Scale- and growth analysis of Atlantic salmon (*Salmo salar*) caught with a bag net near the River Mandalselva, on the Skagerrak coast.

Skjell- og vekstanalyser av atlantisk laks (*Salmo salar*) fanget med kilenot nær Mandalselva, på Skagerrakkysten.

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Preface

This is my master thesis in natural resource management at the Institute of Ecology and Natural Resource Management (INA) at the University of Life Sciences (UMB).

I would like to thank my supervisors professor Reidar Borgstrøm (INA) for good advices and support, professor Thrond Haugen (INA) for statistical help and his good mood, and professor Bror Jonsson (NINA) for guiding me to problems for discussion and sharing his profound knowledge about Atlantic salmon ecology.

Special thanks to my father, Ørnulf Haraldstad, for arousing my interest for fish research, for participating in the field and making me understand the importance of a data set running for several years. I would also like to thank my family and friends for support.

Thanks to Unni Hald for allowing me to fish with a bag net at Stumpodden, Atle Rustabakken (NIVA) and Arne Jensen (NINA) for teaching me Image pro express.

Last, but not least I would like to thank my wife Hilde Terese and son Tobias for reminding me that there may be more important things in life than a master thesis.

Summary

The abundance of wild Atlantic salmon (*Salmo salar*) has declined since the 1970s. The major reason for the recent decline appears to be increased marine mortality. Before 1970s, the native populations of Atlantic salmon were exterminated in several rivers in Southern Norway due to acidification, but in the last two decades many of these have been re-established, due to liming of the rivers.

The aim of this study was to analyse marine growth of Atlantic salmon caught with bag net near the River Mandalselva on the Skagerrak coast in the years 2004-2010. The sampled fish were maturing adults, most of which were probably returning to the River Mandalselva or other rivers in the same area. I determined age and growth of the fish from the scales. The rate of measurement error from the scale reading was low so one reading of each scale was conducted. The sampling error declined when more scales per fish were measured. In this study I measured four scales per fish, a number that both took into account requirements for precision and the amount of work. The number of circuli deposited in the scales and the inter-circuli distances were measured. The growth rate of Atlantic salmon during the first year at sea was positively correlated with the number of circuli present at the end of the same period. The number of circuli deposited after the winter-band was positively related to the catch date. The inter-circuli distances increased rapidly after the smolt had entered the sea, reaching a point of inflection at circuli number six. There was a significant year-to-year variation in the total number of circuli deposited during both first and second growth year at sea. There was a reduction in the peaks of maximum inter-circuli distances for the multi-sea-winter (MSW) Atlantic salmon first growth year at sea over the entire study period, 2001-2008. The total number of circuli deposited during the first growth year at sea differed significantly between the one-sea-winter (1SW) and MSW Atlantic salmon. 1SW fish deposited a higher number of circuli than the MSW fishes.

The observed variations in growth while at sea were probably related to variation in temperature that acted directly on fish growth by affecting physical processes or indirectly by affecting changes in the ecosystem. Findings in this study highlight the importance of considering both circuli number and inter-circuli distances when studying Atlantic salmon growth rather than to solely rely on inter-circuli distances.

Sammendrag

Forekomsten av atlantisk laks (*Salmo salar*) har vært nedadgående siden 1970 tallet. Hovedårsaken til denne nedgangen synes å være økt dødelighet på laksen i havet. I elver i Sør-Norge har mange populasjoner av atlantisk laks blitt utryddet på grunn av sur nedbør. Nye laksebestander er etablert i flere av disse elvene som resultat av kalking av elvevannet, naturlig innvandring av laks fra havet og utsettinger av laks fra naboelver.

Målet med dette studiet var å analysere sjøveksten til atlantisk laks fanget med kilenot nær Mandalselva på Skagerrakkysten i årene 2004-2010. Det innsamlede materialet bestod av kjønnsmoden laks som mest sannsynlig var på gytevandring mot Mandalselva, eller andre elver i området. Alder og vekst på fisken ble bestemt ved skjellanalyser. Målefeilen på enkeltskjell var lav, slik at kun en avlesning per skjell ble gjennomført. Målefeil på enkeltfisk avtok ettersom flere skjell per fisk ble målt. Fire skjell fra hver laks ble målt. Skjellantallet ble bestemt ut fra krav til nøyaktighet og arbeidsmengde. Antall circuli som var avsatt i skjellene og avstandene mellom circuli ble målt. Vekstraten til atlantisk laks første året i sjøen var positivt korrelert med antall circuli dette året. Antall circuli avsatt etter vintersonen var positivt korrelert med fangstdato. Avstanden mellom circuli økte raskt etter at smolten svømte ut i sjøen og nådde et vendepunkt etter circuli nummer seks. Årsvariasjonen i det totale antallet circuli avsatt i både første og andre år i sjøen i tidsperioden 2001-2009 var signifikant forskjellig. Det var en reduksjon i maksimum circuliavstander for flersjøvinter fisk det første året i sjøen for alle årene 2001-2008. Det totale antallet circuli avsatt første året i sjøen var signifikant høyere i skjellene til ensjøvinterfisk enn i skjellene til flersjøvinterfisk.

