



ORIGINAL ARTICLE



WILEY

Increasing temperature associated with increasing grilse proportion and smaller grilse size of Atlantic salmon

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Funding information

SmartSea project; Strategic Research Council; Academy of Finland

Abstract

Effects of temperature on Atlantic salmon (*Salmo salar*) were analysed using Carlin tag recovery data (1985–2014), and mixed-stock catch data (smolt years from 2001 to 2012) in northern parts of the Baltic Sea. During warmer summers, the mean smolt length of the recaptured salmon tended to be smaller, and salmon were recaptured more frequently in feeding grounds closer to the home rivers in the Gulf of Bothnia, while colder summers were associated with more recaptures further south, in the Baltic Main Basin. Moreover, a warmer spring in the smolt year was associated with decreased weight of male grilses in mixed stock data. Further, warmer spring temperatures during the smolt year were associated with a higher proportion of one-sea-winter (1SW) males during the return migration in mixed stock data. These results suggest that the increasing global temperature may affect Atlantic salmon life history demographics.

1 | INTRODUCTION

In recent decades, many Atlantic salmon (*Salmo salar*) stocks have severely declined, and some have become extinct, partly due to intensive fishing and habitat destruction (Hindar, Hutchings, Diserudd, & Fiske, 2011; Mills, Pershing, Sheeham, & Mountain, 2013). Besides this, increasing global temperatures have resulted in large-scale changes in the community structure and demographics of populations (Sydeman, Poloczanska, Reed, & Thompson, 2015). Many species have exhibited changes in morphology, life history, phenology, and genetic structure (Czorlich, Aykanat, Erkinaro, Orell, & Primmer, 2018; Root et al., 2003; Sheridan & Bickford, 2011; Thresher, Koslow, Morison, & Smith, 2007), accompanied by range shifts, population declines, and extinctions (Parmesan & Yohe, 2003; Perry, Low, Ellis, & Reynolds, 2005; Root et al., 2003; Sydeman et al., 2015). Changes in global temperature regimes and an accompanying increase in water temperatures are predicted to cause further depression of population viability, age structure, and adaptive traits

(Jonsson & Jonsson, 2004a; Jonsson & Jonsson, 2009; Perry et al., 2005; Peyronnet, Friedland, & Ó Maoiléidigh, 2008; Beaugrand & Reid, 2012; Piou & Prevost, 2013). In anadromous fish, warmer temperatures are associated with an increased metabolic rate and oxygen use (Barnes, King, & Carter, 2011), faster growth during the freshwater phase, a younger age at smoltification (Jonsson, Jonsson, & Hansen, 2005), an earlier smolt migration (Jokikokko, Jutila, & Kallio-Nyberg, 2016; Otero et al., 2014), higher marine survival (Jutila, Jokikokko, & Julkunen, 2005; Kallio-Nyberg, Jutila, Saloniemi, & Jokikokko, 2004), a faster growth rate in the sea, and younger sea age at maturity (Jonsson, Finstad, & Jonsson, 2012; Jonsson & Jonsson, 2004b; Jonsson, Jonsson, & Hansen, 2003). In addition, temperature affects community structure and population demographics, e.g. marine food webs, density-dependent processes and behaviour in general (e.g. Chaput & Benoit, 2012; Friedland, Chaput, & MacLean, 2005; Jonsson, Jonsson, & Albrechtsen, 2016; Peyronnet et al., 2008; Portner & Farrell, 2008; Todd et al., 2008). Food abundance also varies with temperature: herring, the main prey fish for

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salmon in the northern Baltic Sea, are at their peak when the sea surface temperature is high (Dippner, Hänninen, Kousa, & Vuorinen, 2001; Salminen, Erkamo, & Salmi, 2001).

The rise in sea surface temperature in the Baltic Sea is due to global warming (Jylhä et al., 2009). The Baltic Sea provides an excellent laboratory for studies of increasing temperature on the life history-related feeding migration, growth, and maturation of Atlantic salmon. Compared to North Atlantic stocks, the marine phase of Atlantic salmon in the Baltic Sea is better known due to the more limited geographic scale and accessibility of the marine system, as well as the large amounts of data accumulated during the monitoring and fishing of the stocks over decades (Aro, 2002; ICES, 2016). The Main Basin, the southern part of the Baltic Sea (Figure 1), is the most important feeding ground for immature salmon. However, instead of migrating to south, especially the larger individuals of the northern

stocks remain to feed in the Gulf of Bothnia (GoB) (Salminen, Kuikka, & Erkamo, 1994).

