for linking climate changes and population dynamics (Drinkwater et al., 2010), understanding the reasons for fluctuations in these traits is crucial. Our analyses point to an environmental origin of life-history changes in Korean chum salmon, with phenotypic plasticity as the likely mechanism. However, because harvesting-induced evolution has contributed to observed changes in other Asian chum salmon populations (Morita and Fukuwaka, 2007), and as we have not assessed whether it may have contributed to life-history changes in our study population, further scrutiny is warranted. A major difficulty is that the effects of growth, mortality, and maturation tendency are confounded in time-series of age and size at spawning (Heino et al., 2002). The probabilistic maturation reaction norm (PMRN) approach (Dieckmann and Heino, 2007; Heino and Dieckmann, 2008) has proven helpful in disentangling processes underlying variations in age and length at maturation, but the currently available estimation techniques are not readily applicable to chum salmon from our study population. Suitable techniques are now under development, and will hopefully help further elucidate the oceanic life history of chum salmon.

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**Figure 1** Age at spawning from 1984 to 2008 in female (left panel) and in male (right panel) chum salmon. Filled circles and vertical bars show means and standard errors, respectively. Predicted values for the best models of temporal variation in age at spawning are shown with continuous lines. The best models included a break point in 1993 for females and in 1988 for males.

**Figure 2** Body length at spawning from 1984 to 2008. Left panel: female chum salmon aged 3 years (filled circles), 4 years (open squares), and 5 years (filled triangles); right panel: male chum salmon aged 2 years (open triangles), 3 years (filled circles), and 4 years (open squares). Standard errors are shown by vertical bars (if based on more than two observations). Predicted values for the best models of temporal variation in body length at spawning are shown with continuous lines. The best models included a break point in 1988 for both sexes.

**Figure 3** Body growth in freshwater (FW) and during each consecutive year at sea (SW). Left panel: female chum salmon aged 3 years (filled circles), 4 years (open squares), and 5 years (filled triangles); right panel: male chum salmon aged 2 years (open triangles), 3 years (filled circles), and 4 years (open squares). Standard errors are shown by vertical bars. Once released, fingerlings remain 4-5 months in freshwater; growth in freshwater therefore includes the periods between birth and release and between release and sea migration.

Figure 1

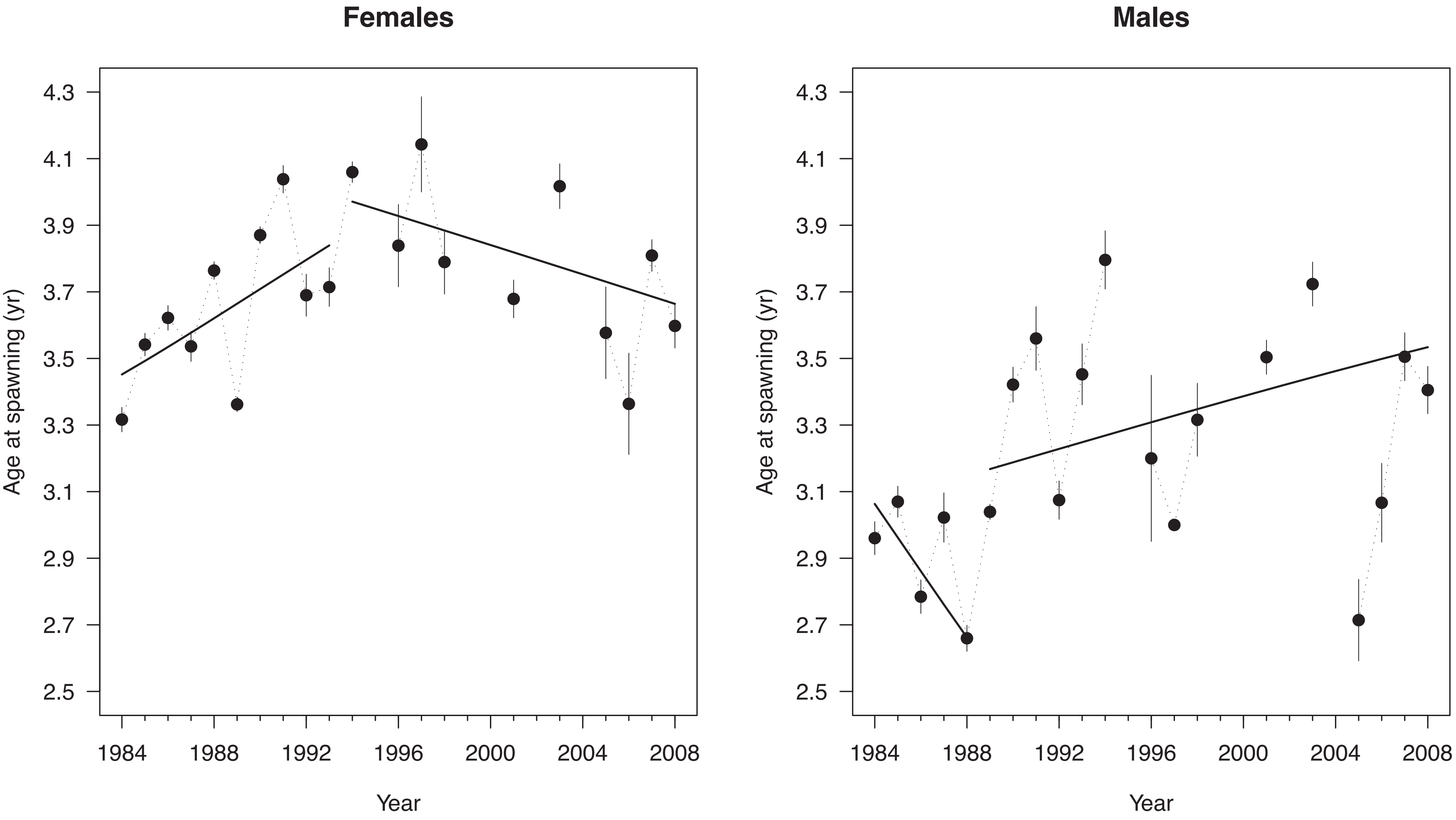
Females
Males
Age at spawning (yr)
4.3
4.1
3.9
3.7
3.5
3.3
3.1
2.9
2.7
2.5
1984
1988
1992
1996
2000
2004
2008
Year