Den observerte vekstvariasjonen i de ulike sjøårene er mest sannsynlig relatert til variasjoner i temperatur. Dette kan virke direkte på fisken ved å påvirke fysiske prosesser eller indirekte ved å føre til endringer i økosystemet av betydning for næringsopptaket. Resultater i denne studien belyser viktigheten av å ta hensyn til både circuliantallet og circuliavstandene ved undersøkelser av veksten til Atlantisk laks, isteden for å stole fullt ut på circuliavstandene alene.

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1. Introduction

The Atlantic salmon (*Salmo salar*) is anadromous, meaning that the species spawn in fresh water, but perform most of their growth in the ocean (Jonsson & Jonsson 2003). The species occurs in temperate and sub-Arctic regions of the North Atlantic Ocean (Klemetsen et al. 2003). The juveniles (parr) spend one to eight years in freshwater before migrating to the sea (Klemetsen et al. 2003). Depending on age at maturity, Atlantic salmon spend one to four (five) years in the ocean before they return with high precision to their home river to spawn (Jonsson et al. 2003). Some individuals die after spawning, but a considerable number may survive and return to the ocean, and thereafter the survivors may spawn for a second time (Jonsson et al. 1991; Fleming 1996). Some male parr attain maturity and spawn together with the anadromous adults (Jones & Ball 1954). In some populations of Atlantic salmon the entire life cycle is completed in fresh water. This is more common in North American than in European rivers (Klemetsen et al. 2003).

The abundance of wild Atlantic salmon has declined since the 1970s (Klemetsen et al. 2003; Jonsson & Jonsson 2004; Annon 2009; Friedland et al. 2009a). Some of this decline may be due to degradation of freshwater habitats (Denschès et al. 2007; Smokorowski & Pratt 2007), excessive rates of exploitation (Jensen et al. 1999), the increase and spreading of parasites such as sea lice (chiefly *Lepeophtheirus salmonis* but also *Caligus elongatus*) and the monogenean *Gyrodactylus salaris* (Johnsen et al. 2008), and possibly also negative effects of escaped farmed Atlantic salmon due to ecological competition, genetic introgression and the spreading of contagious diseases (Jensen et al. 1999; Skaala et al. 2006; Hindar 2007). In parts of Southern Norway, the native populations of Atlantic salmon were exterminated due to acidification during the last century. New populations have been established in many of these rivers due to liming (Haraldstad & Hesthagen 2003; Hesthagen et al. 2011). The strategy employed to re-establish stocks after liming has ranged from natural spawning of strayers, to supplementary stockings of hatchery-reared eggs and fish from donor fish in nearby rivers. These re-established populations contribute significantly to the Atlantic salmon fishery in Norway; estimates being 11-12 % of the total annual rod catches of adult salmon in Norwegian rivers (Hesthagen et al. 2011). However, a major reason for the recent decline in Atlantic salmon appears to be increased marine mortality (Jonsson & Jonsson 2004; Friedland et al. 2009a). In the River Imsa population, marine mortality of Atlantic salmon seems to have doubled between 1980 and 2000 (Jonsson & Jonsson 2004). Furthermore, studies have linked variation in sea-surface temperature (SST) to survival of post-smolts (Friedland et al. 1993; Friedland et al. 2000; Friedland et al. 2005; McCarthy et al. 2008; Todd et al. 2008).

As the fish scales increase in length, circuli is deposited at the scale margin (Dahl 1910). Therefore, inter-circuli distance is a potential valuable tool for comparing growth rates of fish (Fisher & Pearcy 1990). Scale circuli formation rate and inter-circuli distances have been found positively correlated with the growth rate of coho salmon (*Oncorhynchus kisutch*) (Fisher & Pearcy 1990; Fisher & Pearcy 2005), pink salmon (*Oncorhynchus gorbuscha*) (Pearson 1966) and sockey salmon (*Oncorhynchus nerka*) (Bilton & Robins 1971a; Bilton & Robins 1971b). Likewise, the number of circuli and inter-circuli distances of Atlantic salmon scales may reflect the variation in growth rate during the years at sea (Peyronnet et al. 2007). Hence, the growth rate during the first year at sea may correlate with the number of circuli deposited in the first sea annulus of the scale, and the number of circuli after the winter-band may depend on the catch date the following summer.