We investigated the effects of temperature on Atlantic salmon's post-smolt life history by using two types of data. In the first dataset, tag recovery data was applied to test whether the smolt-year temperature affected the smolt length of caught fish (smolt-year classes 1985–2015). Fish from the four main Bothnian Bay rivers were tagged and measured as smolts, and recaptured later during their marine feeding phase throughout the Baltic Sea. These data (limited to smolt-year classes 1985–2004 and dispersal in the second winter year) were also used to study the effects of temperature on feeding dispersal in the sea. The feeding distance was regarded as short if the salmon remained in the Gulf of Bothnia, and long if they migrated further south. In the other dataset, unmarked salmon caught during their spawning migration (year classes 2001–2012)

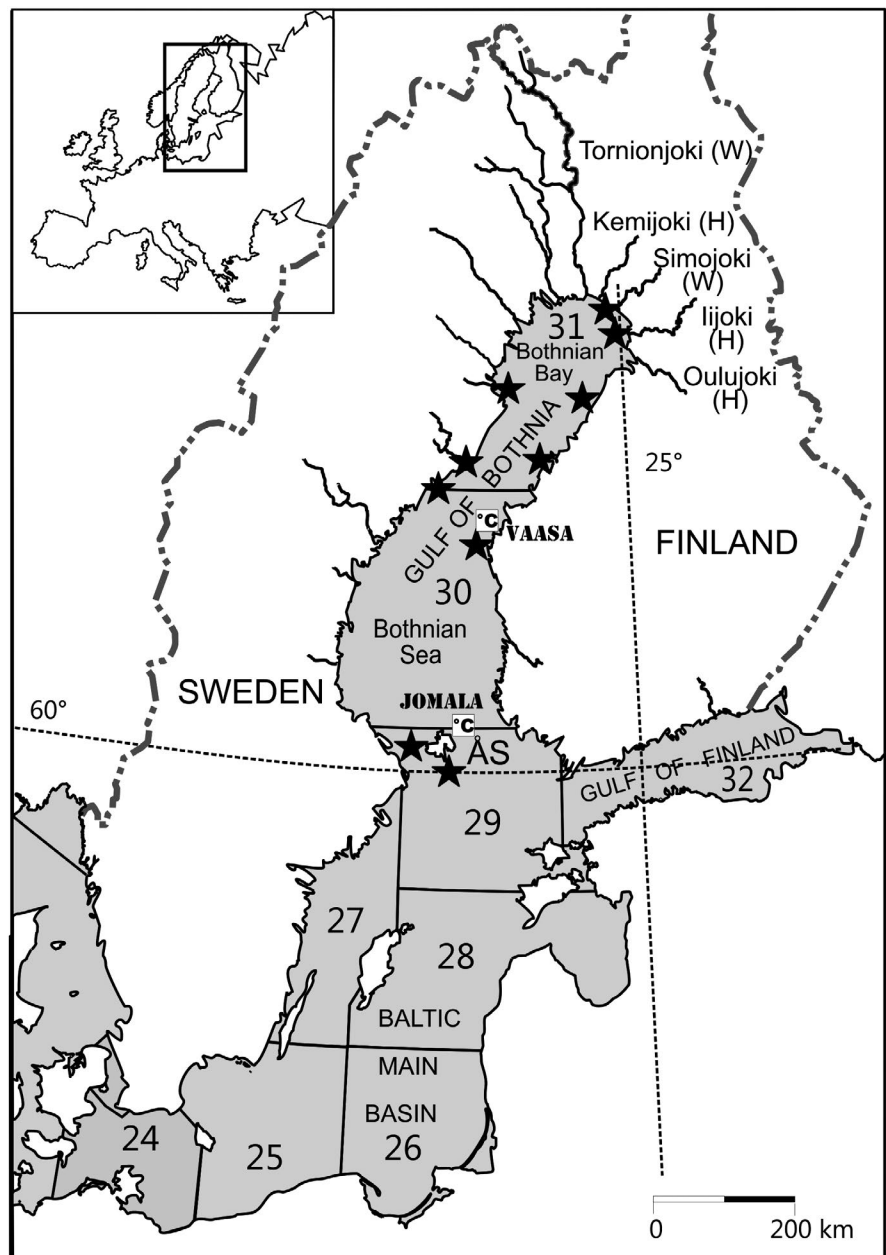


FIGURE 1 Map of the Baltic Sea showing sea areas: Gulf of Bothnia (GoB, ICES rectangles 31 and 30), Bothnian Bay (31), Bothnian Sea (30), Baltic Main Basin (23–28), Archipelago Sea (ÅS, 29), Gulf of Finland (32), and rivers sustaining the Atlantic salmon population. The locations of temperature measurement sites (white square) in Vaasa and Jomala and catch sampling sites for returning salmon (black stars) are shown

TABLE 1 Mixed-stock sea catch sample sizes and the mean grilse weight (kg) of Atlantic salmon (*Salmo salar*) males in smolt-year classes 2001–2012 from the Gulf of Bothnia during the spawning migration, and sample sizes for tag recovery data for tagged smolts of year classes 1985–2004 from the Gulf of Bothnia (GoB) and Baltic Main Basin (MB), during the adult feeding migration

