Master's Thesis

Spatio-temporal differences in the growth of wild and reared Atlantic salmon (*Salmo salar* L.) in the Baltic Sea

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ABSTRACT

The feeding migration to the sea and the associated faster growth is an essential part of the ecology and life history of Atlantic salmon (*Salmo salar* L.). Thus the quantification of growth is an important part of fisheries research. The most productive feeding areas have a key role in the conservation of wild stocks and at the same time ensuring sustainable exploitation of reared stocks. The aims of this study were to investigate if there are spatial, temporal and stock (wild, reared) related differences in the growth of salmon in the Baltic Sea and to determine if individual diet preferences, prey species stock abundance and water temperature affect growth. The absolute length growth of Baltic salmon first and second sea growth season was back-calculated from time series (1989–2010) of archived salmon scales obtained from the main salmon feeding areas (ICES subdivisions (SDs) 25, 26, 28, 30 and 32). During first sea growth season wild salmon caught from SD25 (Main Basin) were fastest growing and individuals caught from SD30 (Bothnian Sea) grew slowest. Reared salmon caught from SD32 (Gulf of Finland) grew fastest during first sea growth season and individuals caught from SD26 (Main Basin) the slowest. During second sea growth season wild salmon caught from SD28 (Main Basin) were fastest growing and individuals caught from SD30 grew slowest. Reared salmon caught from SD25 had the fastest growth during second sea growth season and individuals caught from SD30 the slowest. There was a general increasing trend in the growth of wild salmon, recent growth during first sea growth season being annually 25 cm and during second sea growth season 30 cm. At the beginning of the study period reared salmon growth during first sea growth season was 20 cm, but since 1994 it has stayed close to 25 cm. Their growth during second sea growth season has been increasing through-out the study period from <15 cm close to 30 cm. Wild salmon grew faster than their reared counterparts during both sea growth seasons. Higher trophic position of salmon was associated with increased growth during second sea growth season in the Main Basin. Since trophic position reflects dietary behaviour, this indicates that diet has an influence on growth. Warmer water was associated with decreased growth during first sea growth season in the Gulf of Finland and during second sea growth season in the Main Basin. Salmon populations in the Baltic Sea seem to possess spatial and temporal differences in growth. This study suggests that these differences are explained by stock, dietary prevalence and water temperature.

TIIVISTELMÄ

Syönnösvaellus ja nopea kasvu ovat olennainen osa Atlantin lohen (*Salmo salar* L.) ekologiaa, niinpä kasvunopeuden selvittäminen on tärkeä osa kalatutkimusta. Tuottavimmat syönnösalueet tulisi tietää, jotta olisi mahdollista suojella villejä sekä kalastaa istutettuja lohia kestävän käytön periaatteella. Tämän tutkimuksen tavoitteina oli selvittää Itämeressä elävän villin ja viljellyn Atlantin lohen kasvunopeuden eroja vuosien ja merialueiden välillä. Lisäksi pyrittiin selvittämään, vaikuttavatko saalislajien runsaus, saalislajisuhteet lohen ravinnossa ja veden lämpötila kasvunopeuteen. Absoluuttinen pituuskasvu arvioitiin takautuvalla kasvunmäärityksellä suomuista vuosilta 1989–2010. Suomut oli kerätty pääsyönnösalueilta (ICES osa-alueet (SDt) 25, 26, 28, 30 ja 32). Villin lohen ensimmäisen merivuoden kasvu oli nopeinta SD25:stä (pääallas) ja hitainta SD30:sta (Selkämeri) pyydetyillä yksilöillä, kun taas viljellyn lohen kasvu oli nopeinta SD32:sta (Suomenlahti) ja hitainta SD26:sta (pääallas) pyydetyillä yksilöillä. Villin lohen toisen merivuoden kasvu oli nopeinta SD28:sta (pääallas) ja hitainta SD30:sta pyydetyillä yksilöillä. Viljellyn lohen toisen merivuoden kasvu oli nopeinta SD25:stä ja hitainta Selkämereltä pyydetyillä yksilöillä. Villin lohen molempien merivuosien kasvunopeudessa oli nouseva trendi läpi tutkimusjakson ensimmäisen merivuoden kasvun ollessa viime vuosina keskimäärin 25 cm ja toisen merivuoden kasvun 30 cm vuodessa. Tutkimusjakson alussa viljellyn lohen ensimmäisen merivuoden kasvu oli noin 20 cm, mutta 1994 lähtien se on ollut 25 cm vuodessa. Viljellyn lohen toisen merivuoden kasvu oli tutkimusjakson alussa alle 15 cm, josta se on kohonnut lähes 30 cm:iin vuodessa. Villin lohen keskimääräinen kasvu oli nopeampaa molempien merivuosien aikana verrattuna viljeltyyn. Korkeamman lohen trofiatason ja suuremman kasvunopeuden välillä havaittiin yhteys ensimmäisen merivuoden aikana pääaltaalla, mikä viittaa saalislajisuhteiden vaikuttavan kasvunopeuteen. Lämpimämmän veden ja hitaamman ensimmäisen merivuoden aikaisen kasvun välillä havaittiin yhteys Suomenlahdella sekä lämpimämmän veden ja hitaamman toisen merivuoden aikaisen kasvun välillä pääaltaalla. Itämeren lohella vaikuttaa olevan alueiden ja vuosien välisiä eroja kasvunopeudessa. Tämän tutkimuksen perusteella ne näyttävät johtuvan lohen alkuperästä, ravinnonkäytöstä ja veden lämpötilasta.

Contents

1. INTRODUCTION

Growth is an essential part of the ecology and life history of Atlantic salmon (*Salmo salar* L.) and its quantification is an important part of fisheries research and management (Summerfelt & Hall 1987, Weatherley & Gill 1987). It can be seen as the result of several interlinked processes, the behavioural aspects of obtaining food, the efficiency of bioenergetics of nutrient uptake, deposition, metabolism and cellular growth (Jonsson & Björnsson 1994, De Pedro & Björnsson 2001). While the exploitation rates of some Atlantic salmon stocks have decreased to ecologically sustainable levels, it is still important to study whether management practices cause selective pressures on life-history traits (Allendorf et al. 2008, Hard et al. 2008). To maintain a commercial salmon fishery many salmon populations are supported by stocking and potential adaptations to captivity may then influence the growth potential of wild populations (Whalen & Parrish 1999, Romakkaniemi et al. 2003, Frankham 2008, Hutchings & Fraser 2008). Even in hatchery supplementation programs without intentional selection, increased growth may occur if the absence of predation favours risky feeding behaviour reducing selective payoff from cautious feeding (Devlin et al. 1999). Because wild and reared stocks migrate in the same feeding areas and there is considerable spatial and temporal variation in stock distributions (Kallio-Nyberg 1999, Koljonen 2006) stock specific exploitation is unfortunately very difficult. There is also large variation in the marine growth of Atlantic salmon among populations and years (Jensen et al. 2011). Hence the feeding areas where different Baltic Sea salmon populations produce the most successful individuals should be known to enable sustainable conservation of wild and fishing of reared salmon.

Ocean climate and water temperature during the feeding migration are important environmental factors controlling the growth and survival of salmon. As temperature rises from the minimum, growth rises to a peak and declines with further increases up to a maximum (Salminen et al. 1995, Iwama 1996, Friedland et al. 2000). The effect of a given temperature on salmonid growth depends on interaction among growth, food consumption and temperature (Railsback & Rose 1999). Atlantic salmon is a cold water fish (Barton 1996) and water temperature below 10 °C, which is considered suitable for rapid marine growth, is where salmon are often caught at sea (Reddin & Friedland 1993, Holm et al. 2000). The lower temperature limit for salmonid growth was believed to be approximately 5°C (Elliott & Hurley 1997), but according to Finstad et al. (2004) there is now evidence indicating that salmonids are able to grow at temperatures close to 0 °C, growth being considerably faster for winter than summer acclimatised fish. When temperature is low, metabolic rate is reduced and energetic demands for other aspects of metabolism exceed that available for growth (Brett 1979).

Templeman (1967) and Reddin (1985) stated that during feeding migration salmon spend most of their time close to the surface. They can behaviourally regulate energy costs through microhabitat selection and their physiological optimum for growth is often similar to the behaviourally selected temperature (Jobling 1981, Nislow et al. 1999, Jacobsen & Hansen 2000). In the marine phase they mainly occupy the upper 30 m of the water column (Holm et al. 2004) and avoid water warmer than 11–12 °C by moving to deeper, colder layers (Alm 1958). The most rapid growth in the Baltic Sea takes place in July–September (Salminen et al. 2001). Salmon is particularly receptive to extended day length, eating continuously during the illuminated period of day, which manifests as enhanced growth and can be explained by the vision dependence of hunting and feeding activities (Boeuf & Le Bail 1999). The greater the growth opportunity (°C*day length hours) in late

summer, the greater the proportion of salmon maintaining good growth (Thorpe et al. 1989). Photoperiod and temperature should be considered as interactive factors controlling fish growth (McCormick et al. 2000).

The growth of salmon is largely determined by the amount of available food (Thurow 1968). To survive the demanding feeding migration, postsmolts start consuming high energy content pelagic fish and increase their growth soon after the entering marine habitat (Stefansson et al. 2003, Rikardsen et al. 2004). Salmon feed opportunistically and are considered to be pelagic and mid water predators at sea; however, they tend to select the larger size prey of the available size spectrum supporting rapid growth (Patnaik et al. 1994, Jacobsen & Hansen 2000). Growth in the sea is dependent on interactions with resource distribution. Wider dispersion of prey dampens the formation of dominance hierarchies with the consequent reduction in losses of energy and increase in growth (Jobling et al. 1993, Davison 1997, Martin-Smith & Armstrong 2002). Ultimately growth is positively correlated with the availability and nutritional content of food (Salminen et al. 1995, Barton 1996). Sprat (*Sprattus sprattus* L.) dominates the diet of salmon in the Baltic Main Basin. It decreases or even disappears from the diet in the Bothnian Sea and much of it is replaced by herring *(Clupea harengus membras* L.), but also in smaller amounts by three-spined stickleback (*Gasterosteus aculeatus* L.) and minor amounts of other species. In the Gulf of Finland herring dominates the diet of salmon (Hansson et al. 2001, Ikonen 2006). Renkawitz & Sheehan (2011) noted differences in wild and reared salmon diet, whereas Jacobsen & Hansen (2001) detected no difference between these two stocks. It is not known for sure what food the studied salmon have been eating some time before sampling, but the diets are assumed to approximately match earlier findings. Comparing salmon growth to herring and sprat abundance we may acquire more information on diet and growth interaction in the Baltic Sea.