Smolting and migration from freshwater to saltwater is a critical phase for the survival of the smolts (Handeland et al. 1996), partly because this transformation from fresh water to salt water tolerance is energy demanding (Sheridan 1989; Usher et al. 1991; Handeland et al. 1996), and thus probably affects the growth rate. Low growth rate during a period of low food consumption, followed by a period with excessive growth, called compensatory growth (Arendt 1997), is well documented for Atlantic salmon (Mortensen & Damsgard 1993; Nicieza & Metcalfe 1997; Friedland et al. 2009b). This is demonstrated in a study by Nicieza and Metcalfe (1997), who manipulated the growth rate in a laboratory by either lowering temperature or reducing food availability for two groups of juvenile Atlantic salmon. They found that both groups exhibited compensatory growth after the manipulation, compared with a control group.

After entering seawater, Atlantic salmon post-smolts from Norwegian rivers appear to follow the North Atlantic Current before they eventually turn and migrate out into the open North Atlantic Ocean (Klemetsen et al. 2003). The period of sea entrance and the following month at sea have been considered the time with the highest marine mortality in Atlantic salmon (Friedland et al. 1993; Jonsson et al. 2003; McCarthy et al. 2008). The migration to sea is coinciding with the SST at eight degrees along the Norwegian coast (Hvidsten et al. 1998). Since spring temperature is higher in the southern part of Norway, migration starts earlier here than further north. According to Handeland et al. (2003), an optimal temperature for post-smolt growth is ca 13° C, but will probably decrease with increasing size of the fish (Morita et al. 2010). The post-smolts do not have the same capacity to swim out of areas with unfavourable conditions, in contrast to the adult salmon (Jonsson et al. 1993). Consequently annual variations in temperature and food supply may be decisive for growth and survival of the post-smolt (Friedland et al. 2000). Hvidsten et al. (2009) documented a positive correlation between seawater temperature (SST) at sea entry of the smolts, and the number of returning adult Atlantic salmon from the same cohort. Temperature could act on fish growth directly by affecting physical process or indirectly by affecting changes in the ecosystem (Friedland et al. 2000; Hvidsten et al. 2009). Indirect effects of temperature would include conditions that impact the quality or quantity of food or other aspects of the environment (Friedland et al. 2000). Temperature changes could result in changes in primary- and secondary production, changes in food webs and thereby shifts in predator pressure onto post-smolts and prey availability for post-smolts during their first year at sea. McCarthy et al. (2008) hypothesized that cohort size is probably determined by the growth in month four and five after sea entrance. Another hypothesis suggests that there might be a density-dependent mortality for post-smolts in the coastal areas outside the river mouth, as may be the case in the Miramichi River (Friedland et al. 2009b). These authors found a negative correlation between the size of the smolt cohort and return rate of adults. Their scale analysis suggested a bottleneck for post-smolt survival in week five to seven after entering the Gulf of St. Lawrence. However, there is a general view that Atlantic salmon growth rate at sea is density-independent (Jonsson et al. 1998). Number of adult Atlantic salmon has been found to increase linearly with number of seaward migrating smolts. Probably, the abundance of suitable prey species in the ocean is very high compared to number of Atlantic salmon at sea (B. Jonsson pers comm.).

Age at maturity varies among years within populations (Jonsson et al. 1991). Atlantic salmon maturing after one winter at sea (1SW) range from 1-3 kg in total body mass. Those maturing as two-sea-winter (2SW) fish are usually 4-7 kg, whereas three-sea-winter (3SW) fish usually weigh above 7 kg (Jonsson et al. 1991). Age at maturation may be affected by growth rate during their first year at sea (Hutchings and Jones 1998; Jonsson & Jonsson 1993; Jonsson et al. 2003), heritability for age at sexual maturity (Gjerde et al. 1994) and discharge volume in the home river (Jonsson et al. 1991). In small rivers where the mean flow rate is less than 40 m^3, there is a positive correlation between water flow and mean size and age at maturity (Jonsson et al. 1991).