No. males in catches (mixed stock data)				No. tags recovered (Carlin recovery data)		
Smolt year class	1SW GoB	1–4SW GoB	1SW weight	Smolt year class	GoB 2SW	MB 2SW
2001	82	121	2.3 ± 0.9	1985	2	424
2002	86	112	1.9 ± 0.3	1986	9	401
2003	55	107	2.3 ± 0.4	1987	6	179
2004	101	230	2.1 ± 0.8	1988	76	286
2005	86	176	2.2 ± 0.9	1989	106	146
2006	252	344	2.5 ± 0.8	1990	49	68
2007	191	292	2.0 ± 0.8	1991	58	153
2008	120	285	2.2 ± 0.7	1992	8	54
2009	49	172	1.9 ± 0.6	1993	2	25
2010	35		2.3 ± 0.8	1994	7	67
2011	53		2.2 ± 0.7	1995	3	70
2012	29		1.8 ± 0.5	1996	0	71
				1997	0	87
				1998	0	49
				1999	3	62
				2000	3	82
				2001	0	61
				2002	2	71
				2003	3	79
				2004	1	41
	1,139	1,839			338	2,476

Note: The mixed stock sample sizes are presented for one-sea-winter-old males for known weight (1SW) and for all males (1–4SW) for known age. The tag recovery data of tagged smolts are presented according to the feeding site (Gulf of Bothnia or Main Basin) of the 2SW adult fish during their second winter (December–April).

were used to test whether the temperature during the post-smolt period affected male growth and their return as grilse, i.e. after only one winter at sea.

2 | MATERIALS AND METHODS

2.1 | Data

Baltic Sea lineage is one of the major clades of Atlantic salmon in European waters (Bourret et al., 2013; Säisä et al., 2005). Baltic salmon usually spend two to four years in their natal river before migrating to their feeding grounds in the sea, where they spend another one to three years before migrating back to their natal streams to spawn (Jokikokko, Kallio-Nyberg, & Jutila, 2004; Jutila, Jokikokko, Kallio-Nyberg, Saloniemi, & Pasanen, 2003; Kallio-Nyberg, Romakkaniemi, Jokikokko, Saloniemi, & Jutila, 2015). The northern part of the Baltic Sea, the Gulf of Bothnia, hosts many rivers with stable salmon stocks that are healthier and less depressed than the salmon stocks in the southern range of the Baltic Sea drainage area (ICES, 2011a, 2016).

Currently, Gulf of Bothnia salmon populations have the largest number of released salmon smolts due to intensive restoration efforts and compensatory stocking since the mid-1990s (Jutila, Jokikokko, & Julkunen, 2003). Gulf of Bothnia salmon stocks share similar migration routes and feeding grounds in the sea (Koljonen, 2006), which in turn results in correlated temporal variation in life history traits (Kallio-Nyberg, Jutila, Jokikokko, & Saloniemi, 2006; Kallio-Nyberg, Peltonen, & Rita, 1999).

Our first dataset is based on Carlin-tagged smolts that were recaptured as sub-adults (smolt-year classes 1985–2014). Both wild and reared salmon smolts had been tagged and released into the Tornionjoki, Kemijoki, Simojoki, and Iijoki rivers in the spring (Jokikokko & Mäntyniemi, 2003; Jutila, Jokikokko, & Julkunen, 2003; Kallio-Nyberg et al., 2015; Romakkaniemi et al., 2003). Tagged individuals were recaptured as adults (usually 0.5%–3.0% of tagged smolts) in the Gulf of Bothnia and in the Main Basin (MB) by commercial fishermen, who reported the time of capture, recovery site, and the catch length and weight of the individual salmon (Kallio-Nyberg et al., 2015). Smolt length was already measured during tagging.

The mixed stock catch dataset here consisted of only spawning migrating males (Table 1). Only males were analysed, because they

show substantial variation in age at maturity, i.e. both one-sea-winter (1SW) and multi-sea-winter (MSW) fish are common, while females are mostly MSW fish (Jokikokko et al., 2004; Kallio-Nyberg, Koljonen, & Saloniemi, 2014). The methods and sampling sites remained unchanged between 2001 and 2013, when salmon returning to the spawning grounds were sampled as part of the national EU Data Collection Framework programme (ICES, 2016) (Figure 1). The sea age of each salmon was determined using the guidelines for Atlantic salmon scale reading (ICES, 2011b). All individuals included in this study were sampled during their first spawning migration in the Gulf of Bothnia (Figure 1), and the measured sea age was therefore equal to sea age at first maturity. The sex, bodyweight, and length (total) of the males were recorded. The mixed stock sample in the Gulf of Bothnia may include salmon from more than ten rivers (Koljonen, 2006). The mature salmon in the catch sample from the Gulf of Bothnia were mainly from the stocks of the Tornionjoki, Kalixälven, Byskeälven, Vindelälven, Simojoki, Iijoki, Oulujoki, and Luleälven rivers (Kallio-Nyberg et al., 2014; see Figure 1).

