Growth-history perspective on the decreasing age and size at maturation of exploited Atlantic salmon

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ABSTRACT: Decreases in age and size at maturation have been reported for several exploited fish populations, but little is known about possible changes in individual growth trajectories in the course of exploitation. We investigated changes in growth, age and size at maturation in a declining Atlantic salmon *Salmo salar* population subjected to strong fishing pressure. Based on historical catch records and scale samples collected between years 1948 and 2003, we estimated age and size at maturation and back-calculated individual growth trajectories. The age of the returning salmon declined, smolt size increased and post-smolt growth decreased during the study period. Reductions in age at maturation and shifts in growth trajectories occurred in parallel, suggesting that they were not independent of each other. Although our results cannot distinguish between plastic and genetic effects of exploitation on size and age at maturation, they support the contention that analyses of individual growth trajectories can provide important clues for understanding causes of life-history changes in exploited fish populations.

KEY WORDS: Atlantic salmon · *Salmo salar* L. · Body size · Growth · Fisheries-induced evolution · Maturation · Length at age

INTRODUCTION

Considerable declines have been observed in the abundance of several exploited marine fish stocks over the last decades (e.g. Hutchings 2000, Hutchings & Baum 2005). Population size declines have often been accompanied by marked shifts towards smaller body size and younger age at maturation (e.g. Hutchings & Baum 2005), which can in turn have cascading effects on fish population dynamics through decreased fecundity and population growth (e.g. Hutchings & Fraser 2007). Moreover, as older and thereby usually also larger individuals may be important for the maintenance of genetic variability, a decrease on their relative abundance can negatively affect the viability and adaptability of populations (Birkeland & Dayton 2005).

It has been suggested that the decreasing trends in age and size at maturation observed in many exploited fish populations (reviewed in Dieckmann & Heino 2007) might represent evolutionary responses to exploitation. This is because fisheries targeting large individuals should select against large size and delayed maturity, causing individuals to mature at a younger age and smaller size, the frequency of which would be expected to increase in the population (e.g. Kuparinen & Merilä 2007). Even though the hypothesis of fisheries-induced evolution is generally supported by substantial selection differentials induced by exploitation and the moderate heritability of the age and size at maturation (Law 2007), direct evidence for genetic changes generated by fishing is lacking (Hutchings & Fraser 2007, Kuparinen & Merilä 2007, 2008).

The problem in determining underlying reasons for shifts in the age and size at maturation is that these traits can be easily affected by environmental, physiological and behavioural drivers (e.g. Kraak 2007), so that observed phenotypic changes can be of plastic ori-

gin as well. In particular, growth may play a considerable role in the timing of maturation. In heavily exploited populations, favourable growth conditions arising from reduced competition for resources can promote early maturation through phenotypic plasticity (e.g. Dieckmann & Heino 2007), but similar changes could also result from changes in prevailing thermal regimes (e.g. Crozier et al. 2008). Growth rates could also evolve in response to fisheries-induced selection as a consequence of possible genetic correlations between growth, and the age and size at maturation (Law 2007). On the other hand, observed trends in the age and size at maturation at the population level may simply reflect demographic changes in age and size structure caused by selective fishing (Dieckmann & Heino 2007). Consequently, ruling out alternative explanations has proved difficult (Marshall & McAdam 2007).

Information about possible changes in individual growth trajectories is important for assessing the underlying causes of decreasing age and size at maturation, especially in the absence of genetic evidence of evolution (Hutchings & Fraser 2007, Kuparinen & Merilä 2007). This kind of approach could indicate whether exploited populations might have experienced substantial changes in growth conditions, and whether changes in maturation schedules might simply reflect changes in growth patterns. Therefore, a growth-history perspective should provide a deeper understanding of life-history changes potentially associated with trends in maturation (e.g. Morita et al. 2005, Kuparinen et al. 2008).