The study of stable isotope analysis has the advantage that it provides an assimilated history of feeding relationships. The utility of stable isotope technique depends primarily on differences in the retention of heavier isotopes and excretion of lighter isotopes and in the isotopic ratio between consumers and their diet (DeNiro & Epstein 1981, Minagawa & Wada 1984). The isotopic composition of animal tissue reflects the average diet assimilated over a length of time, unlike stomach content analyses which yield information only about individual diet at a particular point in time (Fry & Sherr 1984, Hobson & Welch 1992). Fry (1988) has shown $\delta^{15}N$ value to correlate more strongly with food web structure than do changes in carbon isotope values. Scale tissue is metabolically inert or it experiences only very little metabolic replacement (Ottaway 1978, Perga & Gerdeaux 2003). Dietary integration is chronologically deposited in the outermost regions of fish scales and it is a widely used source of information regarding dietary history in the last season of growth (Nagai et al. 2004, Hutchinson & Trueman 2006, Hammond & Savage 2009). The observed $\delta^{15}N$ value possibly yields conclusions about trophic position (TP) and food sources (Perry et al. 1999). By comparing salmon TP to that of prey species we may obtain knowledge on prey species proportion in individual Baltic salmon diet.

This study aims to shed light on spatial, temporal and stock (wild, reared) related differences in the growth of salmon in the Baltic Sea. The hypothesis is that growth differs between areas, years and stocks. I also hypothesize that prey stock size, water temperature and prey species proportions in the diet of salmon via the trophic position exploitation of salmon affect growth.

2. MATERIALS AND METHODS

2.1. Study Area

The Baltic Sea (Figure 1) is a semi-enclosed body of brackish water characterized by horizontal and vertical salinity gradients and annual mean water temperature decreases towards the north. Stratification in the Baltic Sea is controlled by occasional salt water intrusions from the North Sea and by river runoff (Schinke & Matthäus 1998, ICES 2012). The surface salinity ranges from around 4 ‰ in the Bothnian Sea and eastern Gulf of Finland to 8 ‰ in the central Baltic and increases to 25 ‰ in the south-west (Jaspers et al. 2011). The study area covers International Council for the Exploration of the Sea (ICES) subdivisions as follows: SDs 25, 26, 28 (excluding Gulf of Riga), 30 and 32.
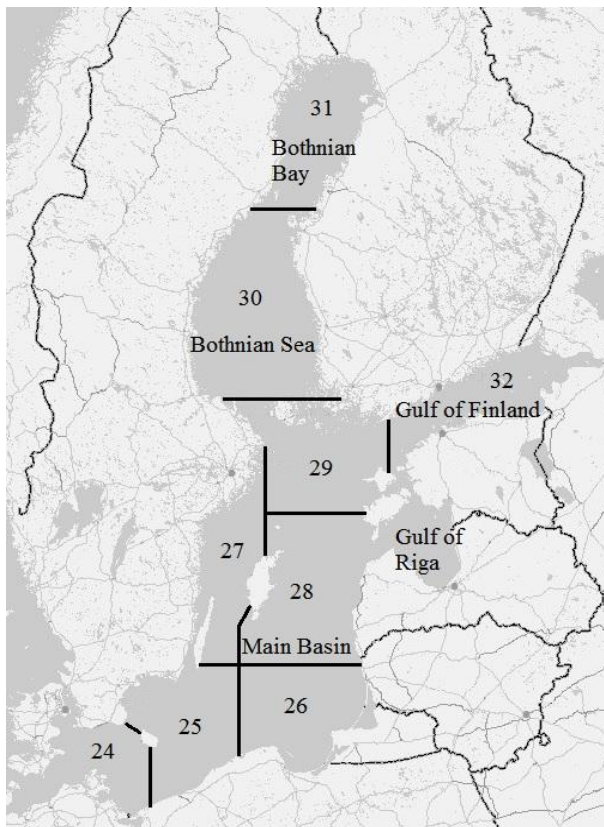
Figure 1. Subdivisions (24-32) of the Baltic Sea according to the International Council for the Exploration of the Sea (ICES) (HELCOM Map and Data Service 2012).

Oceanographic conditions in the central Baltic Sea are strongly linked to atmospheric forcing and since the late 1980s the ecosystem has undergone large changes due to unusual period of strong westerly winds resulting in increased average water temperatures and lack of inflows of saline and oxygen-rich water from the North Sea (Möllman et al. 2005). The geologically young age, salinity and oxygen gradients in the Baltic Sea cause relatively low species diversity (Voipio 1981, MacKenzie et al. 2002).

2.2. Obtaining scales

Archived scale samples were obtained from the Finnish Game and Fisheries Research Institute (FGFRI) and University of Turku from years 1989–2010. Individual total length to the nearest centimetre and place and time of catch was also provided. It is

more practical to determine the growth of length rather than weight as the latter may be affected by changes in condition (Morgan et al. 2000). Since the studied fish were sea recoveries from mark-recapture studies and were Carlin-tagged in their natal river fish farm it was possible to determine if an individual was of reared or wild stock. If the stock was not known, salmon from the rivers Tornionjoki and Simojoki were assumed to be wild and individuals from other rivers reared (Romakkaniemi et al. 2003, FGFRI 2012). Substantially regenerated or otherwise distorted scales were not used. Scales of spawned salmon were not used due to resorption of scale margins during spawning (Crichton 1935).

Before spawning migration salmon often spend one to three years in the sea (Jutila & Pruuki 1988). There were only few scale samples from salmon that were three sea growth seasons (SGS) old and most of them had spawned, thus they were not further studied. As the productivity of many Atlantic salmon stocks are evaluated based on individuals that are one or two SGSs old (Friedland et al. 2000), a similar expression was used in this study. If it was not possible to measure an intact scale, a slightly regenerated scale was sometimes selected and the centre of the scale was approximated. Growth data was analysed and compared between SDs, years and stocks. Groups with one individual were not used in statistical analysis and they are not shown in figures.

2.3. Back-calculation of length

Relationship between fish length and scale radius enables the back-calculation of length at age using scale measurements (Hile 1936, Francis 1990). The distance between scale focus and annulus reflects the length of an individual at the time of annulus formation (Raitaniemi et al. 2000) and this is a widely used approach to estimate the age and growth of fish (Carlander 1987, Busacker et al. 1990). Amount of 3–9 intact scales were selected and soaked in deionized water for 2–3 min to aid separation of dried scales and to loosen any adhering organic particles. The scales were then manually cleaned using a non-lint tissue and impressed on polycarbonate slides. All scale imprints were viewed and to ensure accurate comparison between salmon individuals the most symmetrical scale was selected (Hile 1936).

FGFRI had determined the age of all back-calculated samples. During this study the scale radius and distance between focus and each annulus to the nearest millimetre was measured using a microfiche reader with 25 times magnification. A measurement line according to Heidarsson et al. (2006) from scale focus towards the front edge of scale was used. The number of freshwater years was excluded and only the number of SGSs was determined. The accuracy of scale reading was validated by repeatedly measuring most of the scales by a single person but scales with moderate difficulty in annulus determination were viewed by a second reader and assignments were established in agreement.

Distances from the scale focus to the annuli that formed after freshwater period, I and II SGS were used in the back-calculation of smolt length and lengths after I and II SGS, respectively. The lengths of 922 smolt (Appendix 1), 922 I SGS (Appendix 2) and 246 II SGS (Appendix 3) samples were back-calculated. The back-calculated smolt length deducted from the back-calculated length after I SGS was considered as the growth of I SGS. The back-calculated length after I SGS deducted from the back-calculated length after II SGS was considered as the growth of II SGS. In few occasions it was not possible to determine the position of freshwater annulus because of scale regeneration but growth during II SGS was still determined if the annulus of I and II SGS were visible. Growth was reported to take place in the formation year of the outermost annulus bordering the SGS in question.

Since the length growth of smaller salmon is often faster compared to larger (Austreng et al. 1987, Wootton 1990) but also larger individuals experience increased growth because of the ability to consume larger food items when such are available (Keeley & Grant 2001), in this study length at the beginning of a SGS was not assumed to affect growth. Analysis of the study data also mostly supported this assumption since significant associations (linear regression, $p < 0.05$) between length and growth were found only for reared salmon during I SGS in few years. When Bonferroni correction was used to reduce the chances of obtaining false positive results (Weisstein 2013) these associations were no longer significant.

The highest coefficient of determination of the scale-length relationship was achieved when all scale samples were pooled together and the relationship was explained with power regression trend line (Figure 2) therefore Monastyrsky's (1926, 1930) regression model (Equation 1) was used in the back-calculation of length after I and II SGS as cited in Raitaniemi et al. (2000).
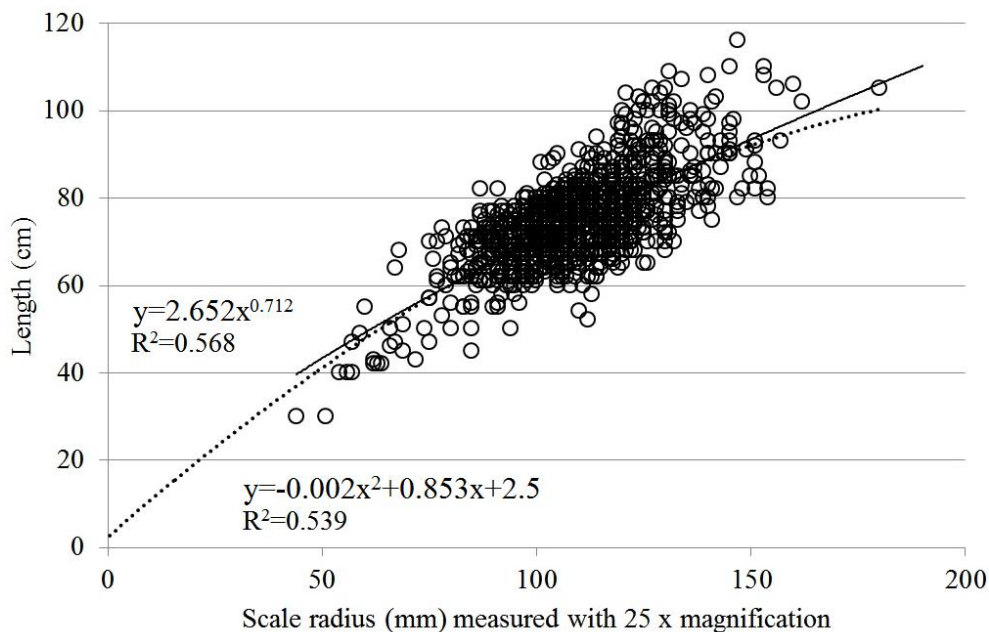

Figure 2. Polynomial and power regression trend lines of scale-length relationship. The intercept of polynomial trend line was set to 2.5 cm at the y-axis to account for growth before scale formation.