In the mixed catch data, the stock of origin of individual fish is unknown, and the data are analysed without information on the river origin of stock. However, in the Appendix S1, we compare the present results with the previously published (Kallio-Nyberg et al., 2014) genetic mixed-model analysis and historical sea age distribution of the male salmon among northern Baltic Sea salmon stocks.

Air temperature data were retrieved from the Finnish Meteorological Institute (www.fmi.fi). The spring or summer air temperature at the Finnish Meteorological Institute air temperature sites at the Vaasa (63°10'N, 21°64'E; close to Gulf of Bothnia rivers) and Jomala weather stations (60°18'N, 19°19'E; close to the Main Basin of the Baltic Sea) were chosen, as these coastal sites are near the smolt migration areas. The correlation between annual temperatures measured at Vaasa and Jomala was statistically significant (summer temperatures; Spearman correlation: $p < .001$, $r = .895$, $n = 12$). Post-smolts migrate mainly to the Bothnian Bay for 1–2 months, and after this, feeding salmon migrate to the southern Gulf of Bothnia (Bothnian Sea) or the Main Basin of the Baltic Sea (Jutla, Jokikokko, & Ikonen, 2009; Kallio-Nyberg et al., 1999).

The abundance of herring aged 0+ in the Gulf of Bothnia was estimated using the 1+ herring abundance data from the previous year (ICES, 2012), i.e. the smolt year. Young herring are the most important prey for salmon in the first summer in the Gulf of Bothnia (Salminen et al., 2001).

2.2 | Statistical methods

We used linear regression to test whether the smolt-year temperature affected the length of the recaptured smolts. The summer air temperature in Vaasa during the smolt year was used as a predictor for smolt growth (i.e. smolt years between 1985 and 2015). When all recaptured Carlin-tagged Simojoki and Tornionjoki salmon were

included, the mean (\pm std) annual sample size for smolts was 419 (± 354 , $n = 12,570$ smolts, for 30 years), and for wild smolts only 77 (± 83 , $n = 2,018$; 26 years). Smolt size is not a good response variable for reared salmon, as size varies according to rearing history, rearing conditions, and hatchery (Jokikokko, Kallio-Nyberg, Saloniemi, & Jutla, 2006). The summer temperature measured at the Vaasa station was used, because the highest post-smolt numbers, according to Jutla et al. (2009), are in June in the Bothnian Bay near Vaasa, and the mortality of post-smolt is highest at the beginning of sea life.

To test whether the temperature of the smolt year affected the spatial distribution of feeding salmon, we used logistic binomial regression models, with the recapture site (the Gulf of Bothnia versus the Main Basin) as the binomial response variable, and smolt length and air temperature in the smolt year as predictors. All 2SW (19–23 months at sea, November–March) salmon that had been tagged and released as smolts in the Bothnian Bay Tornionjoki, Kemijoki, Simojoki, and Iijoki rivers (Jutla, Jokikokko, Kallio-Nyberg, et al., 2003; Kallio-Nyberg et al., 1999, 2015) were included in the analysis. The total number of recoveries of 2SW salmon was 2,814 from the smolt years 1985–2004 (Table 1). The spring air temperature at Jomala was used in the models, because salmon migrate to the southern Gulf of Bothnia in the second winter if they stay in the Gulf (Kallio-Nyberg et al., 1999). Interactions between predictors were calculated for all models, but only the models with the lowest AIC (Akaike information criteria) are reported.

The correlation (Spearman correlation) between the annual abundance of young herring (1985–2007) in the Bothnian Sea and air temperature (Jomala, Vaasa) was applied as a measure of food availability. The abundance of 0+ herring for a particular year was estimated using the abundance of 1+ herring from the following year (ICES, 2012). The abundance of young herring in the Bothnian Sea is associated positively with the feeding migration of salmon in the Bothnian Sea and marine survival (Kallio-Nyberg et al., 1999; Kallio-Nyberg, Saloniemi, Jutla, & Jokikokko, 2011).

The growth of 1SW male salmon was analysed from mixed stock data (year-level data) using linear regression. The air temperature in the smolt year was used as a predictor across the 12 years (i.e. smolt years between 2001 and 2012). The weight of all males independent of origin and weight for these 410 wild and 866 reared individual fish were used as the response variable for the proxy of first-year sea growth. The sample size and mean weight of all 1SW male salmon in each smolt-year class is presented in Table 1. The air temperature of the smolt year was measured in the spring at the Jomala and Vaasa stations.

The effect of temperature on the probability of returning as grilse was analysed as a binomial log-linear model in the mixed stock data (as 1, i.e. matured in the first year, versus 0 for later maturing, 2SW or older; see data in Table 1; Carlin recovery data). The air temperature in the smolt year measured in the summer at the Jomala station in 2000–2009 was used as a predictor. The Jomala temperature was used, because the feeding salmon migrate to the southern Gulf of Bothnia or the Main Basin of the Baltic Sea. Currently, nearly all salmon return to spawn before the fourth sea winter (Kallio-Nyberg et al., 2014); but see the Appendix S1 for historical data.