Atlantic salmon *Salmo salar* L. is an economically valuable species intensively targeted by both commercial and recreational fisheries. During the 20th century, Atlantic salmon populations in North America and Europe have rapidly declined, leading to the extinction of nearly 300 populations and the endangerment of one-third of the remaining populations (World Wildlife Fund 2001). A shift towards maturation at the age of 1 sea winter (SW) has been observed in many declining populations, with a corresponding reduction in the proportion of large multi-sea-winter (MSW) fish in the spawning stock (e.g. Welton et al. 1999, Quinn et al. 2006, Hindar et al. 2007). However, even though changes in age and/or size at maturation have often been documented in historical catch records, little is known about possible changes in individual growth trajectories during the corresponding periods (e.g. Bielak & Power 1986). Such information is essential for understanding environmental and evolutionary processes that may underlie shifts in age and size of fish maturation. In particular, smolt size and growth during the first year at sea are critical for the timing of maturation in Atlantic salmon (Friedland & Haas 1996, Jons-

son & Jonsson 2007) and, therefore, possible changes in post-smolt growth should be carefully investigated.

Here, we focus our study on an exploited, endangered Atlantic salmon population in the southernmost limit of the species' endemic distribution in northern Spain. Using complete freshwater angling catch records and archival scale samples extending back to the 1940s, we examined variation in growth trajectories and trends in age and size at maturation of adult salmon returning for spawning in freshwater. Our specific aim was to investigate if patterns seen in age at maturation might be linked to changes in salmon growth histories. Simultaneous variations in timing of maturation and growth may reflect (1) an evolutionary response to selective exploitation of large, older salmon, or (2) environmental changes affecting maturation indirectly through altered growth conditions. We evaluated these alternative hypotheses by investigating trends in maturation and patterns in growth histories at the juvenile and post-smolt stages, and by comparing growth histories linked to alternative maturation strategies.

MATERIALS AND METHODS

Study population and data collection. The River Asón is located in northern Spain and drains into the Bay of Biscay and into the North Atlantic at 43° N. The main stem of the river is 42 km long, but only the lower 33 km stem is usually accessible, depending on flow. The juvenile phase in freshwater usually lasts for 1 to 2 yr, after which smolts migrate to the sea, where they spend a further 1 to 3 yr in the marine feeding grounds located in the North Atlantic. Adult salmon enter the Asón in all months of the year, but peak spawning migrations occur during spring and early summer (García de Leániz & Martínez 1988). The river has supported fisheries for hundreds of years. However, since 1949 the exploitation in the river has been restricted to rod and line only, over a constant fishing season from mid-March to mid-July (Consuegra et al. 2005a). Complete and accurate annual rod and line salmon catches have been reported since 1949, and despite some inter-annual variation there has been a clear declining trend in catches since 1970 (Consuegra et al. 2005b; Fig. 1a). Salmon catch per unit fishing effort has declined even more steeply than these absolute catch numbers, since the number of angling licences sold has simultaneously increased. The average length of angled salmon also decreased during the second half of the 20th century (Fig. 1b) and particularly around the late 1980s and early 1990s, when salmon <65 cm in length (which can confidently be classified as 1SW fish or 'grilse', observed from back-calculation data)
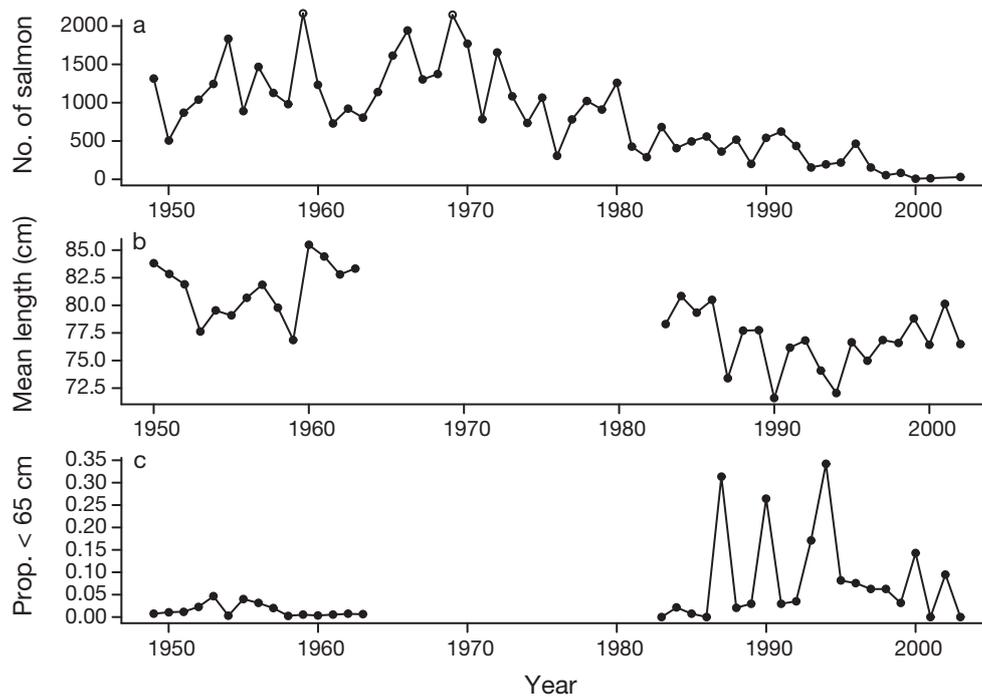
Fig. 1. *Salmo salar* L. Rod and line Atlantic salmon catches in the River Asón during the period 1949–2003. (a) Number of salmon angled during the fishing season (March–July), (b) mean length of salmon caught, (c) proportion of salmon of length <65 cm in the annual catch