Figure 2

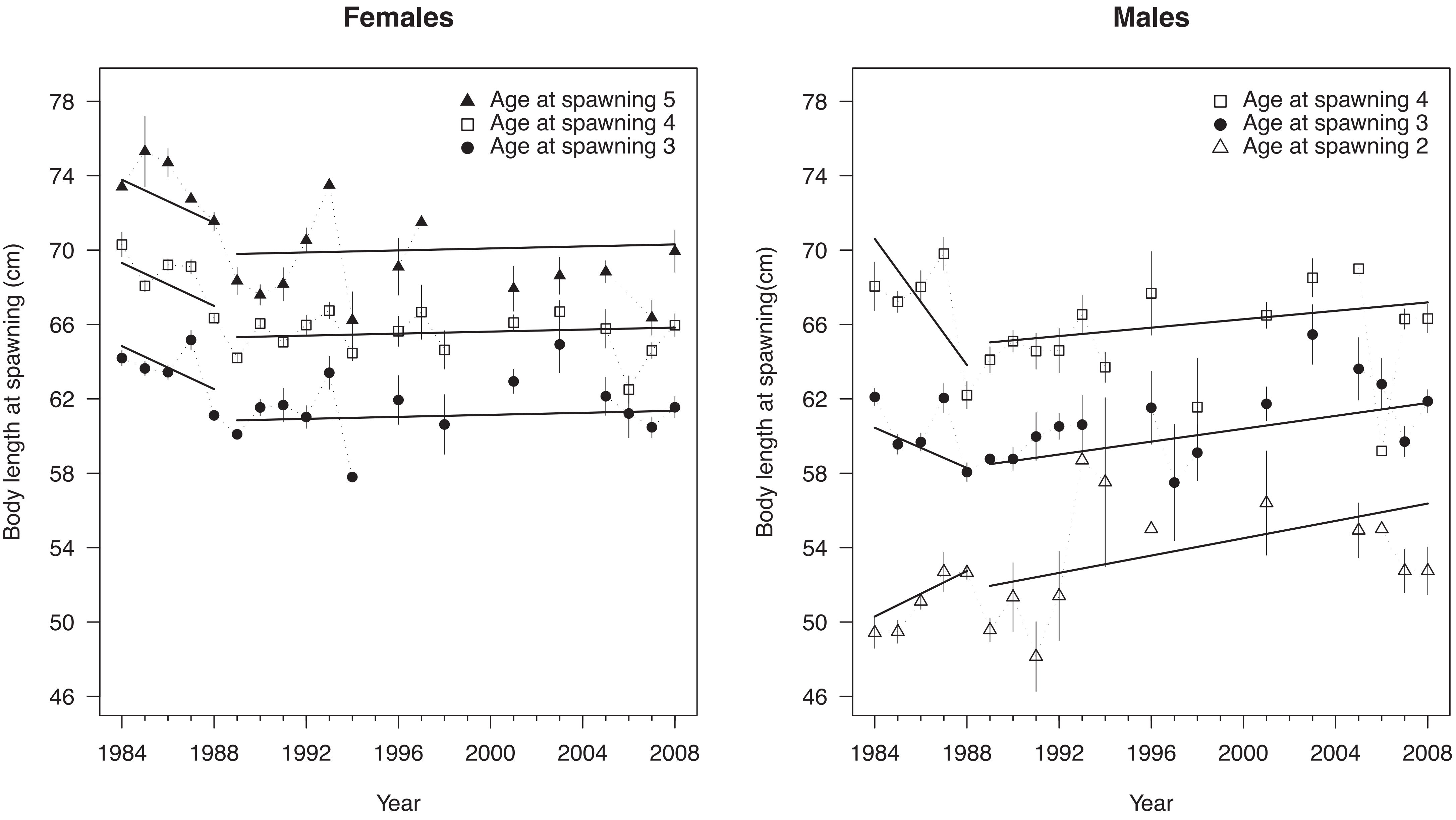
Females
Age at spawning 5
Age at spawning 4
Age at spawning 3
Body length at spawning (cm)
78
74
70
66
62
58
54
50
46
1984
1988
1992
1996
2000
2004
2008
Year
Males
Age at spawning 4
Age at spawning 3
Age at spawning 2
Body length at spawning(cm)
78
74
70
66
62
58
54
50
46
1984
1988
1992
1996
2000
2004
2008
Year