Equation 1: $L_i = (S_i/S)^b L$

In the model:

L = fish body length at capture

L_i = back-calculated fish length at time of annulus formation at age i

S = scale radius at capture

S_i = scale radius at the time of annulus formation

b = constant from power regression equation (0.712, SE = ± 0.288)

Obtaining scales from adult salmon has become a frequently used method of generating data on smolt length (Bagliniere & Maisse 1985). Due to the absence of individuals smaller than 40 cm, the lengths of smolts were back-calculated with a model

where a set intercept accounts for body growth before scale formation starts (Raitaniemi et al. 2000). When the intercept at the y-axis was set to 2.5 cm to account for the growth before scale formation (Heidarsson et al. 2006), a polynomial trend line had the highest coefficient of determination (Figure 2) and a suitable model (Equation 2) according to Raitaniemi et al. (2000) was used for smolt length back-calculation.

Equation 2: $Li = (aSi^2 + bSi)*(L-c)/(aS^2 + bS)$

In the model:

L, Li, S, S i= as previously mentioned

a = constant from polynomial equation (-0.002, SE = ± 0.0)

b = constant from polynomial equation (0.853, SE = ± 0.108)

c = intercept point at y-axis (2.5, SE = ± 5.878)

2.4. Sea water temperature

Sea water temperatures from May to October were used since most of salmon growth takes place during that time (Larsson 1984, Salminen et al. 2001). Temperatures from 5–30 m depth in May, June, September and October and from 10–30 m depth in July and August were used since those are the depths where salmon is assumed to dwell (Alm 1958, Holm et al. 2004). Sea water average temperatures were according to ICES (ICES 2012). Temperature was assumed to affect similarly both stocks since they feed in the same areas (Kallio-Nyberg 1999, Wootton 1990) and thus wild and reared salmon samples were pooled together studying the effect of temperature on growth. The growth of salmon was assumed to peak and begin to decrease after a certain temperature (Salminen et al. 1995, Iwama 1996, Friedland et al. 2000)

2.5. Prey species abundance

According to Kallio-Nyberg et al. (2004) the abundance of salmon prey species and climatic factors are directly or indirectly associated. The Estimates of herring and sprat stock abundance were from FGFRI (FGFRI 2011) and ICES (ICES 2011) reports. The age groups of herring with average length of 19 cm or less in SDs 25, 26, 28 and 30 and all age groups of sprat were assumed as suitable prey for salmon (Mikkonen et al. 2011). The effect of herring stock abundance on the growth of salmon after year 2005 and in SD32 was not analysed since the study of Mikkonen et al. (2011) did not cover that period of time and area. Also there were no sprat statistics from SD32 thus the effect of sprat stock abundance on growth in SD32 was not studied. Therefore in SDs 25, 26, 28 and 30 the relationship between the growth of salmon and the abundance of herring was analysed in 1988–2005 and between the abundance of sprat in 1988–2009. The amount of herring and sprat was pooled since salmon feed on both of them when available (Hansson et al. 2001). Samples of wild and reared salmon were pooled together when studying the effect of prey species abundance on growth since they utilize prey stocks in the same manner (Jacobsen & Hansen 2001). Also the study data supported this since the TPs of wild and reared individuals differed only in two years (t-test, p<0.05).

2.6. Stable isotope analysis

The stable isotope analyses of scales were limited to the outermost margin of the scale, representing the growth of last season as suggested by Wainwright et al. (1993) and Satterfield & Finney (2002). Scale marginal increments were removed with a scalpel detaching as much as possible of the outermost annulus without removing any of the

circulus from prior growth and stored in individual Eppendorf tubes (Hutchinson & Trueman 2006). Margins from 5–9 scales from the same fish were pooled to ensure sufficient mass of material, after which they were dried overnight in room temperature. Samples were soaked for 2 min in 1.2 HCl to remove extraneous carbonates, rinsed five times in deionized water and placed into weighted tin capsules to dry overnight at a constant temperature of approximately 60 °C (Fry 1988, Perga & Gerdeaux 2003, Kennedy et al. 2005, Hammond & Savage 2009). Tin capsules were weighed without sample beforehand to ensure sufficient amount of at least 0.2 mg sample for stable isotope ratio determination.

Isotope compositions were determined at the University of Jyväskylä with a Carlo Erba Flash EA 1112 elemental analyser coupled with Thermo Finnigan DELTA[plus]-Advantage mass spectrometer (CF-IRMS). Pike (*Esox lucius*) white muscle with known isotopic composition was used as a working standard to ensure the accuracy of analyses. Cladocerans sampled from different Baltic Sea areas were used as TP baseline organisms for determining salmon areal TP. The isotope values of cladocerans and salmon prey species were collected from the Bothnian Sea, Gulf of Finland and Main Basin area (Kiljunen et al. 2008, Kiljunen unpubl. data) (Table 1). The $\delta^{15}N$ values from the Main Basin were used for SDs 25, 26 and 28 when determining salmon areal TP. Stable N isotope values were expressed in delta (δ‰) notation relative to the international standard, atmospheric air N^2 as described by Fry (2006). The stable isotope ratios of sprat, herring, three-spined stickleback and cladocerans were assumed stable throughout the study period.

Table 1. $\delta^{15}N$ ratios of cladocerans, salmon prey species and their standard deviations (SD) (Kiljunen et al. 2008, Kiljunen unpubl. data).

Area	Sample	$\delta^{15}N$ ‰ Mean ± SD
Bothnian Sea	Herring	9.9±0.4
	Sprat	8.7±0.4
	Three-spined stickleback	9.0±0.3
	Cladocerans	4.1±2.4
Main Basin	Herring	10.8±0.3
	Sprat	9.5±0.7
	Three-spined stickleback	10.0±(–)
	Cladocerans	4.8±3.3
Gulf of Finland	Herring	11.6±0.6
	Sprat	10.0±0.4
	Three-spined stickleback	11.2±0.8
	Cladocerans	4.5±0.6

When the δ^{15}N ratios of Baltic salmon scales observed in this study were compared to the δ^{15}N ratios of muscle (Valkonen unpubl. data), the mean δ^{15}N ratio of muscle was 0.64 ‰ higher. This value was added to the δ^{15}N ratios of salmon scales for better reflecting the composition of salmon prey species. A trophic fractionation factor of 2.9 ‰ (Kiljunen et al. 2008) was used in isotope analysis. Trophic position (TP) was calculated according to Vander Zanden et al. (1997) (Equation 3).

Equation 3: $TP_{salmon} = (\delta^{15}N_{salmon} - \delta^{15}N_{cladocerans})/\Delta^{15}N + 2$

In the model Δ = trophic fractionation factor 2.9 ‰

It was assumed that δ^{15}N ratios are not affected by salmon size or environment (Sweeting et al. 2007a, Sweeting et al. 2007b, Hammond & Savage 2009) which was supported by the lack of relationship between size and scale δ^{15}N ratios (linear regression, p>0.05) observed in this study. Since the areal distribution of sea migration is independent of the duration of migration (Kallio-Nyberg et al. 2000), the outermost growth increments of scale II SGS were assumed to also reflect the diet of I SGS. Because salmon feed opportunistically (Jacobsen & Hansen 2000) TP of salmon was assumed to be associated with prey abundance which was partly supported by the study data (linear regression, p<0.05). In all SDs the TP of herring is the highest of salmon prey species, followed by three-spined stickleback and sprat (Kiljunen et al. 2008). Thus it was assumed that increase in the TP of salmon reflects higher herring and three-spined stickleback proportion in the diet at the expense of sprat and qualitative proportions of prey species in the diet of salmon were determined.

2.7. Statistical analyses

The growths of all cohorts were assumed to follow normal distribution as Magnifico (2007) describes and vast majority of the group variances were equal. Thus it was assumed that the hypothesised spatial and temporal growth differences will be effectively observed with the analysis of variance (ANOVA). T-test was used to analyse stock related growth differences. The pairwise comparisons of the observed growth differences were done with t-test when two groups were compared and with TukeyHSD when there were more than two groups. In four instances TukeyHSD pairwise comparison did not detect significant growth differences between years even though ANOVA detected, probably because of the uneven number of individuals in test units (Stevens 1999). Thus in those instances LSD-test was used instead. Also in two instances ANOVA only bordered significant while TukeyHSD pairwise comparison detected significant differences.

Because of the observed quite high variance inflation factor in the collinearity diagnostics (Pan & Jackson 2008) of water temperature and prey species abundance and the assumed associations between the factors affecting the growth of salmon, the effect of temperature, prey species abundance and salmon TP on growth was studied with partial correlation analysis. When the correlation between growth and one of the three factors was studied, the remaining factors were set as controlling. IBM SPSS Statistics (version 20) was used for statistical analyses.

3. RESULTS

3.1. Spatial growth differences

There were statistically significant spatial differences in the growth of wild salmon (Figures 3 & 4) during I ($ANOVA_{9.944,\ 264}$, p<0.001) and II SGS ($ANOVA_{3.867,\ 71}$, p<0.05).