became more abundant in the annual catches (Fig. 1c). Throughout the second half of the 20th century, annual exploitation rates by anglers in the R. Asón have been high (mean = 0.40; García de Leániz et al. 1992, Hindar et al. 2007), particularly for large MSW fish which have sustained exploitation rates >80% (García de Leániz et al. 1992).

Since 1949, each salmon legally caught in the river Asón has been systematically registered, by recording the length and weight of the fish, and the date and location (pool) of capture (Garcia de Leaniz & Martinez 1988). A sample of scales was also collected from most fish though many of these were lost or damaged during storage. Salmon in the River Asón have always been a valuable catch, and potential biases arising from possible discards of small fish in favour of trophy fish have never been reported and are not expected to have occurred. The scales available for analysis of individual growth trajectories originate from 460 salmon caught in the Asón during the years 1948–50, 1957, 1961–63, 1988–93 and 2000–03 (Table 1).

Estimation and analyses of growth trajectories. Scale impressions were made on clear cellulose acetate strips using a pressure roller. Only scales with a clear nucleus were analysed, usually 2 to 3 scales per fish. The impressions were then scanned on a Minolta MS 6000 microfiche reader at 2 magnifications ×23

(whole scale), and ×50 (close-up of freshwater age). Age was determined from printed copies of the enlarged scale impressions, and distances from the scale focus (nucleus) to the end of freshwater growth

Table 1. *Salmo salar*. Overview of the analysed Atlantic salmon data from the River Asón: total angling catch, number of fish analysed from the catch and their sea-age class frequencies. SW = sea winter

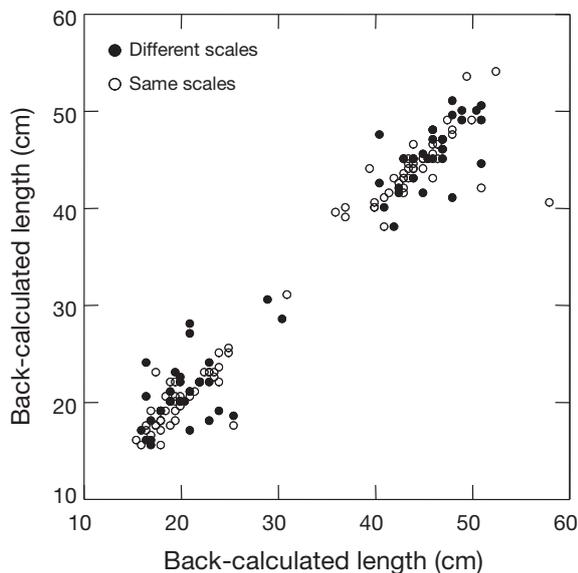| Capture year	Angling catch	No. fish analysed	1SW	2SW	3SW
1948	318	24	0	14	10
1949	411	2	0	2	0
1950	320	4	0	1	3
1957	801	12	1	9	0
1960	917	1	0	0	1
1961	552	42	1	11	30
1962	559	56	0	36	20
1963	476	40	0	12	28
1988	238	29	0	29	0
1989	101	47	3	42	2
1990	85	32	7	21	4
1991	101	1	0	1	0
1992	226	72	4	68	0
1993	75	47	11	34	2
2000	7	7	1	6	0
2001	15	15	0	14	1
2003	29	29	0	29	0