In the present study I examined the growth of Atlantic salmon caught in a bag net in the coastal waters in Mannefjorden, the southernmost fjord in Norway. The fish were maturing adults, and the majority of them were probably on their return to the local River Mandalselva. My goal was to answer the following questions: How high was the measurement and sampling error from the scale readings? Was the growth rate positively correlated with circuli formation rate? I used both inter-circuli distances and circuli number to study growth. Since the smolting is an energy demanding process, compensatory growth or a bottleneck for growth in the weeks after the smolts had entered seawater should be expected. Did the growth rate vary during the growth years at sea and between age groups? The growth variation may be linked to variation in sea-surface temperature (SST). Did the growth rate during the first year at sea determine the age at maturation?

2. Study area

2.1 Stumpodden

Stumpodden (58°01´N; 7°44´Ø) is a cape situated one-kilometre south-west of the outlet of the River Mandalselva (Fig 1), in the Mannefjorden, the southernmost fjord in Norway. Bag net fishing has probably been performed at Stumpodden since the 1870s (Lund, local fisherman, pers comm.). The seabed is mainly sand, with bedrock near the shore. Depth varies, dependent on water currents and wind conditions. Storms from south may change the depth several meters. The bag net was set 20 meters from the shore, at the end of a leader net attached to the shoreline. The depth at the bag net site may vary between three and five meters. The dominant current is westbound with the coastal current. The water discharge in the River Mandalselva affects temperature, salinity, turbidity and current conditions at Stumpodden. The surrounding fjord, Lindesnes- Mannefjorden, is a national protected salmon fjord which gives the local salmon population a protection against farming activity, intervention in the outlet of the river and fjord systems (Miljøverndepartementet 2007).

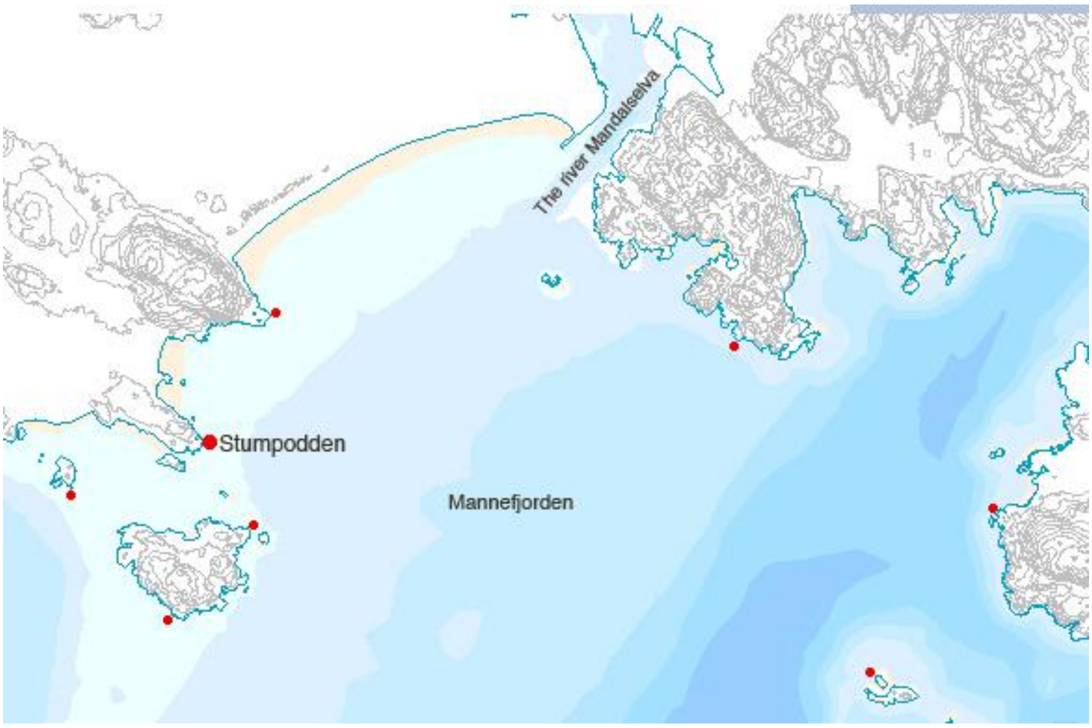

Fig 1 The fjord, Mannefjorden with the cape Stumpodden, the outlet of River Mandalselva and bag net localities (red dots). The shades of blue illustrate sea depth (Mandal kommune).