There were also spatial differences in the growth of reared salmon during I (ANOVA, $_{13.070, 656}$, p<0.001) and II SGS (ANOVA$_{6.030, 173}$, p<0.001).
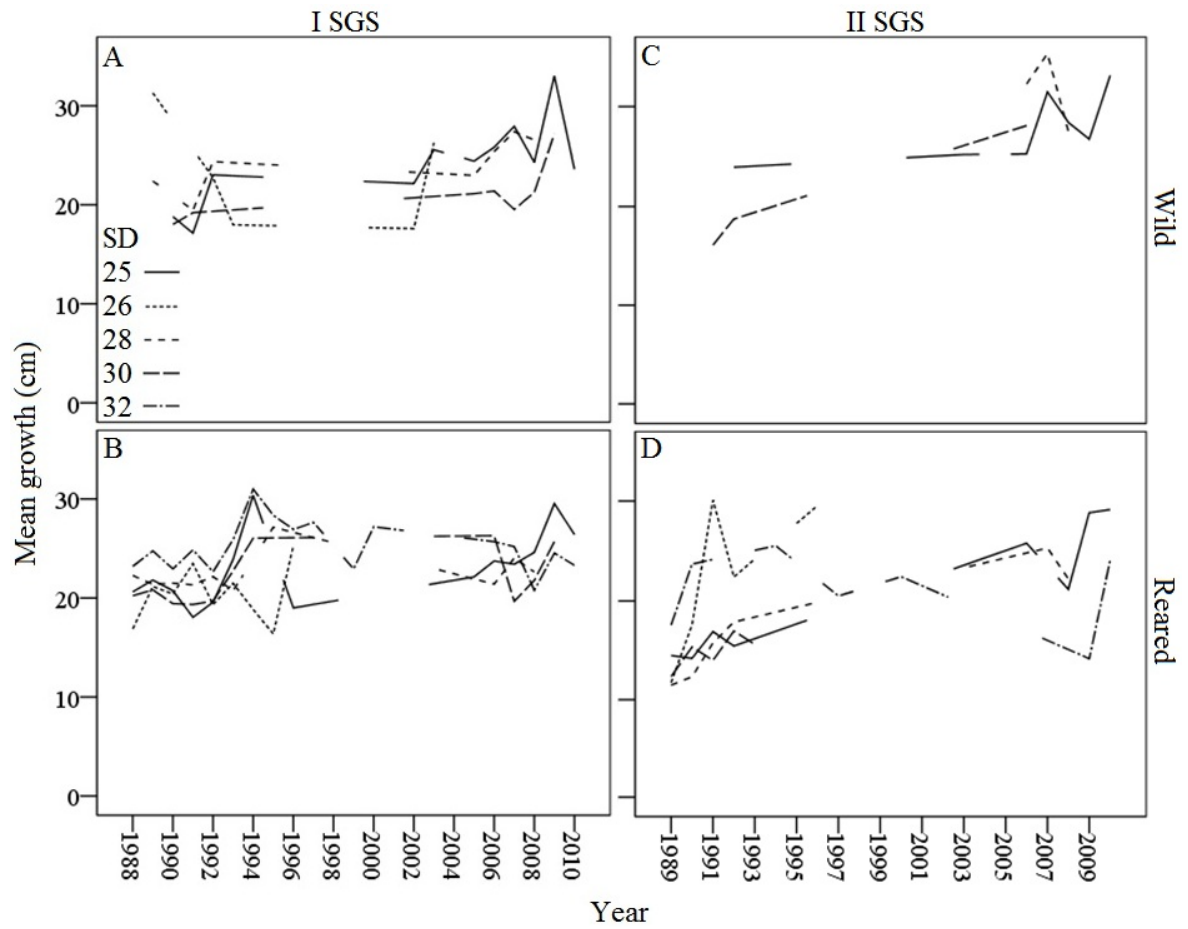

Figure 3. The growth of wild and reared Baltic salmon during I and II sea growth season (SGS) in studied years and International Council for the Exploration of the Sea (ICES) subdivisions (SDs). Figure A) The I SGS of wild salmon, B) The I SGS of reared salmon I SGS, C) The II SGS of wild salmon and D) The II SGS of reared salmon.
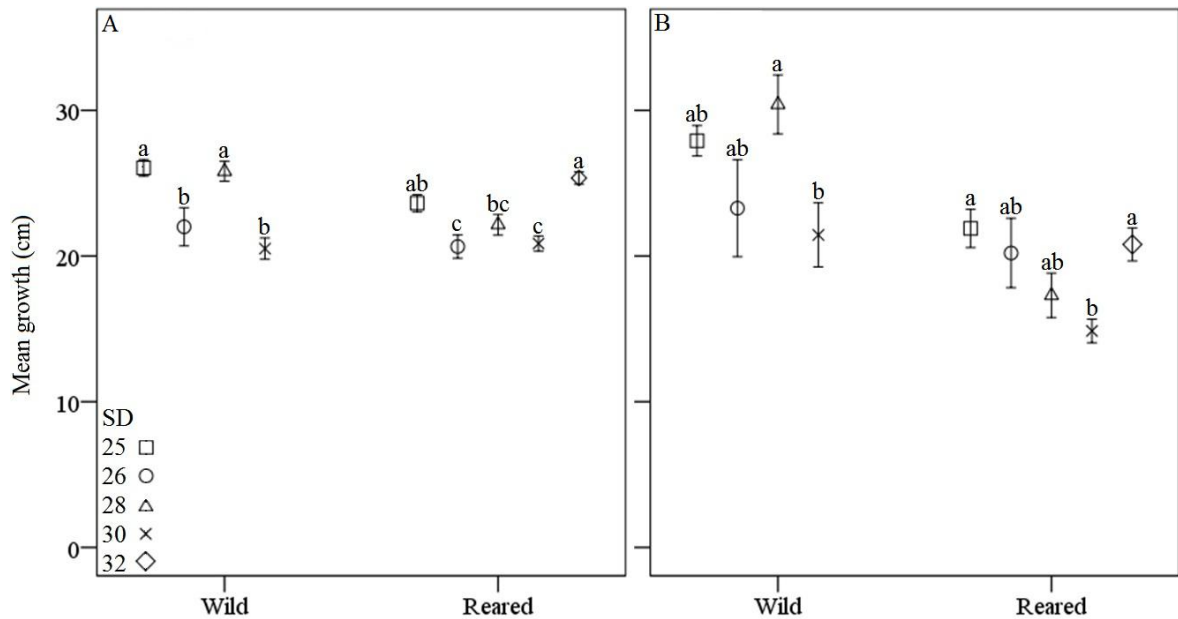
Figure 4. The growth of wild and reared Baltic salmon during first (A) and second (B) sea growth season in the International Council for the Exploration of the Sea (ICES) subdivisions (SDs). The symbol in the middle of the vertical bars shows the mean and bars ±1 SE. The growths of those wild or alternatively reared salmon that do not differ significantly (TukeyHSD, p>0.05) between SDs have error bars marked with the same letter.

When growth data was compared between SDs in every one of the studied years separately it was found that there were significant spatial differences during I SGS in the growth of wild salmon in 2008 (ANOVA$_{3.573, 47}$, p<0.05) (Figure 5) and in the growth of reared salmon in 1991 (ANOVA$_{2.779, 70}$, p<0.05). There were also spatial differences in the growth of reared salmon during II SGS in 1991 (ANOVA$_{4.101, 34}$, p<0.05) and 2009 (ANOVA$_{12.597, 14}$, p<0.05).
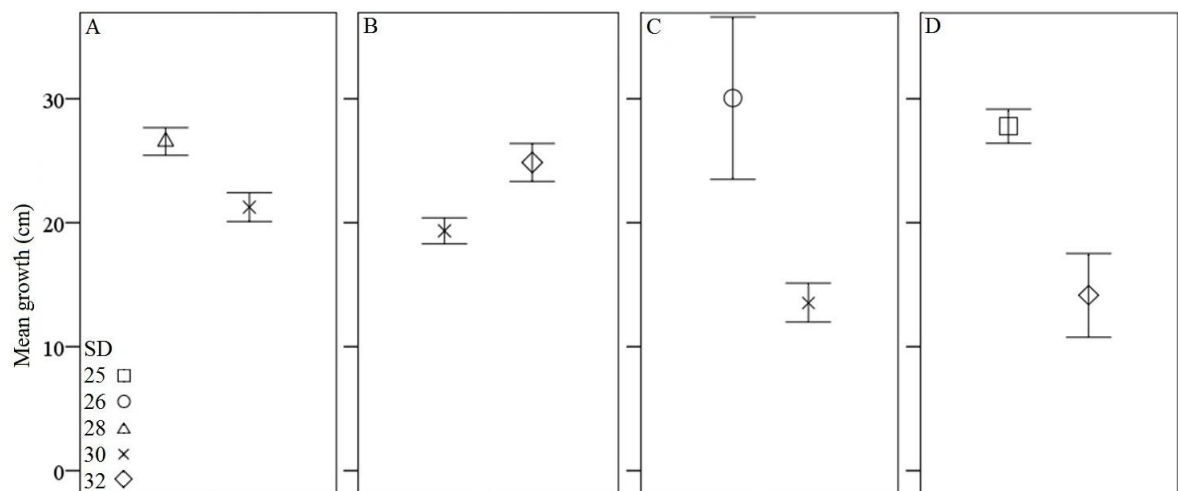
Figure 5. Spatial differences (Figures A, B, C = TukeyHSD, p<0.05; D = t-test, p<0.05) in the growth of Baltic salmon between the International Council for the Exploration of the Sea (ICES) subdivisions (SDs) when studied years were analysed separately. The symbol in the middle of the vertical bars shows the mean and bars ±1 SE. Figure A) The I SGS of wild salmon in 2008, B) The I SGS of reared salmon in 1991, C) The II SGS of reared salmon in 1991 and D) The II SGS of reared salmon in 2009.