Fig. 2. *Salmo salar*. Reliability in back-calculated smolt lengths and post-smolt growth, based on 2 blind estimates taken on either the same or different scales from each individual (intra-class r smolt length = 0.84, post-smolt growth = 0.78)

(smolt length), the beginning and end of each winter at sea, and the edge of the scale (scale radius) were measured to the nearest 0.5 mm along the 360° axis (Friedland et al. 2000). Lengths at age were back-calculated according to Friedland et al. (1996):

$$B_i = (S_i/T)\,L \qquad (1)$$

where B_i is the back-calculated length at age i, S_i is the scale radius at age i, T is the total scale radius to edge of scale and L is the length of fish at capture. This back-calculation assumes a simple proportional model of fish growth in relation to scale growth (Francis 1990) and is the most common method of back-calculation of salmon scales (e.g. Friedland et al. 1996, Davidson & Hazelwood 2005). To ascertain the precision of the back-calculations, we estimated the repeatability of back-calculated salmon lengths, measuring the scales of 75 ind. twice in a double blind fashion (Fig. 2). Repeatability, calculated as the average measures intra-class correlation coefficient (SPSS v. 13.0), was 0.84 for back-calculated smolt lengths (95% CI = 0.75 to 0.90) and 0.78 for back-calculated size to the first SW (95% CI = 0.65 to 0.86).

The age and size of salmon angled in freshwater were considered to be their age and size at maturation, since virtually all returning salmon (>99%) are first-time spawners in the River Asón (Consuegra et al. 2005b). In addition to these traits, back-calculations provided information about freshwater age and full growth trajectories of each salmon. The particular interest of this study was to detect overall trends in growth, and age and size at maturation from late 1940s to early 2000s, rather than in comparing catches between individual years. To this end, we focused on investigating differences in salmon life histories between the 4 temporally distinct groups formed by the data: the first group covering years 1948–50, the second 1957–63, the third 1988–93 and the fourth 2000–03. Within each group the fish analysed originated from the same or temporally similar cohorts, so that any evolutionary or long-term environmental trends in salmon life histories should be mostly seen between groups, rather than within groups.

Between catch-year groups, trends in the freshwater age and age at maturation were analysed using an ordered logistic regression model with a 'cloglog' link function (McCullagh 1980). To investigate whether shifts in the length at maturation were due to changes in maturation ages only, or due to changes in size at age as well, we modelled length at each maturation age class (i.e. 1SW, 2SW and 3SW) separately, by having the catch-year group as a fixed predictor and the smolt year as a random effect, to account for possible correlations between individuals that migrated to sea (and did their marine growth) during the same period. Smolt length and post-smolt growth were both modelled with catch-year group and age at maturation as fixed effects and smolt year as a random effect, i.e. with the assumption being that fish that entered the sea in the same year might be related. Hence, the approach used estimates the general level of the response variable for the fish in each group of catch years, but also accounts for annual variations within catch-year groups. The association between smolt length and post-smolt growth was investigated by examining the correlation coefficient. To account for possible correlations between individuals that smolted in the same year, we also modelled post-smolt growth with a linear mixed-effect model, with smolt length as a predictor and smolt year as a random effect. All statistical analyses were performed with R statistical package.