3 | RESULTS

3.1 | Effects of temperature on smolt length and feeding area

In the 30-year data for the Carlin-tagged and recaptured Bothnian Bay wild and reared salmon (smolt-year classes 1985–2014), a decrease of 6.4 mm was observed in mean smolt length with a one-degree Celsius increase in the smolt-year mean summer temperature (in Vaasa; smolt length = $275.1 - 6.4 * \text{temperature}$; $F_{(1,28)} = 5.05$, $p = .033$, $R^2 = .153$) (Figure 2). When the study was limited to wild smolts (26 years of data), the decrease in smolt size with increasing temperature was somewhat lower (smolt length = $212.7 - 3.7 * \text{temperature}$; $F_{(1,24)} = 2.89$, $p = .102$, $R^2 = .108$).

If the spring of the second sea winter (19–23 months at sea) (Figure 3) was warm (temperature about 4–5°C in Jomala), salmon fed more frequently (Table 2, model M1) in the Gulf of Bothnia (northern Baltic) than in the Baltic Main Basin (southern Baltic). The preference for a northern feeding area increased with larger smolts (Table 2, model M2). The higher abundance of young herring in the Gulf of Bothnia in 1985–2007 also reflected the higher summer air temperature (Jomala: $r = .658$, $p < .001$, $n = 23$; Vaasa: $r = .627$, $p = .001$, $n = 23$).

3.2 | Effects of temperature on growth and the probability of returning as grilse

The mean spring air temperature monitored in the Gulf of Bothnia was a good predictor for 1SW male weight (Jomala: weight = $2.737 - 0.152 * \text{temperature}$, $F_{(1,10)} = 13.3$, $p < .005$, $R^2 = .570$; Vaasa: weight = $2.489 - 0.114 * \text{temperature}$, $F_{(1,10)} = 6.8$, $p < .025$, $R^2 = .406$). The grilse mean weight decreased by 150 g per one-degree Celsius increase in mean air temperature (Figure 4) in Jomala, while in Vaasa it was essentially the same. When the study

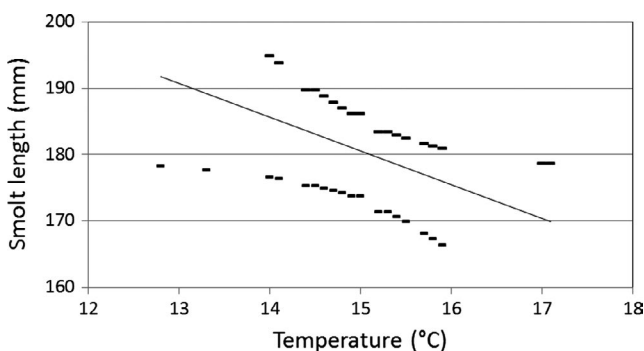


FIGURE 2 The model predicted Atlantic salmon smolt length from the tag recovery data (Table 1) in relation to temperature (°C) (summer air temperature in the Gulf of Bothnia, in Vaasa; $p = .032$). Regression: length (mm) = $275.1 - 6.38 * \text{temperature}$, $R^2 = .153$. The model predicting a linear trend (continuous line) between smolt length and the summer air temperature in the smolt year, with 95% confidence limits of the mean (broken lines), is presented

was limited to 1SW hatchery males, the decrease was 160 g per one-degree Celsius increase in mean air temperature at Jomala (weight = $2.953 - 0.161 * \text{temperature}$, $F_{(1,10)} = 9.53$, $p = .012$, $R^2 = .487$). Probably due to the small sample size ($n = 410$), the decrease was not significant for wild males weight = $2.019 - 0.062 * \text{temperature}$, $F_{(1,10)} = 0.73$, $p = .412$, $R^2 = .068$).

After smolting, northern Atlantic salmon stocks usually migrate to the southern parts of the Baltic Main Basin to feed and return to their native rivers in the north close to maturation (after one to four sea years) (Table 1: mixed data; catch sites in Figure 1). Mixed stock samples of the smolt-year classes 2001–2009 indicate that the probability of returning as grilse increases as a function of the increasing air temperature (summer air temperature at Jomala: $\chi^2 = 3.70$, $df = 1$, $p = .054$). Mean air temperatures between 15 and 16°C are critical to the decision to return (Figure 5).

4 | DISCUSSION

An increasing temperature in the smolt year was associated with smaller smolt and grilse, and an increasing grilse proportion in our long-term data on Atlantic salmon in the Baltic Sea. An increasing temperature in the Gulf of Bothnia was also associated with more recaptures in the feeding grounds closer to the home rivers during the second sea winter.