3.2. Temporal growth differences

An increasing trend in the growth of wild salmon during I SGS was seen throughout the study period (linear regression, p<0.001) (Figure 6). A similar trend was seen with reared salmon at the beginning of the study period lasting approximately until mid-1990s (linear regression, p<0.001). Also an increasing trend in the growth of both stocks during II SGS was observed (linear regression, p<0.001).
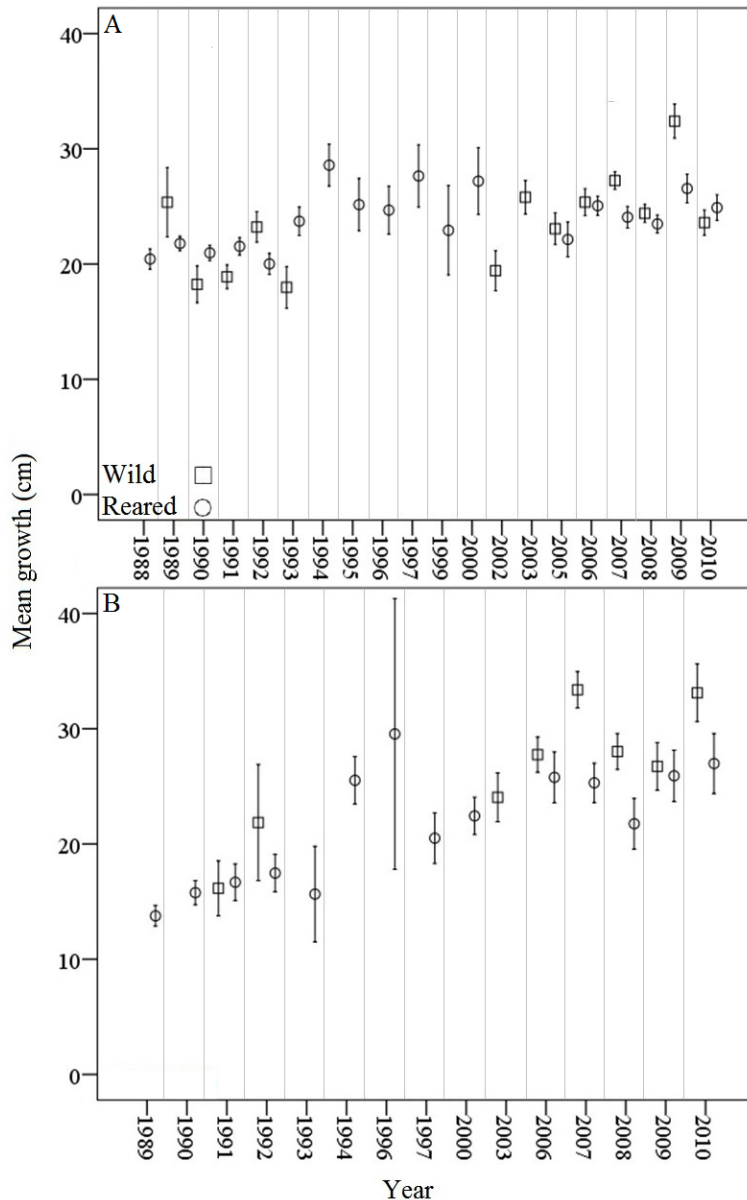
Figure 6. The growth of wild and reared Baltic salmon in studied years during first (A) and second (B) sea growth season. The symbol in the middle of the vertical bars shows the mean and the bars ±1 SE.

When growth data was compared between years in all studied SDs separately differences in the growth of wild salmon during I SGS were detected in SDs 25 (ANOVA$_{4.632, 128}$, p<0.001) and 26 (ANOVA$_{3.482, 26}$, p<0.05) (Figure 7). The growth of reared salmon during I SGS differed temporally in SDs 25 (ANOVA$_{2.047, 156}$, p<0.05), 30 (ANOVA$_{1.847, 131}$, p=0.059) and 32 (ANOVA$_{1.789, 208}$, p<0.05), though in SD30 ANOVA only bordered significant while pairwise comparison detected significant differences.
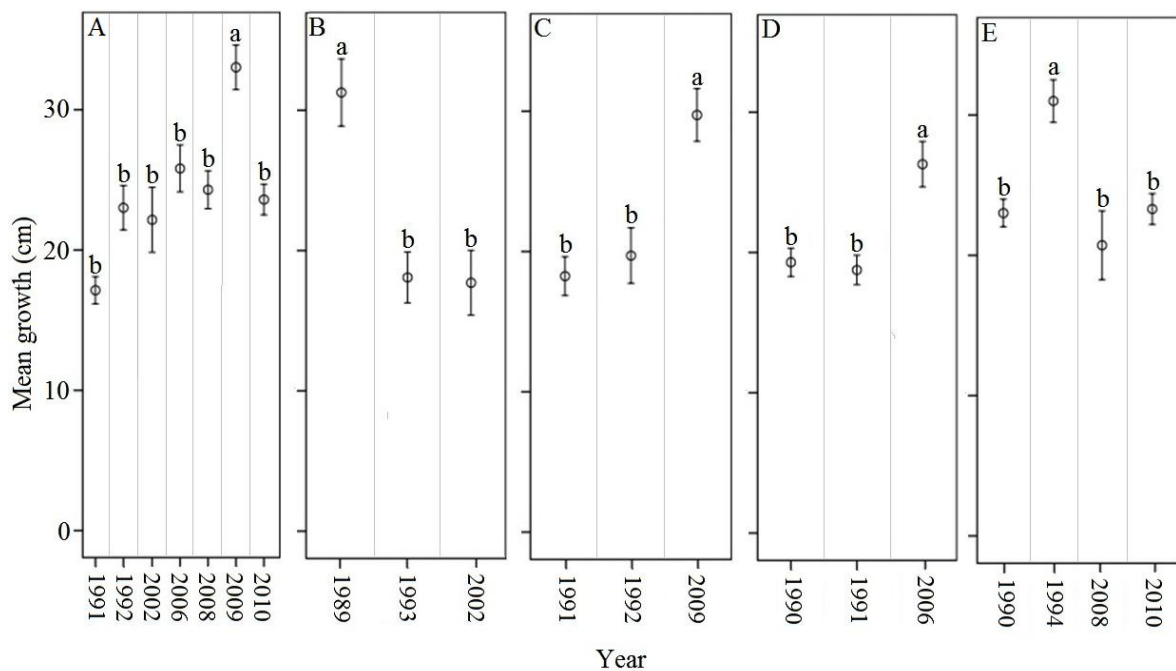
Figure 7. Significant temporal differences (Figures A, D & E = TukeyHSD, $p<0.05$; B & C = LSD, $p<0.05$) in the growth of Baltic salmon first sea growth season when the studied International Council for the Exploration of the Sea (ICES) subdivisions (SDs) were analysed separately. The symbol in the middle of the vertical bars shows the mean and bars ± 1 SE. The growths of those years that do not differ have error bars marked with the same letter. Figure A) Wild salmon in SD25, B) Wild salmon in SD26, C) Reared salmon in SD25, D) Reared salmon in SD30 and E) Reared salmon in SD32.

During II SGS the growth of wild salmon had significant temporal differences in SD30 (ANOVA$_{8.102, 9}$, $p<0.05$) and reared salmon in SDs 25 (ANOVA$_{4.737, 47}$, $p<0.05$) and 32 (ANOVA$_{2.912, 22}$, $p<0.05$) (Figure 8).
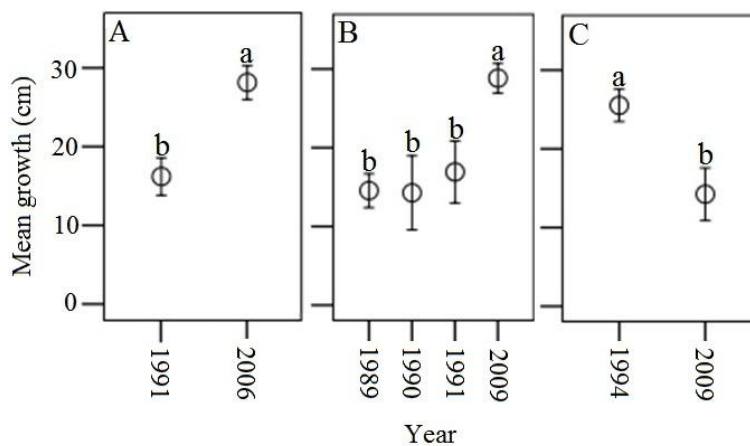
Figure 8. Significant temporal differences (TukeyHSD, $p<0.05$) in the growth of Baltic salmon during second sea growth season when the studied International Council for the Exploration of the Sea (ICES) subdivisions (SDs) were analysed separately. The symbol in the middle of the vertical bars shows the mean and bars ± 1 SE. The growths of those years that do not differ significantly have error bars marked with the same letter. Figure A) Wild salmon in SD30, B) Reared salmon in SD25 and C) Reared salmon in SD32.

3.3. Growth differences of wild and reared salmon

The overall growth of wild salmon was significantly faster compared to reared during I (t-test$_{3.542, 920}$, p<0.05) and II (t-test$_{7.469, 244}$, p<0.05) SGS (Figure 9).
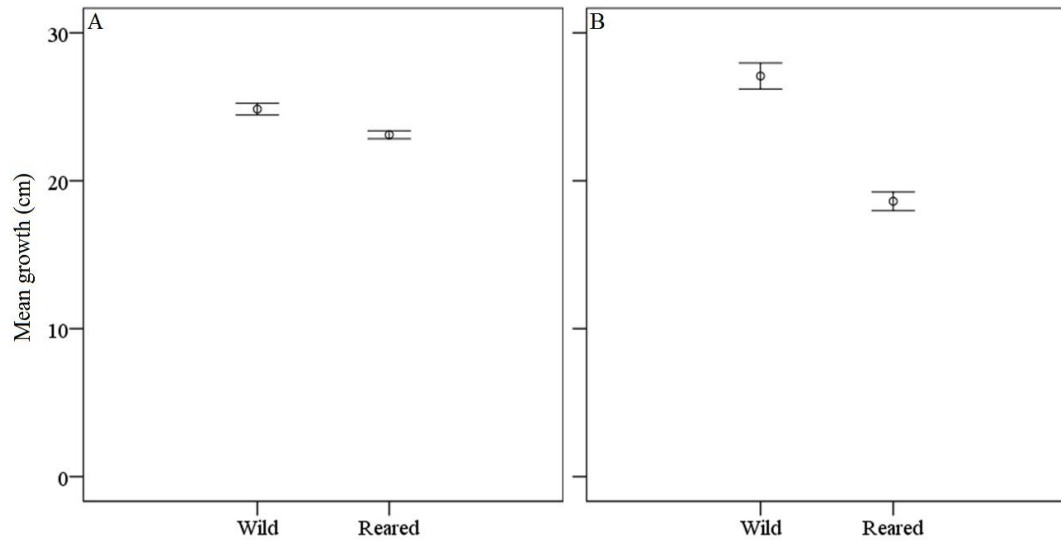
Figure 9. Differences (t-test, p<0.05) between the growth of wild and reared Baltic salmon during first (A) and second (B) sea growth season. The symbol in the middle of the vertical bars shows the mean and bars ±1 SE.