Figure 3

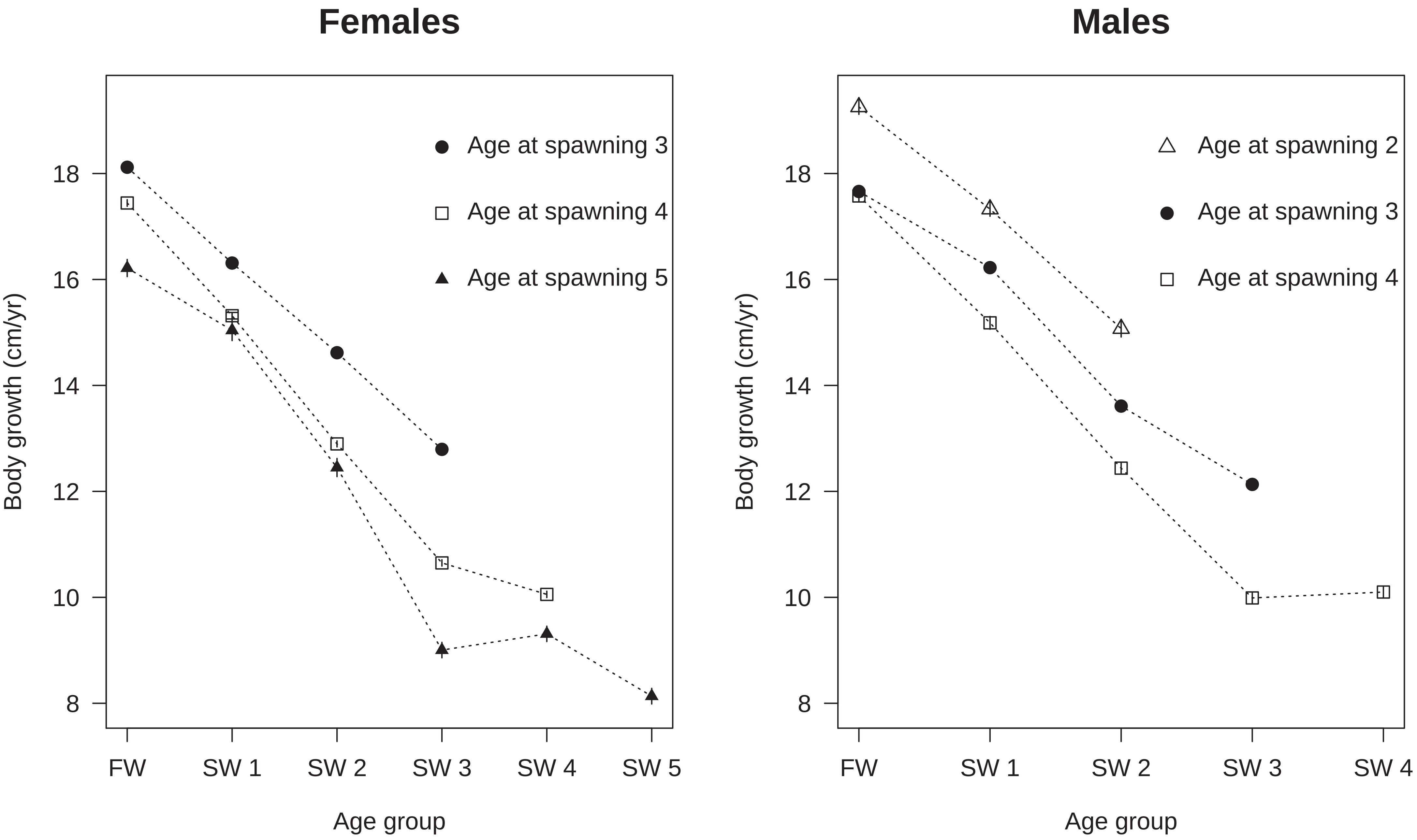
Females
Males
Body growth (cm/yr)
8
10
12
14
16
18
FW
SW 1
SW 2
SW 3
SW 4
SW 5
Age group
Age at spawning 2
Age at spawning 3
Age at spawning 4
Age at spawning 5

**Table 1** Support for models predicting age at spawning, body length at spawning, and growth. $\Delta_i$ is the AIC difference between model $i$ and the model with the minimum AIC, and $w_i$ is the Akaike weight for model $i$. Large values indicate strong support for a model (Burnham and Anderson, 2002).

**Table 2** ANOVA tables for the best models of temporal variation in body growth at sea in female (denominator df = 11,448) and male (denominator df = 6,283) chum salmon from 1980 to 2008.

**Table 3** Regression coefficients for environmental effects on the body growth of female and male chum salmon in the Bering Sea from 1980 to 2008. "Limited data set" refers to the subset of years for which zooplankton estimates are available (insert which years – it's not in the methods). Growth is measured in cm/yr, CPUE as the number of fish caught per 30 tans of research gillnet (one tan is 50 m long), zooplankton in mg $m^{-3}$, SST in ˚C, and PDO and ALPI in units of change in Pacific Decadal Oscillation index and in Aleutian Low Pressure Index, respectively. The abbreviations "NS" (not significant) and "NA" (not available) indicate the absence of an effect and the absence of data, respectively.