Water temperatures in the rivers and sea are known to be linked to down-migrating salmon smolts (Juttila et al., 2005). Salmon smolts tend to leave their home river in the spring, when conditions are optimal (“the smolt window”; Otero et al., 2014), typically when the sea surface temperature reaches between 9 and 12°C in river mouths in the Bothnian Bay (Juttila et al., 2005). Spring and summer sea surface

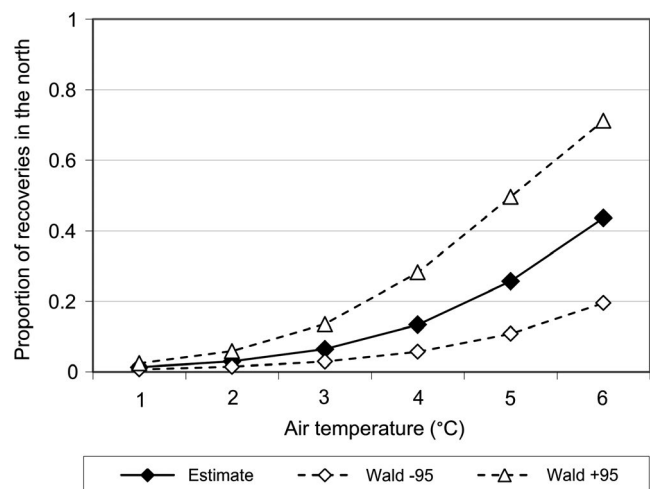


FIGURE 3 The proportion of Atlantic salmon tag recoveries in Baltic Sea feeding areas in the northern (Gulf of Bothnia) relative to the more southern Baltic Main Basin during their second winter (19–23 months in the sea, Dec–April) in relation to the spring air temperature (°C) of their smolt year at the Jomala weather station (60°18'N, 19°19'E). Wald confidence limits (–95 and +95) are presented

TABLE 2 Feeding ground preference models [Gulf of Bothnia (GoB) or Main Basin (MB)] for tagged Atlantic salmon smolts, recovered as adults during their second sea winter, in relation to the annual spring air temperature (year) in the corresponding smolt year in the Gulf of Bothnia (Jomala) ($n_{GoB} = 338$; $n_{MB} = 2,476$) (M1), or in relation to both the air temperature in the smolt year and their smolt length (cm) ($n_{GoB} = 303$; $n_{MB} = 2,277$) (M2)

Migration model	Effect	Estimate	SE	df	Wald χ^2	Pr > $ \chi^2 $	AIC
M1	Intercept	-5.101	0.248	1	421.57	<0.001	1,831.6
	Temperature	0.877	0.057	1	199.40	<0.001	
M2	Intercept	-9.110	0.543	1	281.60	<0.001	1,566.9
	Temperature	0.813	0.061	1	179.51	<0.001	
	Smolt length	0.199	0.023	1	76.22	<0.001	

Note: All tagged Atlantic salmon smolts released in 1985–2004 into the Bothnian Bay and subsequently recovered as adults are included.

Abbreviation: AIC, Akaike information criterion.

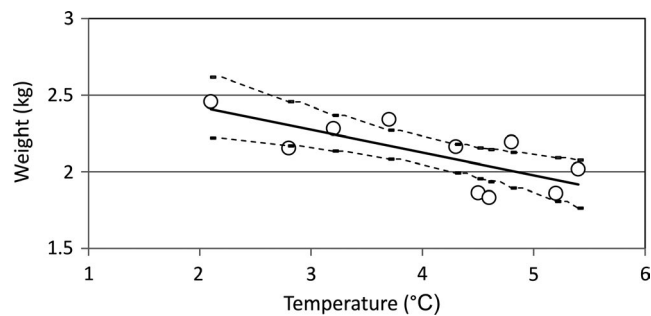


FIGURE 4 The model-predicted weight of 1SW Atlantic salmon males in the mixed-stock catch data (Table 1) in relation to the spring air temperature of the smolt year (°C) (at Jomala; $p = .005$). Regression: $\text{Weight} = 2.737 - 0.152 * \text{air temperature}$, $R^2 = .406$. Annual observations (open circles) and the model-predicted linear trend (continuous line) between the weight of 1SW males and the spring temperature in the smolt year, with 95% confidence limits of the mean (broken lines), are presented. The model is based on data from 12 years, but only 10 observations are shown, because the values for two years were the same

temperatures in the Baltic Sea vary parallel with air temperature (Stramska & Białogrodzka, 2015).