When the growth of wild and reared salmon was compared separately in studied SDs it was observed that during I SGS wild salmon grew faster compared to reared in SDs 25 (t-test$_{2.182, 284}$, p<0.05) and 28 (t-test$_{3.869, 162}$, p<0.05) (Figure 10) and during II SGS in SDs 25 (t-test$_{3.526, 89}$, p<0.05), 28 (t-test$_{5.029, 38}$, p<0.05) and 30 (t-test$_{3.116, 63}$, p<0.05).

Figure 10. The growth of wild and reared Baltic salmon during first (A) and second (B) sea growth season in the International Council for the Exploration of the Sea (ICES) subdivisions (SDs). The symbol in the middle of the vertical bars shows the mean and bars ±1 SE. The growth of those wild and reared salmon in the same SD that do not differ significantly (t-test, p>0.05) have error bars marked with the same letter.

When the growth of wild and reared salmon was compared in all studied years and SDs separately it was observed that wild salmon grew faster during I SGS in 2007 in SD25 (t-test$_{2.227,40}$, $p<0.05$) (Figure 10) and in 2008 in SD28 (t-test$_{2.204, 26}$, $p<0.05$). During II SGS wild salmon grew faster in 2008 in SD25 (t-test$_{2.632, 13}$, $p<0.05$).

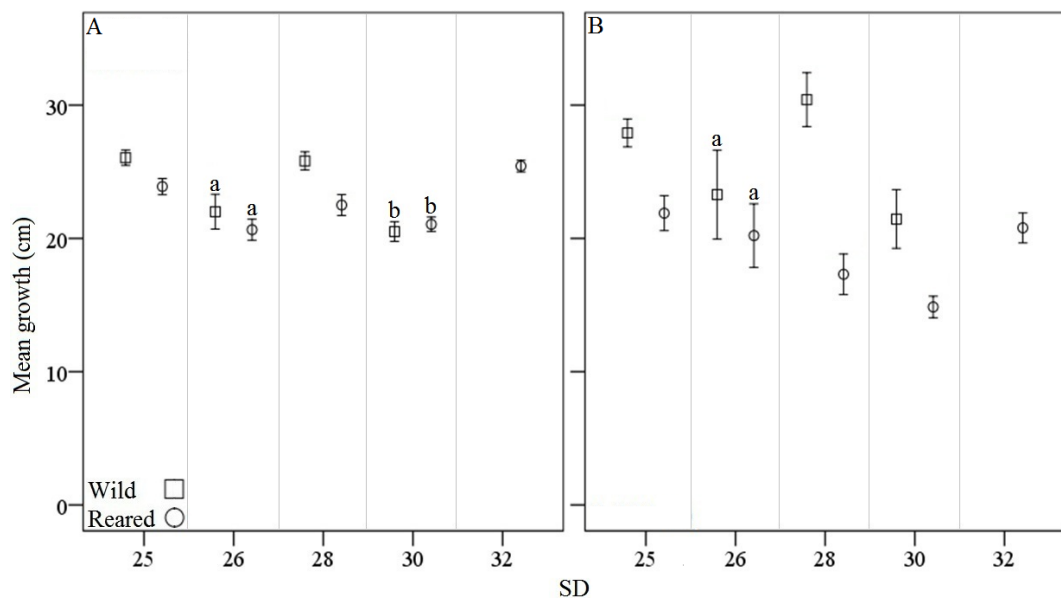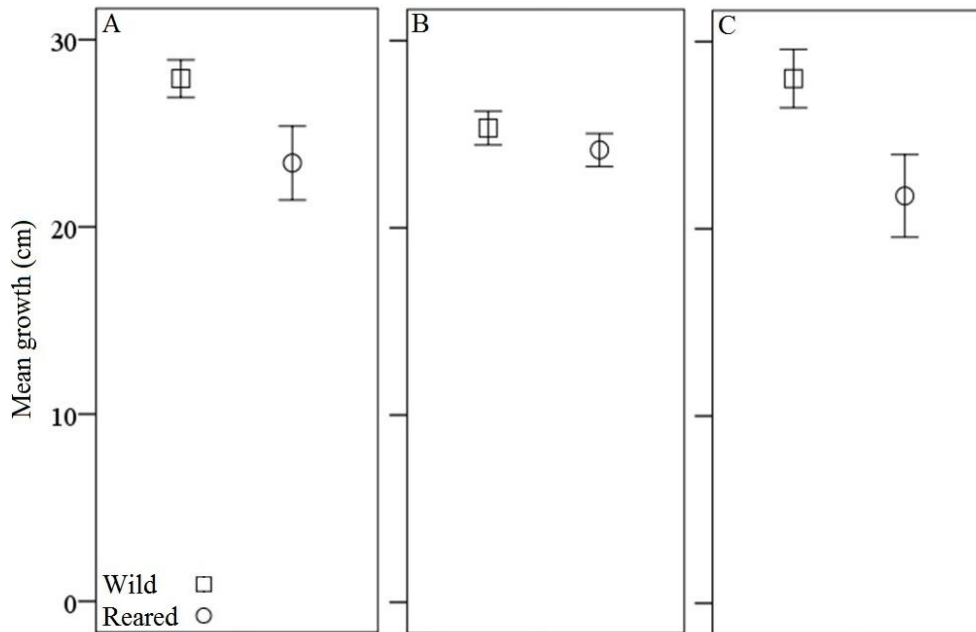Figure 10. Significant differences (t-test, $p<0.05$) between the growth of wild and reared Baltic salmon when studied years and the International Council for the Exploration of the Sea (ICES) subdivisions (SDs) were analysed separately. The symbol in the middle of the vertical bars shows the mean and bars ±1 SE. Figure A) The growth of I SGS in 2007 in SD25, B) The growth of I SGS in 2008 in SD28 and C) The growth of II SGS in 2008 in SD25.

3.4. Effect of temperature, prey abundance and trophic position on growth

An association between higher temperature and decreased growth during I SGS was found in SD32 (partial correlation, $r=-0.299$, $p<0.001$) (Figure 11). Higher temperature was also associated with decreased growth during II SGS in SD25 (partial correlation, $r=-0.578$, $p<0.05$). When describing the association between temperature and growth during I SGS a 4th order polynomial trend line had the highest coefficient of determination and according to it fastest growth took place at approximately 4 ^{o}C temperature. Since that is not true according to several authors (Elliott & Hurley 1997, Friedland et al. 2000, Holm et al. 2000, Iwama 1996) a quadratic polynomial trend line with the next highest coefficient of determination was selected to describe the association between temperature and growth during I SGS. Quadratic polynomial trend line was also used to describe the association between temperature and growth during II SGS since it had the highest coefficient of determination.
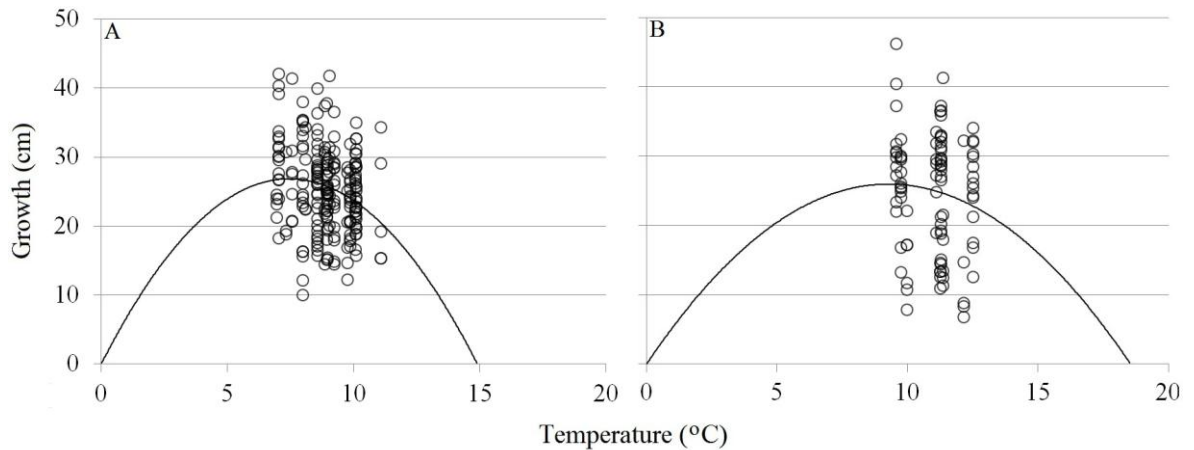
Figure 11. The significant relationships (partial correlation, p<0.05) between the growth of salmon and water temperature in the International Council for the Exploration of the Sea (ICES) subdivision 32 during first sea growth season (A) and 25 during second sea growth season (B). The circles represent individual fish.