RESULTS

During the study periods 1948–50 and 1957–63, 2SW and 3SW salmon were the dominant sea-age groups (Table 1). This reflects the composition of the entire salmon catch reasonably well, as the annual proportions of salmon small enough to be 1SW were very low (Fig. 1c), The probabilities of maturation at different sea ages, estimated by ordered logistic regression (Fig. 3), did not differ significantly between the first 2 catch-year groups (t_{213} = –0.05, p = 0.48). During the years 1988–93, 2SW salmon became more
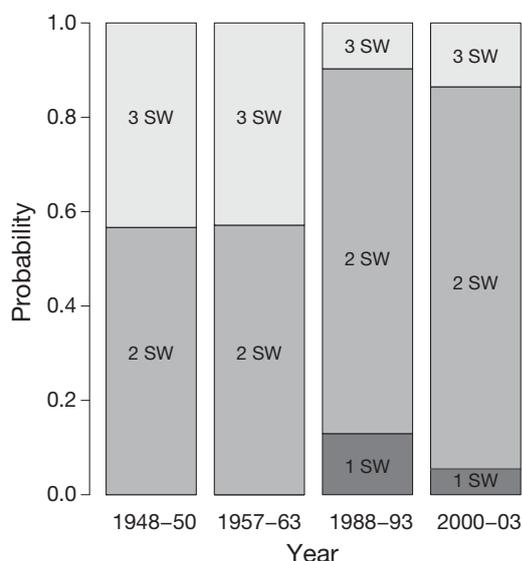
Fig. 3. *Salmo salar*. Probabilities of maturing as 1 sea-winter (SW), 2SW and 3SW salmon, estimated by an ordered logistic regression model for 4 catch year groups

abundant than 3SW salmon, and the incidence of 1SW salmon (~11%) increased too (Table 1). The increase in young, 1SW salmon in the catch can also be detected by the increase in the abundance of <65 cm ind. in the total salmon catches during late 1980s and early 1990s, although variations between years are also substantial (Fig. 1c). The observed changes in life histories and in the relative abundance of different age classes can also be seen in a significant increase in the estimated probabilities of maturation at 1SW and 2SW, and in a decreased probability of maturation at 3SW between years 1957–63 and 1988–93 (t_{377} = 5.40, p < 0.01; Fig. 3). During the period 2000–03 1SW salmon became again less abundant in the salmon catch (note that sample sizes correspond to catch sizes; Table 1) but the maturation probabilities estimated for these years did not significantly differ from the period 1988–93 (t_{262} = –1.08, p = 0.13), suggesting that the major change in the age composition of the spawning stock might have occurred between the early 1960s and late 1980s. Smolt age did not vary significantly over the study period, and nearly all fish migrated to sea as either 1- (58.7%) or 2- (40.7%) year-old smolts.

Average lengths (± SD) of fish maturing as 1SW, 2SW and 3SW salmon were 61.5 ± 3.1, 77.5 ± 4.1 and 93.1 ± 4.5 cm, respectively. As 1SW salmon were well represented only in the sample from 1988–93, changes in their length over time could not be investigated. For 2SW and 3SW salmon, the linear mixed-effect models could not detect any significant changes in age-specific lengths at maturation over the study period (2SW: $F_{3,12}$ = 1.73, p = 0.21; 3SW: $F_{3,7}$ = 2.98, p = 0.11).