In recent years, smolt migration has started earlier as a result of earlier thermal springs (in Finland, defined as the period when mean day and night temperatures remain above 0°C and below 10°C in the Gulf of Bothnia) (Jokikokko et al., 2016; Otero et al., 2014). In this study, an increasing air temperature in the Gulf of Bothnia was associated with a smaller mean smolt size of recaptured Atlantic salmon. A larger smolt size is known to improve marine survival in general for both wild and reared salmon smolts (Jokikokko et al., 2006; Kallio-Nyberg et al., 2011). Survival increases up to a smolt length of 140–220 mm when it levels off in the Bothnian Sea (Salminen, Kuikka, & Erkamo, 1995). High survival promotes a large year-class size, followed by the stock's greater reproduction capacity. However, even if wild smolts are often smaller, their survival is better than that of reared smolts, and the difference in survival between wild and reared smolts increases in years when the average survival is low (Saloniemi, Jokikokko, Kallio-Nyberg, Jutila, & Pasanen, 2004).

Survival rates after the post-smolt stage tend to be high when sea surface temperature and herring abundance are also high (Salminen

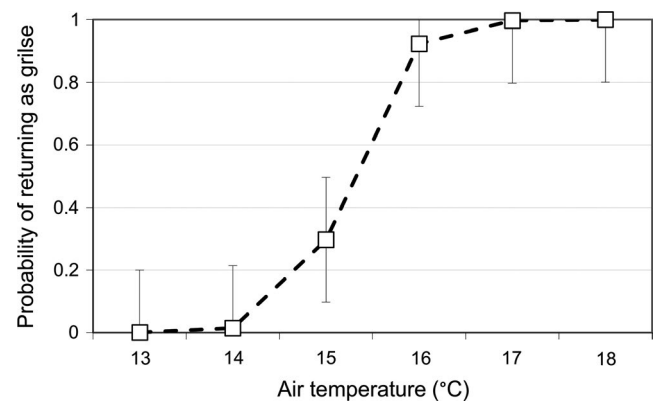


FIGURE 5 The probability of Atlantic salmon male spawning as grilse (1SW) in relation to the summer air temperature (°C) in their smolt year for smolt-year classes 2001–2009 in the Gulf of Bothnia. (SAS GENMOD: Type 3 analysis: air temperature at Jomala: $\chi^2 = 3.70$, $df = 1$, $p = .054$). The 95% standard error bars are presented

et al., 1995). During colder summers, small smolts are likely to have lower survival, causing mean smolt size to increase in those years. Selection against small smolts is likely to remove the weakest individuals with less competitive ability and less favourable genotypes. Sea temperature is likely to be the main environmental factor determining if smolts migrate to the south into the Baltic Main Basin, because in warm years, prey fish abundance in the north, in the Gulf of Bothnia, is high, and as a result, salmon marine survival is high for those years (Kallio-Nyberg et al., 2004, 2006).

The recovery data used in the present analysis included different Bothnian Bay stocks (Tornionjoki, Iijoki, and Simojoki salmon), comprising both reared and wild smolts. Reared salmon released as smolts more often remain in northern feeding areas than salmon born in the wild (Jutila, Jokikokko, Kallio-Nyberg, et al., 2003; Kallio-Nyberg et al., 2015). Nevertheless, Kallio-Nyberg et al. (1999) demonstrated that although salmon stocks differed in their life history traits, their spatial distribution during the feeding season varied synchronously according to environmental factors. When young herring are abundant in the Bothnian Sea, all salmon stocks tend largely to remain in the Bothnian Sea during the second sea winter (Kallio-Nyberg et al., 1999).

Earlier smolt migration due to global warming (Otero et al., 2014) may also affect sea migration. Post-smolts (under 24 cm) feed on surface fauna (Jutla & Toivonen, 1985), and during their first summer in the sea, they shift their diet from invertebrates to prey fish (Salminen et al., 2001). Zooplankton and young herring are abundant during warm springs in the Gulf of Bothnia (Dippner et al., 2001). Herring are the main prey fish for piscivorous salmon in the Gulf of Bothnia (Karlsson, Ikonen, Mitans, & Hansson, 1999; Salminen et al., 2001), and a high herring abundance in the Gulf of Bothnia is associated with salmon continuing to feed in the Gulf of Bothnia (Kallio-Nyberg et al., 1999; Salminen et al., 1994). Nevertheless, colder winter months may cause slower growth in salmon in the Bothnian Sea compared with the Main Basin (Jevrejeva et al., 2004).

Our long-term data suggest that increasing temperatures are associated with the smaller mean sizes and younger age (1SW) of returning male salmon in the Baltic Sea. When time spent feeding at sea increases, the risk of dying at sea before spawning also increases. The benefits of continuing to feed in the sea to gain a larger size may be less than the cost of waiting and being exposed to increased mortality (Jonsson & Jonsson, 2007). Staying in the Gulf of Bothnia instead of migrating south and returning as grilse may be an advantageous reproduction strategy for males, especially after warmer growing conditions in the smolt year.

Other factors such as selective fishing are also known to affect the age structure of spawning salmon (Jokikokko & Jutla, 2005; Jørgensen et al., 2007; Kokkonen, Vainikka, & Heikinheimo, 2015). Size-selective fishing tends to remove fast-growing individuals and cause maturation at a younger age (Kokkonen et al., 2015). Fishing may have reduced the proportion of older, and thus larger, fish in the spawning stock. Such selection may have stronger negative effects in females, because their fitness is strongly associated with a higher number of larger eggs, which is typical of larger females.