No relationship between the growth of salmon and prey species abundance was found in any of the studied SDs (partial correlation, p>0.05). No associations were found between TP and the growth of salmon during I SGS, but higher TP was associated with increased growth during II SGS in SD25 (partial correlation, r=0.631, p<0.05) (Figure 12).
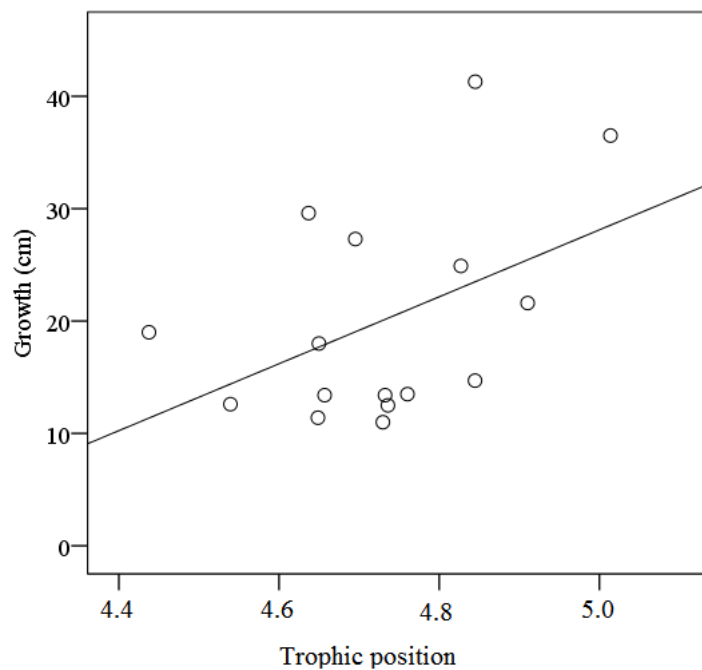

Figure 12. The significant relationship (partial correlation, p<0.05) between the trophic position and growth of salmon during second sea growth season in subdivision 25 of the International Council for the Exploration of the Sea. The circles represent individual fish.

4. DISCUSSION

4.1. Spatio-temporal and origin related differences in growth

The overall annual growth of Atlantic salmon in the Baltic Sea has been increasing during the study period and the hypothesis that there are temporal growth differences was supported. The large temporal variation in the growth salmon observed in this this study was also described by Jensen et al. (2011). Drinkwater et al. (2003) stated that low frequency and high amplitude changes in the abundance of salmon populations are common. According Huusko & Hyvärinen (2012) variation in size has an association with the abundance of salmon thus it is possible that the faster growth observed in this study is associated with low abundance. Larsson (1984) noted that in 1930-1980 there was a decreasing trend in the growth of northern Baltic Sea river stocks but the results of this study show that growth has increased since 1988. This possibly implies that the habitat conditions of salmon in the Baltic Sea have improved. The Baltic Sea regime shift in the late 1980s and early 1990s when the ecosystem changed from cod (*Gadus morhua* L.) dominance to more sprat dominated ended in 2005 (Möllmann et al. 2009), might have partly caused the observed faster growth at those times and the rising growth trend. Unfortunately there were gaps in sample time series and consequently growth was not determined throughout the study period.

The hypothesis that Baltic salmon has spatial growth differences was partly supported, since the results indicated faster growth in the Main Basin and the Gulf of Finland compared to the Bothnian Sea. The observed faster growth in the Main Basin is in accordance with Christensen & Larsson (1979) and underlines the resources and habitat of the area. As post-smolts respond to migration cues they may be forced to swim against currents (Salminen et al. 1994) creating energy deficits as fish swim to avoid undesirable conditions (Friedland 1998, Kallio-Nyberg et al. 1999). The demanding migration (Jutila et al. 2003) might be one reason for the surprisingly slow growth in SD26, but why the same effect is not noted in other parts of the Main Basin is unclear. Alm (1934) found growth differences between river stocks small but consistent indicating a genetic origin in the variation of growth. Since the samples from SD26 originated from the same rivers as samples from SD25 the observed growth differences are probably not of genetic origin.

Salminen et al. (2001) stated that feeding conditions in the Bothnian Sea seem to differ from the southern areas of the Baltic Sea and the Gulf of Finland, which might have contributed to the observed slower growth in the Bothnian Sea. According to Larsson (1984) the productivity is lower in the Gulf of Bothnia because of the shorter growth season compared to the Main Basin. If conditions in the Bothnian Sea are unfavourable, wild salmon migrate further, but reared salmon instead could exhibit slower growth, with an inherited tendency to lower migratory activity (Salminen 1997). The fact that Salminen et al. (1994) and Kallio-Nyberg et al. (1999) noticed only a small proportion of salmon to spend their feeding migration in the Bothnian Sea might be because of the poor growth conditions observed in this study for both origins and SGSs there. Until 2006 slower growing Neva salmon were released in the Bothnian Sea (Salminen 1997, Helle et al. 2011) which might have contributed to the slower growth there. Also Salminen et al. (1995) detected better growth in the Gulf of Finland and stated that this could be because of the good feeding conditions in the area. The habitat conditions in the Gulf of Finland seem to be sufficient for reared salmon since all the salmon sampled from the Gulf of Finland were reared.

The results supported the hypothesis that the growth of wild and reared salmon differ since wild salmon was observed to grow faster. Reared salmon smolts were longer

compared to wild (t-test, p<0.05) (Appendix 1) which possibly affected the fact that the lengths of wild and reared salmon did not differ after I SGS (t-test, p>0.05) (Appendix 2), even though the overall growth of wild salmon during I SGS was higher compared to reared. The fact that the average length growth of smaller individual is usually faster compared to larger individual (Austreng et al. 1987, Wootton 1990) probably increases the growth of wild salmon during I SGS more compared to reared because of the smaller size of wild smolts observed in this study. However, also the larger smolt size of reared salmon is expected to increase growth, since larger size enables them to feed on larger prey when such is available (Keeley & Grant 2001) and there is an energetic advantage from feeding on larger prey (Kerr 1971).

Although only few relationships between length and growth were detected in this study and the effect of length on growth was not further considered, precise estimates of the relationship between length and growth could have made it possible to more accurately tell if the observed growth during a SGS was slow or fast when related to the length at the beginning of SGS in question. The growth during I SGS may in reality be larger than observed in this study since smolt lengths acquired in tagging experiments (Larsson 1984, Jokikokko et al. 2006) were smaller compared to the back-calculated smolt lengths in this study. This is possibly because back-calculation models may produce approximately 1.5 cm overestimated smolt lengths but often the error will be small in proportion to fish length (Heidarsson et al. 2006). Also smolt size is positively associated with survival (Jokikokko et al. 2006), thus larger smolts may have been selected in the study data.

Due to faster growth of wild salmon they were longer compared to reared after II SGS (t-test, p<0.05) (Appendix 3). Many studies have noted opposite results compared to this study and have attributed faster growth of reared salmon to domestication and adaptation to hatchery conditions (Gjederm 1979, Kallio-Nyberg & Koljonen 1997, Devlin et al. 1999, Frankham 2008, Vainikka et al. 2010). However, Jonsson et al. (2003) found the growth at sea to be similar for wild and reared salmon and Jonsson et al. (1996) reported wild salmon to grow better at sea.

If reared individuals have been subjected to unintended selection they may have greater potential for processing food, grow fast in favourable environments, but have higher routine costs of living (Millidine et al. 2009). Increases in metabolic demands may be compensated to some extent by an increase in food conversion, but most of the elevated growth must be met by increased nutritional intake (Jonsson & Björnsson 1994). If reared salmon have higher routine costs of living and thus increased nutrition requirements, in optimal circumstances they are able to outgrow their wild conspecifics, but wild conditions are often far from optimal. When climate, nutrition or some other factor is unsatisfactory for high growth, wild salmon are probably able to grow faster, as observed here. When growth is used as a proxy for survival (Friedland et al. 2000), it seems that wild salmon cope better in all studied SDs during their II SGS and in all but SD30 during I SGS.

4.2. Effect of temperature, prey abundance and diet on growth

The responses of biological systems to climate are diverse and likely to lead to changes in salmon populations, but it is difficult to interpret physical and biological correlations as they do not necessarily prove causality, though they may be used for initial exploratory purposes (Overland et al. 2010). Furthermore, Köster et al. (2005) stated that when statistical analyses reveal changes in the growth of salmon correlating with sea water temperature they do not necessarily indicate the underlying processes. Even when the effect of environmental variable on the physiology of salmon is known, it is difficult to evaluate the outcome at population level (MacKenzie & Köster 2004) and detecting the

responses of fish population to climate and other factors is difficult because of the very large number of influential factors.

The hypothesis that water temperature affects salmon growth was partly supported by the results since in the Gulf of Finland and the Main Basin growth was negatively related to water temperature. This is in contrast with several authors (Salminen et al. 1995, Kallio-Nyberg et al. 2004, Vainikka et al. 2010, Overland et al. 2010, Jensen et al. 2011) who reported increased growth, especially in northern populations, associated with increased water temperature. Since the late 1980s water temperature has risen in the Baltic Sea (Möllman et al. 2005) both in the surface (MacKenzie & Schiedek 2007) and deeper layers (MacKenzie & Köster 2004). It seems that the increased water temperature may chance the habitat less favourable for salmon growth. Regional climate types account for low frequency and high amplitude changes in population abundance which are typically similar for closely situated populations (Drinkwater et al. 2003, Overland et al. 2010, Jensen et al. 2011, Huusko & Hyvärinen 2012). This may be partly responsible for the limited significant spatial growth differences observed when the studied years were analysed separately.

Also the positive effect of warming water temperature via prey fish abundance on salmon growth is expected, since these factors are positively related (Margonski et al 2010). Kallio-Nyberg et al. (2011) reported larger smolts to benefit from warm summer months since different food items are available for small and large individuals. Though the back-calculated mean length of reared smolts was larger compared to wild, the faster growth of neither stock was associated with increased water temperature. During the warmest summers moths when salmon seeks colder and deeper water layers (Alm 1958, Holm et al. 2004) it is possible that acquiring prey may be more difficult since salmon is dependent on vision when hunting (Boeuf & Le Bail 1999).

As hypothesized the trophic position of salmon, and consequently diet preference, was associated with growth but only during II SGS in the Main Basin. Since Hansson et al. (2001) observed the diet of salmon to be dominated by sprat in the Main Basin, increased growth associated with feeding on higher TP is presumably due to increase in the normally low herring and three-spined stickleback proportion in the diet. Thus it seems that in the Main Basin area the growth of salmon is enhanced when sprat based diet is complemented with other prey species. The lack of associations between the growth and TP of salmon in other parts of the Baltic Sea possibly implies that often the growth of an individual is not affected by its diet preference and that whether salmon feeds on herring, sprat or three-spined stickleback, it does not affect growth.