**Table 1**

| Model | Age at spawning |  | Body length at spawning |  | Growth |  |
|---|---|---|---|---|---|---|
|  | $\Delta_i$ | $w_i$ | $\Delta_i$ | $w_i$ | $\Delta_i$ | $w_i$ |
| **Females** |  |  |  |  |  |  |
| Break in 1988 | 29.7 | < 0.001 | 0 | 1.000 | 0 | 1.000 |
| Break in 1993 | 0 | 0.949 | 27.8 | < 0.001 | 124.5 | < 0.001 |
| Break in 1998 | 6.0 | 0.047 | 31.8 | < 0.001 | 141.3 | < 0.001 |
| Quadratic | 11.0 | 0.004 | 33.8 | < 0.001 | 124.5 | < 0.001 |
| Linear | 80.2 | < 0.001 | 36.2 | < 0.001 | 250.4 | < 0.001 |
| Null (constant) | 121.4 | < 0.001 | 41.9 | < 0.001 | 337.9 | < 0.001 |
| **Males** |  |  |  |  |  |  |
| Break in 1988 | 0 | 1.000 | 0 | 1.000 | 0 | 1.000 |
| Break in 1993 | 84.5 | < 0.001 | 21.2 | < 0.001 | 68.6 | < 0.001 |
| Break in 1998 | 110.6 | < 0.001 | 15.3 | < 0.001 | 64.5 | < 0.001 |
| Quadratic | 121.9 | < 0.001 | 20.3 | < 0.001 | 61.2 | < 0.001 |
| Linear | 140.4 | < 0.001 | 28.6 | < 0.001 | 124.9 | < 0.001 |
| Null (constant) | 326.8 | < 0.001 | 35.1 | < 0.001 | 146.5 | < 0.001 |

**Table 2**

| | df | *F* | *P* |
|---|---|---|---|
| **Females** | | | |
| Intercept | 1 | 13,737 | < 0.001 |
| Age at spawning | 1 | 2,845 | < 0.001 |
| Ocean age | 2 | 3,343 | < 0.001 |
| Years 1984-1988 | 1 | 69 | < 0.001 |
| Years 1989-2008 | 1 | 5.6 | 0.018 |
| Period | 1 | 122 | < 0.001 |
| Ocean age × Years 1984-1988 | 2 | 14 | < 0.001 |
| Ocean age × Years 1989-2008 | 2 | 59 | < 0.001 |
| Ocean age × Period | 2 | 10 | < 0.001 |
| **Males** | | | |
| Intercept | 1 | 39,875 | < 0.001 |
| Age at spawning | 1 | 1,504 | < 0.001 |
| Ocean age | 2 | 1,337 | < 0.001 |
| Years 1984-1988 | 1 | 17 | 0.001 |
| Years 1989-2008 | 1 | 0.7 | 0.4 |
| Period | 1 | 80 | < 0.001 |
| Ocean age × Years 1984-1988 | 2 | 4.5 | 0.011 |
| Ocean age × Years 1989-2008 | 2 | 24 | < 0.001 |
| Ocean age × Period | 2 | 7.2 | < 0.001 |

**Table 3**

| | Limited data set | | | | Full data set | | | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | Standard Error | *t* | *P* | Estimate | Standard Error | *t* | *P* |
| **Females** | | | | | | | | |
| Chum salmon | -0.005 | 0.001 | -4.49 | < 0.001 | -0.005 | 0.0007 | -7.75 | < 0.001 |
| Pink salmon | 0.001 | 0.0005 | 1.87 | 0.06 | NS | NS | NS | NS |
| Zooplankton | 0.006 | 0.0004 | 11.73 | < 0.001 | NA | NA | NA | NA |
| SST | NS | NS | NS | NS | 0.79 | 0.1 | 8.07 | < 0.001 |
| PDO | 0.29 | 0.05 | 6.18 | < 0.001 | 0.40 | 0.043 | 9.22 | < 0.001 |
| ALPI | -0.11 | 0.015 | -7.56 | < 0.001 | NS | NS | NS | NS |
| **Males** | | | | | | | | |
| Chum salmon | -0.006 | 0.001 | -4.67 | < 0.001 | -0.004 | 0.0009 | -3.92 | < 0.001 |
| Pink salmon | NS | NS | NS | NS | NS | NS | NS | NS |
| Zooplankton | 0.002 | 0.0008 | 2.97 | 0.003 | NA | NA | NA | NA |
| SST | 0.69 | 0.21 | 3.21 | 0.001 | 0.89 | 0.14 | 6.32 | < 0.001 |
| PDO | 0.25 | 0.07 | 3.39 | < 0.001 | 0.36 | 0.07 | 5.45 | < 0.001 |
| ALPI | -0.09 | 0.02 | -3.80 | < 0.001 | NS | NS | NS | NS |

## APPENDIX A

**Table 1** Number of female and male chum salmon sampled from 1984 to 2008, by age at spawning. Females aged 2 and males aged 5 at maturation were very few, and have therefore been excluded. No data were collected in 1995, 1999, 2000, and 2002. For 2001 and 2003 (*), no scale measurements were available; only age and body length at spawning were measured.