A comparison between the current and historical records (Alm, 1934) of age at maturation shows a trend towards younger spawning, especially among hatchery-produced smolts (Figures S1 and S2). Early spawning fish were rare, and repeat spawning was common in the 1930s, but the Atlantic salmon spawning age distribution in the Bothnian Bay is currently very narrow. In the current data (2000–2014), the mean spawning age for Tornionjoki wild females was 2.2 years (reared females 2.0 years), and 1.8 years for wild spawning males (reared males 1.3 years) (Figure S2). The low proportion of repeat spawning fish (2.8% in Simojoki stock, 1997–2003; Jokikokko, & Jutla, 2005) results in an even smaller size in ascending salmon.

An increasing temperature is likely to change the migration behaviour and decrease the age at maturity of Atlantic salmon populations. At the same time, fishing mortality acts in the same direction by favouring faster life cycles and a smaller spawning size. Hatchery rearing also causes smolts to grow faster, and become larger but less competitive in the wild (Jonsson et al., 2003).

Observed changes in life history traits (Friedland, Hansen, Dunkey, & MacLean, 2000; Hutchings & Jones, 1998; Jonsson et al., 2016; Kallio-Nyberg et al., 1999) have previously been associated

with phenotypic plasticity, which may be the first step in adjusting to changing environments (Sydeman et al., 2015). The maturation period is known to have high heritability, and minor genes have been regarded as its most likely basis, but a single major locus, either alone or with minor loci, is also found behind the trait (Lafuente & Beldade, 2019). New studies (Ayllon et al., 2015; Barson et al., 2015; Czorlich et al., 2018) have found a very simple one-locus system that predicts much of the variation in age at maturity of Atlantic salmon along the north Atlantic coast, including the Baltic Sea. The early maturation allele was dominant in males but recessive in females.

The response to selection and especially the rate of response depend on the genetic basis of the traits. Strong natural selection can decrease frequencies of relevant alleles and even remove them entirely from the population. Erosion of genetic variation (and associated phenotypes) is fast and more permanent if the phenotype is based on a single locus. For example, genetic variation for migration timing has been nearly fixed in Chinook salmon (*Oncorhynchus tshawytscha*) as a consequence of dam construction (Thompson et al., 2019). The timing of spawning migration is variable for both Atlantic and Pacific salmon, and warming is likely to affect the timing of migration for both (Quinn, McGinnity, & Reed, 2015).

However, the difference in dominance patterns in males and females is likely to somewhat slow the erosion of genetic variation. The present study included only male returners, because females of the same age are not physiologically able to reproduce. However, the data (based partly on another dataset) in Figure S2b of the Appendix S1 shows a similar spawning age trend for females and males. On average, female spawners are older than male spawners. Although domestication tends to decrease spawning age, the difference in spawning age between the sexes remains. The trend towards a smaller maturation size is also associated with a more male-biased sex ratio (Figure S2a in the Appendix S1) in populations with the youngest (and smallest) males.

A fast decrease in the mean spawning age and size of Atlantic salmon males is a probable scenario, with increasing climate temperatures and other anthropogenic interventions in the Baltic Sea Atlantic salmon populations. We may be witnessing permanent evolutionary changes (Crozier & Hutchings, 2014) in Atlantic salmon populations in the Baltic Sea. Anthropogenic impacts at many levels are changing the genetic and ecological structure of not only the Atlantic salmon populations but river and marine ecosystems in general, as well as the human economy based on recreational and commercial fishery.

ACKNOWLEDGEMENTS

Warm thanks to Dr Craig Primmer and Dr Tutku Aykanat for valuable discussions and useful comments on the manuscript during the work. We thank the staff of the Natural Resources Institute Finland (Luke), and especially the staff in the tagging office, for their major efforts in running the tagging programme, and the Swedish and Finnish Data Collection teams for their considerable work in collecting salmon data in accordance with the EU Data Collection Framework. The present study was partly funded by the SmartSea

project, the Strategic Research Council of the Academy of Finland, and Luke.

AUTHOR CONTRIBUTIONS

Irma Kallio-Nyberg: study conception, data analysis, manuscript preparation, drawing of figures. Irma Saloniemi: study conception, manuscript preparation, data analysis. Marja-Liisa Koljonen: data generation, manuscript preparation, coordination of tag return data collection.

DATA AVAILABILITY STATEMENT

National Data Collection Programme under Council Regulation (EC).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Kallio-Nyberg I, Saloniemi I, Koljonen M-L. Increasing temperature associated with increasing grilse proportion and smaller grilse size of Atlantic salmon. *J Appl Ichthyol*. 2020;36:288–297. <https://doi.org/10.1111/jai.14033>