Use of tissue stable isotope composition as a proxy for diet requires that the isotopic composition of salmon diet is constant (Trueman et al. 2005). The assumption that the δ^{15}N ratios of cladocerans and consequently sprat, herring and three-spined stickleback were stable throughout the study period could have biased the results if slight changes in δ^{15}N baseline occurred. It is unclear if the observed decreasing trend in salmon TP (linear regression, $p<0.05$) took place because of chance in diet or baseline δ^{15}N.

The hypothesis that prey stock abundance affects salmon growth was not supported by the results since no relationship between salmon growth and prey stock abundance was found. The results were partly supported by Kallio-Nyberg et al. (2004) who described that larger salmon in the Main Basin are not affected by fluctuations in sprat and herring abundance. Also according to Karlsson et al. (1999) in some years sprat and herring biomass in the Main Basin explains the mass of salmon spawners. In contrast to the observations made in this study Kallio-Nyberg et al. (2011) stated that high herring

abundance increases the growth of salmon in the Bothnian Sea. Salminen et al. (2001) reported that herring is probably the key factor influencing salmon stock fluctuations and growth in the Bothnian Sea. Also Kallio-Nyberg et al. (2004) observed the prey abundance in the Bothnian Sea to be important for the success of salmon stocks migrating from the northern Gulf of Bothnia. Though most of these migrants are represented in the Main Basin samples (Christensen & Larsson 1979). It seems that salmon in the Baltic Sea are able to find sufficient sustenance even during years of low prey stocks so that prey stock fluctuations do not affect the growth of salmon.

5. CONCLUSIONS

The Main Basin seems to be providing the fastest growth for both wild and reared salmon stocks whereas growth is slowest in the Bothnian Sea. The general temporal growth trend has been increasing possibly because the habitat conditions of salmon in the Baltic Sea are sufficient or even improving to enable efficient growth. Since the growth of wild salmon is faster compared to reared it seems that they are better adapted to life in the Baltic Sea.

If sea water temperature continues to rise in the future the growth of some salmon populations may become slower. Generally the growth of salmon is not affected by diet preference or prey stock abundance but in the Main Basin availability of other prey species in addition to sprat may positively affect growth.

ACKNOWLEDGEMENTS

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APPENDIX

Appendix 1. Back-calculated mean lengths (cm) ±S.E. of Atlantic salmon smolts in studied years and International Council for the Exploration of the Sea (ICES) subdivisions (SDs). "W" equals wild, "R" reared. The number of samples is indicated in the parenthesis.

Year	SD25 W	SD25 R	SD26 W	SD26 R	SD28 W	SD28 R	SD30 W	SD30 R	SD32 R
1987		23.7±2.2(5)		22.8±1.3(5)		22.8±2.0(4)		22.5±1.8(7)	29.6±1.2(4)
1988		23.0±1.0(11)	27.6±0.4(2)	21.9±1.4(12)	27.7±0.8(4)	25.1±0.8(20)		23.1±0.6(27)	29.2±1.1(14)
1989	20.9±0.8(2)	21.9±1.6(9)		21.3±1.2(8)		24.6±0.6(15)	22.0±2.0(5)	21.0±0.6(23)	27.7±0.8(17)
1990	22.2±3.9(3)	22.7±0.8(7)		22.5±1.3(10)	24.7±1.3(5)	22.8±1.0(15)	24.1±0.7(8)	21.6±0.4(22)	27.9±0.8(17)
1991	22.7±1.3(7)	25.0±1.1(11)	21.5±0.8(9)	22.0±1.1(11)	24.2±0.5(5)	23.5±1.1(3)		24.6±0.8(23)	25.1±2.2(5)
1992		26.0±0.9(4)	21.7±0.8(5)	21.9±1.0(14)		22.7±1.8(3)		26.1±0.6(2)	27.9±0.8(19)
1993		29.0±3.0(3)		23.7±2.2(4)				24.6±0.1(2)	27.5±0.8(16)
1994				28.2±2.5(3)		23.7±1.7(2)			28.5±1.2(7)
1995		26.4±2.8(3)		25.8±1.3(2)					26.1±2.2(7)
1996									26.0±1.3(7)
1998									26.9±0.5(3)
1999									30.5±1.5(4)
2001	22.5±1.0(4)		23.0±1.4(6)						
2002	20.0±1.0(10)		19.1±1.3(5)						
2004	24.4±1.0(6)	26.3±1.2(5)			24.5±0.4(3)		23.8±1.0(4)		
2005	22.4±0.6(18)	27.7±0.8(20)			25.0±0.9(7)	24.2±3.0(2)	23.8±1.4(2)	31.2±1.3(12)	28.4±0.6(31)
2006	22.4±0.4(27)	28.2±0.9(15)			22.8±0.3(33)	26.1±2.1(15)	25.0±1.4(3)	25.2±4.2(3)	24.2±0.6(21)
2007	23.0±0.6(20)	27.9±0.7(37)			23.3±0.8(17)	25.4±1.2(11)	22.5±0.9(11)	25.9±0.7(8)	22.9±1.5(7)
2008	21.7±0.7(17)	26.1±0.8(11)					21.9±3.1(2)	30.6±0.9(3)	25.0±1.0(15)
2009	21.3±0.6(15)	25.4±1.0(16)							22.6±1.2(15)

Appendix 2. Back-calculated mean length (cm) ±S.E. of Atlantic salmon after first sea growth season in studied years and International Council for the Exploration of the Sea (ICES) subdivisions (SDs). "W" equals wild, "R" reared. The number of samples is indicated in the parenthesis.

Year	SD25 W	SD25 R	SD26 W	SD26 R	SD28 W	SD28 R	SD30 W	SD30 R	SD32 R
1988		44.4±2.5(5)		39.7±1.0(5)		45.0±3.4(4)		42.8±2.4(7)	52.8±1.7(4)
1989		44.8±2.1(11)	58.9±2.8(2)	43.1±2.7(12)	52.5±1.4(4)	46.4±1.7(20)		43.8±1.6(27)	53.9±1.6(14)
1990	39.7±2.8(2)	42.7±3.6(9)		41.8±2.0(8)		46.1±2.1(15)	40.1±1.8(5)	40.5±1.3(23)	50.2±1.5(17)
1991	39.3±4.2(3)	40.7±1.6(7)		46.0±2.6(10)	44.2±1.5(5)	44.2±2.6(15)	43.3±1.5(8)	41.0±1.1(22)	52.4±2.1(17)
1992	45.7±2.5(7)	44.5±2.6(11)	45.1±2.7(9)	41.4±3.5(11)	48.5±2.6(5)	45.6±5.4(3)		44.4±1.3(23)	47.7±5.9(5)
1993		49.9±4.4(4)	39.7±3.2(5)	43.4±2.9(14)		43.5±2.8(3)		48.9±2.0(2)	53.8±2.5(19)
1994		59.4±12.3(3)		42.6±3.8(4)				50.6±13.2(2)	58.5±1.7(16)
1995				44.5±5.8(3)		50.8±3.4(2)			56.9±3.0(7)
1996		45.4±5.1(3)		51.1±5.0(2)					53.0±4.1(7)
1997									53.6±3.6(7)
1999									49.8±4.4(3)
2000									57.7±4.2(4)
2002	44.6±2.7(4)		40.6±3.4(6)						
2003	45.5±2.5(10)		45.2±1.4(5)						
2005	48.8±2.6(6)	48.5±1.9(5)			47.5±2.9(3)		44.9±1.3(4)		
2006	48.2±1.8(18)	51.4±2.0(20)			50.4±1.7(7)	45.6±6.7(2)	45.2±2.8(2)	57.5±2.5(12)	54.1±1.2(31)
2007	50.3±1.1(27)	51.6±2.0(15)			50.2±1.1(33)	50.6±2.7(14)	42.2±5.2(3)	44.8±4.5(3)	49.3±1.2(21)
2008	47.3±1.5(20)	52.5±1.4(37)			49.8±1.6(17)	48.0±2.1(11)	43.9±1.6(11)	47.6±2.3(8)	43.2±2.2(8)
2009	54.7±1.7(17)	55.7±2.2(11)					49.1±1.8(2)	56.3±9.4(3)	49.5±1.4(15)
2010	45.0±1.1(15)	51.8±2.5(16)							45.9±1.8(15)

Appendix 3. Back-calculated mean length (cm) ±S.E. of Atlantic salmon after second sea growth season in studied years and International Council for the Exploration of the Sea (ICES) subdivisions (SDs). "W" equals wild, "R" reared. The number of samples is indicated in the parenthesis.

Year	SD25 W	SD25 R	SD26 W	SD26 R	SD28 W	SD28 R	SD30 W	SD30 R	SD32 R
1989		60.6±2.4(6)		51.5±2.0(5)		56.6±4.1(4)		55.2±3.5(7)	66.4±2.4(6)
1990		54.4±5.8(5)		58.4±4.0(8)		51.3±0.6(5)		56.0±2.2(17)	81.5±6.3(2)
1991		55.2±5.5(6)		70.0±9.3(4)		55.2±3.4(6)	55.2±3.6(4)	52.7±2.6(19)	
1992	63.3±12.8(3)	54.0±0.9(3)		63.5±17.2(2)		50.9±5.7(2)	58.5±3.4(2)	57.1±2.6(10)	
1993								54.0±5.6(2)	
1994									68.9±5.6(4)
1996				68.4±13.6(2)					
1997									60.6±2.4(2)
2000									72.2±5.6(3)
2003	69.8±3.3(4)		63.9±6.0(6)						
2006	74.1±3.4(6)	72.7±3.7(6)			79.7±4.9(3)		73.0±2.9(4)		
2007	83.5±5.1(3)				86.5±3.6(3)	70.9±5.0(2)			
2008	77.0±2.1(9)	68.5±4.1(6)			74.4±4.3(7)	67.1±4.8(8)			
2009	74.5±4.2(11)	74.3±3.0(12)							51.6±1.5(3)
2010	85.5±3.3(7)	84.3±5.2(4)							77.9±1.0(3)