Therefore, the observed decreasing trend in the average length at maturation detected in the 460 scale samples (1948–50: 85.1 cm; 1957–63: 85.9 cm; 1988–93: 76.1 cm; 2000–03: 77.8 cm) and the similar trend seen in the total annual catches (Fig. 1b) are likely to have arisen from changes in the age structure of the spawning stock (Fig. 3). The length of smolts was not significantly associated to age at maturation ($F_{2,433}$ = 0.21, p = 0.81), but smolt length varied depending on the catch year (Fig. 4a). No significant changes in backcalculated smolt lengths could be detected between 1948–50 and 1957–63 (t_{195} = 0.01, p = 0.50), but a significant increase in smolt length was evident between 1957–63 and 1988–93 (t_{377} = –2.07, p = 0.02; Fig. 4a). The decrease in smolt length seen between 1988–93 and 2000–03 (Fig. 4a) was not significant (t_{262} = 1.45, p = 0.07). As in the case of smolt length, no association between post-smolt growth and age at maturation was detected ($F_{2,433}$ = 2.05, p = 0.13). The temporal patterns seen in post-smolt growth were generally opposite, but slightly more drastic (Fig. 4b): post-smolt growth decreased from years 1948–50 to years 1957–63, albeit not significantly (t_{195} = 1.64, p = 0.05), and further decreased from years 1957–63 to years 1988–93 (t_{377} = 1.84, p = 0.03), after which it again increased to years 2000–03 (t_{261} = –3.12, p < 0.01). In addition to the general temporal trends in the smolt length and post-smolt growth, there were also some
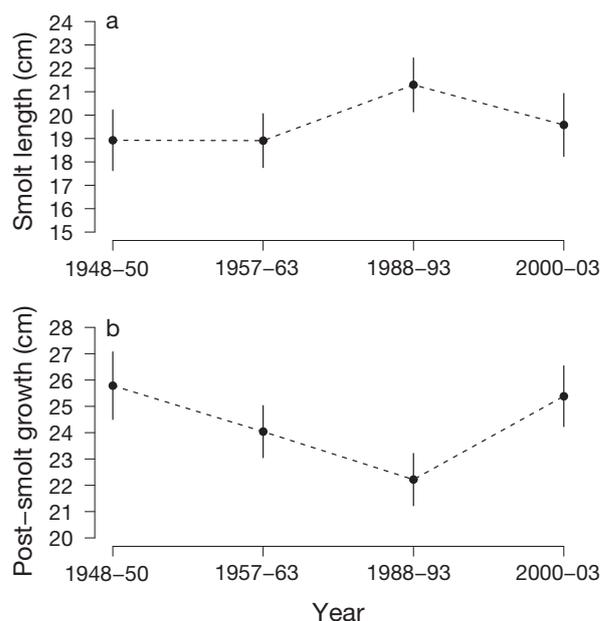

Fig. 4. *Salmo salar*. Temporal trends in (a) smolt length and (b) post-smolt growth. Average smolt length and post-smolt growth (●) and their standard errors (vertical lines) are estimated for 4 catch-year groups using a linear mixed-effect model in which smolt year is treated as a random effect

annual variations about them. This was reflected in the SD of the random effect of the year of smolting, which was 1.33 for smolt length and 0.61 for post-smolt growth. As suggested by the simultaneous shifts in smolt length and post-smolt growth (Fig. 4), these lengths were negatively correlated (Pearson's r = −0.50, t_{455} = −12.34, p < 0.01), so that one 1.0 cm increase in smolt length was predicted to decrease post-smolt growth by −0.62 cm (t_{434} = −11.63, p < 0.01).

DISCUSSION

The analysis of salmon life histories in the River Asón shows that the sea age of adult salmon caught by anglers during the fishing season (mid-March to July) changed considerably during the second half of the 20th century (Figs. 1c & 4), and that these changes were accompanied by changes in patterns of juvenile and post-smolt growth (Fig. 3). At the same time, salmon catch has shown a steady decline (Fig. 1a), suggesting that the abundance of at least the early-running component of the population has declined markedly. In the River Asón, early-running salmon are predominantly large MSW salmon, whereas small 1SW salmon (grilse) are common among late-running individuals that enter the river only during summer and early autumn (Consuegra et al. 2005a). Therefore, fishing in the Asón is to some extent age- and size-selective, as it tends to target early-running fish (Consuegra et al. 2005a).