**Table 1**

| | Females | | | Males | | |
|---|---|---|---|---|---|---|
| | Age at spawning (yr) | | | Age at spawning (yr) | | |
| Spawning year | 3 | 4 | 5 | 2 | 3 | 4 |
| 1984 | 123 | 52 | 2 | 22 | 87 | 17 |
| 1985 | 113 | 124 | 3 | 31 | 111 | 44 |
| 1986 | 123 | 133 | 19 | 65 | 90 | 26 |
| 1987 | 66 | 70 | 2 | 21 | 46 | 23 |
| 1988 | 206 | 316 | 67 | 198 | 116 | 68 |
| 1989 | 392 | 184 | 15 | 57 | 375 | 77 |
| 1990 | 88 | 303 | 33 | 15 | 62 | 82 |
| 1991 | 18 | 115 | 24 | 5 | 12 | 33 |
| 1992 | 59 | 51 | 19 | 5 | 52 | 10 |
| 1993 | 21 | 48 | 1 | 2 | 19 | 21 |
| 1994 | 1 | 77 | 6 | 5 | 0 | 44 |
| 1996 | 10 | 16 | 5 | 2 | 4 | 4 |
| 1997 | 0 | 6 | 1 | 0 | 3 | 0 |
| 1998 | 4 | 15 | 0 | 0 | 13 | 6 |
| 2001* | 59 | 63 | 15 | 6 | 53 | 72 |
| 2003* | 7 | 43 | 8 | 0 | 13 | 34 |
| 2005 | 14 | 9 | 3 | 7 | 13 | 1 |
| 2006 | 7 | 4 | 0 | 1 | 12 | 2 |
| 2007 | 26 | 79 | 5 | 12 | 24 | 61 |
| 2008 | 41 | 40 | 6 | 6 | 35 | 38 |

## APPENDIX B

## GROWTH ESTIMATIONS

### Back-calculation method

To determine which back-calculation method was the most appropriate for our data, two preliminary analyses were performed. The first one consisted in detecting the presence of so-called "growth effects", which cause older fish to have significantly larger scales than equally-sized younger fish (Campana, 1990; Wilson *et al.*, 2009). This was achieved by comparing the fit of a regression model of scale length-at-catch on body length-at-catch with that of a model including age as covariate, assuming that a significant and positive age term can serve as evidence for growth effects. The log-likelihood ratio test used for model comparison favoured the formulation including age ($F = 86.25$, $p < 0.001$) and according to which scale length-at-catch increased significantly ($p < 0.001$) by $0.2 \pm 0.011$mm each year and by $0.016 \pm 0.002$ mm/cm increment in body length-at-catch. The second analysis consisted in determining whether the relationship between scale length-at-catch and fork length-at-catch varied across cohorts (see Carlander, 1981). This was done using a linear model in which cohort was added as predictive factor in interaction with either (log-transformed) fork length-at-catch or (log-transformed) body length-at-catch (see Francis, 1990). As cohorts and age classes are fully confounded if a cohort consists of only one age class, we limited this latter analysis to the cohorts comprising at least two age-at-catch classes. Regardless of whether we assumed a scale-proportional or a body-proportional hypothesis (i.e. whether scale length-at-catch was a function of body length-at-catch or the opposite) and of whether variables were log-transformed or not, a significant cohort effect was detected (Predictor $\times$ Cohort interaction effect –

Females: 2.51 < $F_{13,2979}$ < 6.5, $p < 0.001$; Males: 4.06 < $F_{14,1995}$ < 8.77, $p < 0.001$). Such effect implies that the scale length – body length relationship varies between cohorts and that the back-calculation of body length-at-age should therefore account for this variation.

Based on these analyses, we chose the biological intercept (BI) method (Campana, 1990) to back-calculate lengths-at-age. This method allows correcting for growth effects (Campana, 1990; Secor and Dean, 1992; Sirois et al., 1998) and circumventing the problems arising from the above-mentioned cohort effects, as it does not rely on the definition of a scale length-body length regression. However, it relies on the major assumption that scale and body length and growth are proportional.

## Analyses and Results

The statistical methods used to analyse scale length data are the same as the ones used to analyse body length data.

### Length at spawning

*Change in length at spawning with age at spawning*

Individuals spawning later were larger: scale length at spawning (Fig. B.1) significantly increased with age at spawning in females (LME model: $\beta = 0.25 \pm 0.008$ mm/yr,) and in males ($\beta = 0.32 \pm 0.008$ mm/yr).

*Temporal variation in length at spawning*

In both females and males, the best model for temporal variation in scale length at spawning was a threshold model with a break point in 1988 (Fig. B.1, Table B.1). Scale length at spawning in females increased prior to 1989 (LME model: $\beta_a = 0.1 \pm 0.011$ mm/yr, $p < 0.001$) and decreased subsequently ($\beta_b = -0.01 \pm 0.003$ mm/yr, $p < 0.001$), after a slight downward shift between the two periods

($\beta_{\mathrm{p}} = -0.1 \pm 0.02$ mm/yr, $p < 0.001$). In males, the patterns were age-dependent (prior to 1989: $\beta_{\mathrm{a \times age}} = -0.05 \pm 0.01$ mm/yr, $p < 0.001$; after 1989: $\beta_{b\times\mathrm{age}} = -0.005 \pm 0.002$ mm/yr, $p = 0.004$). At age 2, scale length at spawning slightly increased over time before 1989 ($\beta_{\mathrm{a}} = 0.17 \pm 0.03$ mm/yr, $p < 0.001$) and remained constant thereafter ($\beta_{\mathrm{b}} = 0.02 \pm 0.006$ mm/yr, $p = 0.051$). The slopes changed from slightly positive at young age to slightly negative in 4-year-old individuals prior to 1989 and in both 3- and 4-year-old individuals after 1988 (Fig. B.1). No shift in scale length at spawning was detected between periods ($\beta_{\mathrm{p}} = -0.01 \pm 0.07$ mm, $p = 0.92$; $\beta_{\mathrm{p \times age}} = 0.01 \pm 0.02$ mm, $p = 0.65$).

## Discussion: Challenges inherent to using back-calculation methods

In contrast to body length at spawning, we found that female and male scale length at spawning mostly increased prior to 1988 and decreased thereafter. Unless unexpected and non-negligible scale resorption occurred every year, and unless the extent of such resorption varied considerably between years, this mismatch between temporal patterns in scale length and body length at spawning implies that the relationship between scale growth and somatic growth varies over time, potentially in response to changes in selective pressures or in the environment. Hence, back-calculating body length-at-age calls for caution. In particular, unless we understand how different external factors affect the relationship between scale growth and body growth, applying the biological intercept back-calculation method, which assumes constant proportionality between body growth and scale growth in space and time (Campana, 1990; Morita and Matsuishi, 2001), might produce artifactual patterns. However, although a variety of other back-calculation methods exist (reviewed in Francis, 1990), the biological and mechanistic assumptions underlying each of them render their application equally controversial. Despite the remarkable effort invested into reviewing and clarifying back-calculation methods (see for e.g., Francis, 1990; Morita and Matsuishi, 2001; Schirripa, 2002; Li et al., 2008), the differential merits and limitations of alternative approaches remain difficult to appreciate.

**Figure B.1** Scale length at spawning from 1984 to 2008. Left panel: female chum salmon aged 3 years (filled circles), 4 years (open squares), and 5 years (filled triangles); right panel: male chum salmon aged 2 years (open triangles), 3 years (filled circles), and 4 years (open squares). Standard errors are shown by vertical bars (if based on more than two observations). Predicted values for the best models of temporal variation in scale length at spawning are shown with continuous lines. The best models included a break point in 1988 for both sexes.

**Table B.1** Support for models predicting scale at spawning. $\Delta_i$ is the AIC difference between model $i$ and the model with the minimum AIC, and $w_i$ is the Akaike weight for model $i$. Large values indicate strong support for a model (Burnham and Anderson, 2002).

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Figure B.1

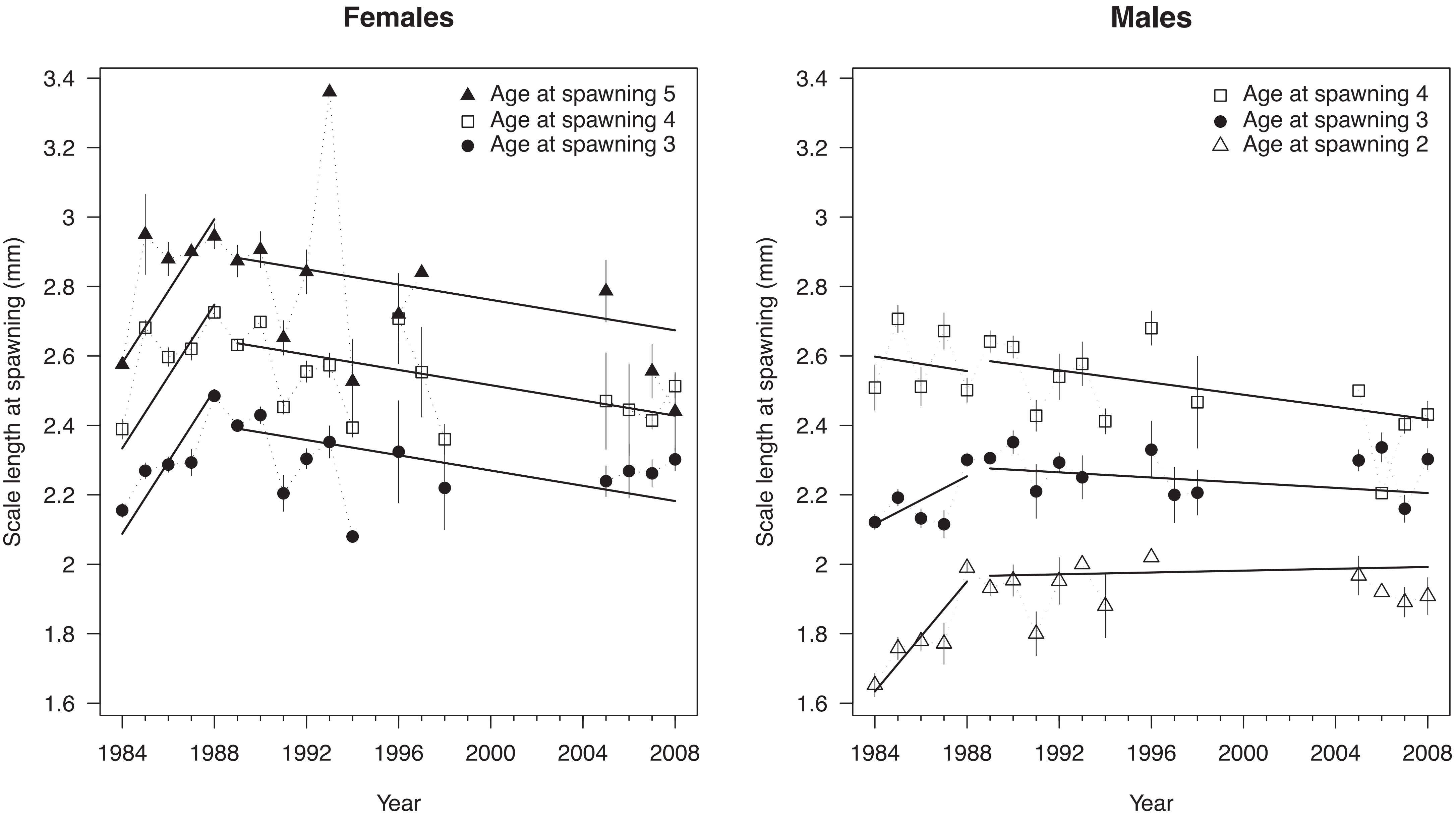

Females
Males
Scale length at spawning (mm)
Year
Age at spawning 5
Age at spawning 4
Age at spawning 3
Age at spawning 2
3.4
3.2
3
2.8
2.6
2.4
2.2
2
1.8
1.6
1984
1988
1992
1996
2000
2004
2008