Negative correlations between smolt length and post-smolt growth have been documented previously for Atlantic salmon (e.g. Nicieza & Braña 1993, Jonsson & Jonsson 2007). In contrast, post-smolt growth and age at maturation do not appear to exhibit any general association: in some populations rapid growth during the first sea-summer has been shown to result in early maturation (Nicieza & Braña 1993), but there is also evidence to suggest that poorly growing salmon tend to mature earlier because the advantage of postponing maturation is small (Jonsson & Jonsson 2007). In the case of the Asón population, smolt length and post-smolt growth were negatively correlated, and a connection between the temporal patterns in these traits and in the age at maturation could be detected: an increase in smolt length was accompanied by a decrease in post-smolt growth (Fig. 4), as well as a shift towards early maturation (Fig. 3), all the major shifts being observed in the transition from the early 1960s to late 1980s.

Temporal patterns of growth trajectories in the Asón coincided with changes in ages at maturation, but these patterns were similar among all individuals independent of the age at which they matured, as no asso-

ciation between age at maturation and smolt length or post-smolt growth could be detected. Synchrony in growth and maturation changes still suggests that they might be related, for instance so that declining age at maturation could have resulted from the same processes that affected smolt length and post-smolt growth. On the other hand, as changes in growth were similar in all salmon independent of the age at which they matured, a direct correlation between growth and age at maturation should not be expected (and was not detected). If there was a functional relationship between smolt size and age at maturation, we should have seen differences in smolt size between young and old maturing salmon, which is not the case. Therefore, the results rather suggest that the observed changes in salmon life histories might have been caused by some factors that were experienced by all the individuals (i.e. affected the whole population). Such a factor could be, for example, a decline in population abundance (e.g. Hutchings & Fraser 2007) or changes in the climatic conditions (Nicieza & Braña 1993, Davidson & Hazelwood 2005, Todd et al. 2008).

During the period 1996–2000, salmon spawners (mostly late-running) sampled in the River Asón were found to be on average 0.5 SW younger and 7 cm smaller than salmon caught by anglers (early-running) during the same season (Consuegra et al. 2005a). However, it is unknown whether such differences in age and size at maturation of early- and late-running salmon have changed over time. Therefore, the decreasing trend in the age at maturation detected in this study applies only to the fishery component (early-running) of the population, and may not necessarily hold true for the entire spawning stock. Nevertheless, there are a few reasons to believe that the life-history patterns seen in early-running salmon might still apply for the entire population: (1) patterns in smolt length and post-smolt growth were similar among all sea-age classes (Fig. 4), suggesting that these changes were due to common conditions experienced by all juveniles, and (2) previous molecular genetic studies focusing on this population have suggested a genetic basis for variation in run timing (Consuegra et al. 2005a), and indicated that a decrease in size and age at maturation might result from anglers selectively removing large early-running fish from the population during a fixed fishing season (García de Leániz et al. 1992; Consuegra et al. 2005a). Overexploitation of large MSW fish entering the river early in the season will inevitably cause small, late-running fish to be better represented among the spawning stock. As the heritability of run timing and age at maturation is substantial in Atlantic salmon (Garcia de Leaniz et al. 2007), late-running, early-maturing fish might then become more abundant in subsequent generations. Thus, our

study does not rule out the hypothesis of fisheries-induced evolution, although it cannot provide direct evidence for it either. A common change in environmental conditions inducing changes in growth might, in principle, also result from an evolutionary change: a shift towards earlier maturation could decrease population fecundity (e.g. Hutchings & Baum 2005) and reduce competition among juveniles. Increasing juvenile growth might increase smolt length and decrease post-smolt growth as a consequence of a negative correlation between these traits (e.g. Nicieza & Braña 1993, Jonsson & Jonsson 2007).

The results of this study show that shifts towards earlier maturation in an exploited fish population have occurred in parallel with changes in growth histories, suggesting that the trends seen in maturation might reflect a change at the level of life histories rather than just in the population structure. It remains a considerable challenge to assess whether changes in salmon growth are a cause or a consequence of decreasing age and/or size at maturation, whether genotypic changes are involved and, ultimately, whether fishing is the underlying factor driving the patterns. Our study emphasizes the importance of looking not only at trends in age at maturation, but also at changes in individual growth histories. Such a broad perspective will allow researchers to gain a better understanding of drivers underpinning variation in entire life histories instead of just the maturation component (Kuparinen et al. 2008).

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