**Table B.1**

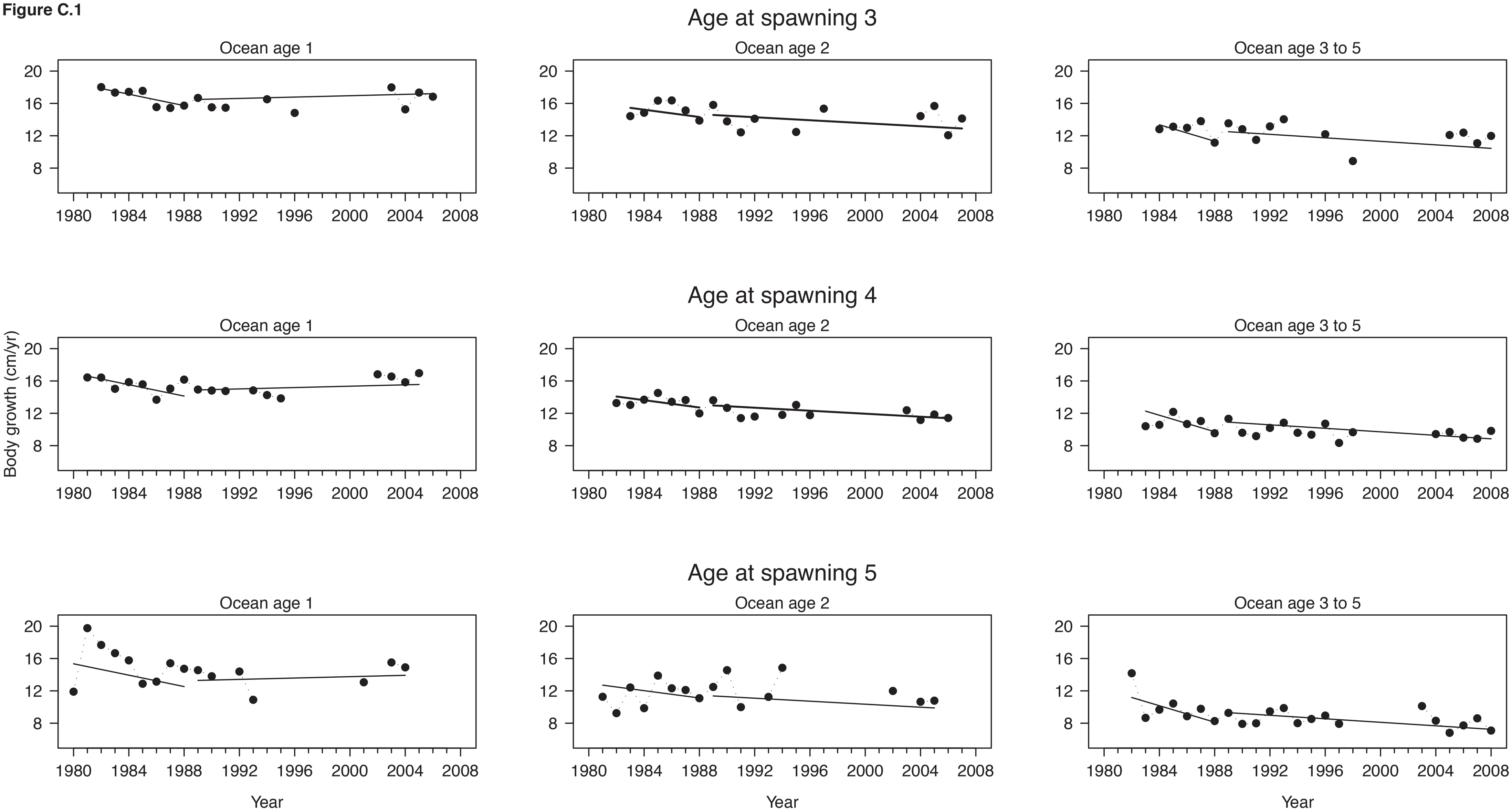
| | | |
|---|---|---|
| **Females** | | |
| Break in 1988 | 0 | 1.000 |
| Break in 1993 | 88.6 | < 0.001 |
| Break in 1998 | 113.5 | < 0.001 |
| Quadratic | 99.4 | < 0.001 |
| Linear | 111.1 | < 0.001 |
| Null (constant) | 111.5 | < 0.001 |
| **Males** | | |
| Break in 1988 | 0 | 0.797 |
| Break in 1993 | 4.8 | 0.072 |
| Break in 1998 | 15.7 | < 0.001 |
| Quadratic | 3.6 | 0.131 |
| Linear | 33.2 | < 0.001 |
| Null (constant) | 70.7 | < 0.001 |

## APPENDIX C

**Figure C.1** Mean body growth at sea in female chum salmon from 1984 to 2008. Rows correspond to increasing ages at spawning (3 years to 5 years) and columns correspond to increasing ocean ages (1 year to 5 years; ocean ages 3 years to 5 years are combined). Predicted values for the best models of temporal variation in body growth are shown with continuous lines. The best models included a break point in 1988.

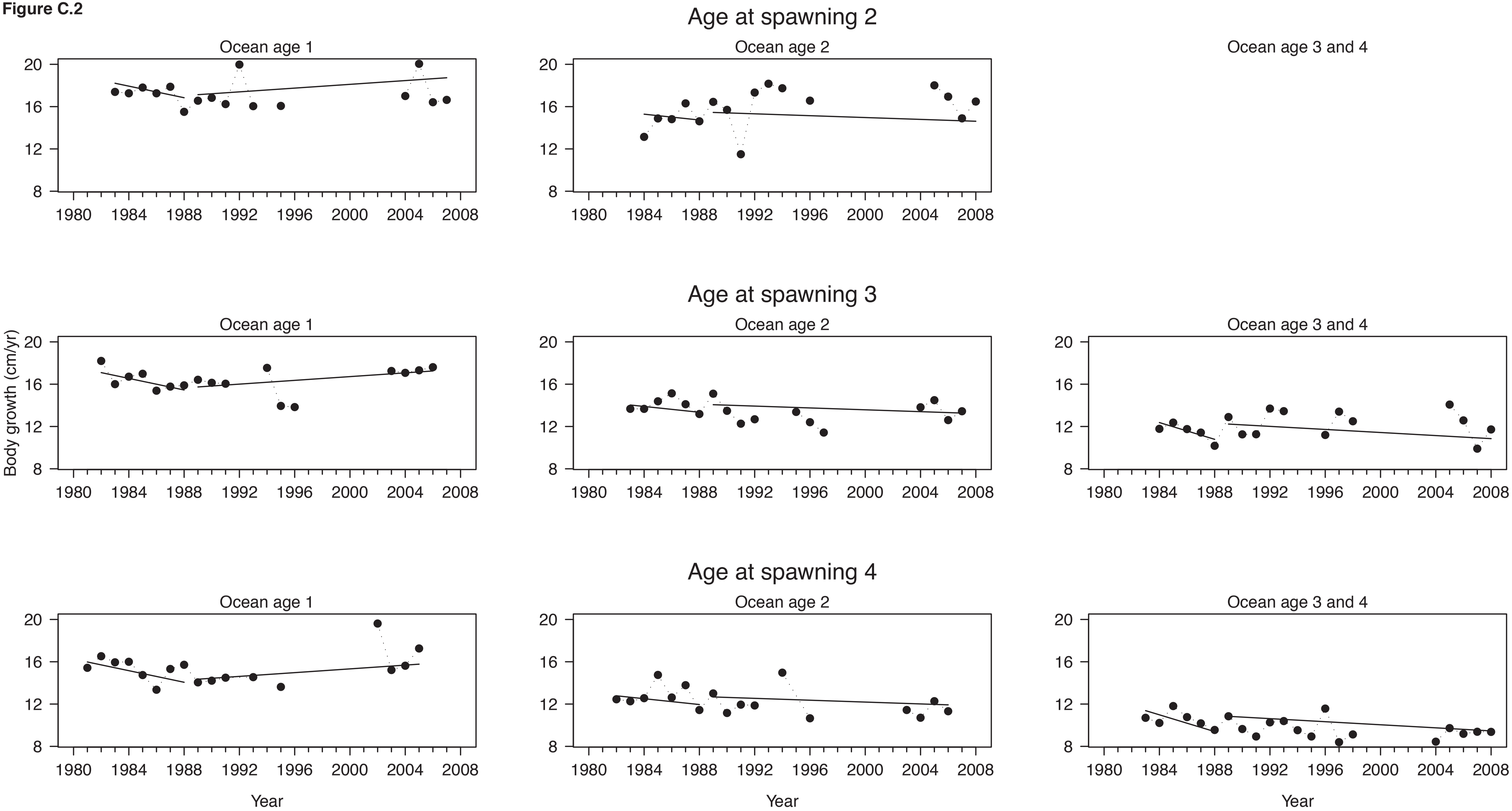
**Figure C.2** Mean body growth at sea in male chum salmon from 1984 to 2008. Rows correspond to increasing ages at spawning (2 year to 4 years) and columns correspond to increasing ocean ages (1 year to 4 years; ocean ages 3 years and 4 years are combined). Predicted values for the best models of temporal variation in body growth are shown with continuous lines. The best models included a break point in 1988.

**Figure C.1**



Age at spawning 3
Ocean age 1
Ocean age 2
Ocean age 3 to 5
Age at spawning 4
Ocean age 1
Ocean age 2
Ocean age 3 to 5
Age at spawning 5
Ocean age 1
Ocean age 2
Ocean age 3 to 5
Body growth (cm/yr)
20
16
12
8
1980
1984
1988
1992
1996
2000
2004
2008
Year

**Figure C.2**


Age at spawning 2
Age at spawning 3
Age at spawning 4
Ocean age 1
Ocean age 2
Ocean age 3 and 4
Body growth (cm/yr)
Year
20
16
12
8
1980
1984
1988
1992
1996
2000
2004
2008