The bag net catches of Atlantic salmon in the Mandal municipality increased after liming programs were initiated in the River Mandalselva and other nearby rivers in the late 1990`s

(Haraldstad & Hesthagen 2003) (fig 2). The annual salmon coastal catch in Mandal municipality is today around five metric tonnes (Baklien, statistics Norway, pers comm.). The decline in annual catches during the last years is probably due to a reduction in the length of the fishing season, which is determined by the Norwegian environmental authorities. Several bag nets were located nearby Stumpodden.

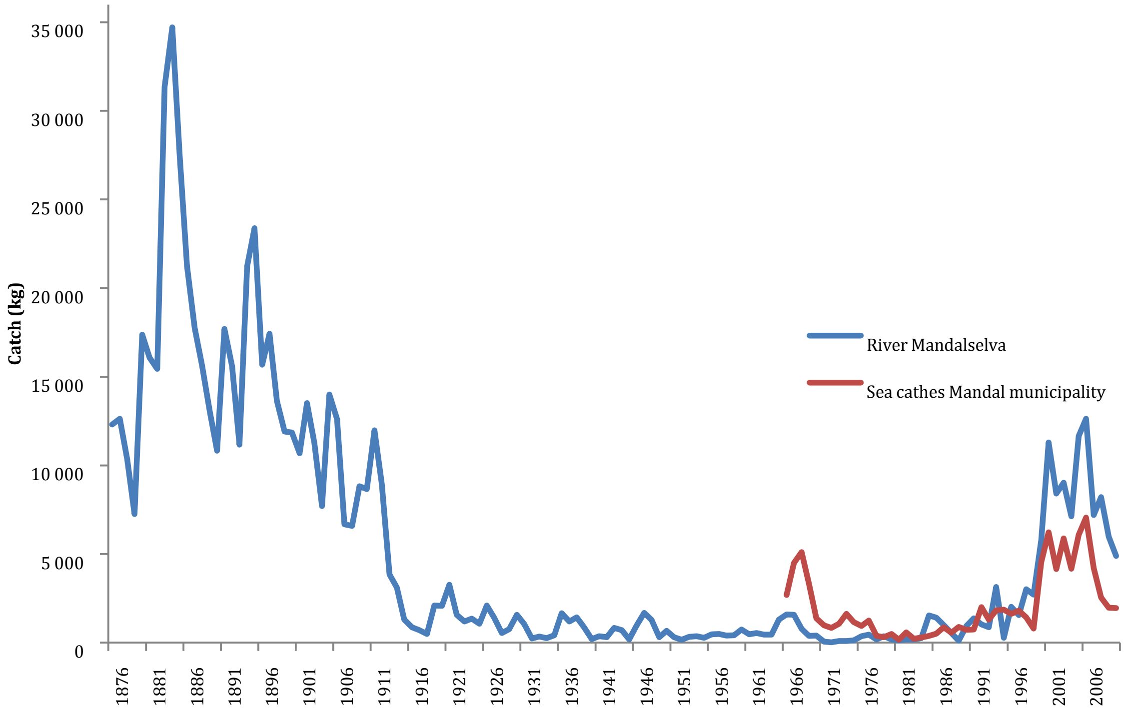

Fig 2 Annual catches in the River Mandalselva (blue line), and coastal fisheries within Mandal municipality (red line) (Statistics Norway 2011).

2.2 The River Mandalselva

The Atlantic salmon caught at Stumpodden were captured on their spawning migration. A large portion of this salmon is probably hatched in Mandalselva, and heading for their home river to spawn. Although high proportions of released smolt from the neighbouring River Audna and River Lygna were recaptured as mature fish in other rivers in southern Norway (Staurnes et al. 1996). Of the freshwater returns, 31,1% were reported in the River Mandalselva. The River Mandalselva flows through Aust-Agder and Vest-Agder counties (Fig 3). Atlantic salmon may ascend the lowermost 48 km of the river, from the outlet near Mandal city to Kavfossen in Bjelland (Haraldstad and Hesthagen 2003). The river catchment is 1809 km^2, with an average water discharge at 89 m^3 near the outlet. The watercourse is regulated for hydroelectric power production in six power plants. Two power plants are situated in the lowermost 48km were the Atlantic salmon might ascend. There are seven liming stations in the river catchment.

Fig 3 The River Mandalselva, with the largest lakes, tributaries, liming stations(Kalkdoserer) and power plants(Kraftverk). (Haraldstad og Hesthagen 2003).

In the early 15th century approximately 250 tonnes of Atlantic salmon may have been captured annually in the River Mandalselva (Haraldstad and Hesthagen 2003). According to Peder Claussøn Friis (Kvalheim 1959), 140 metric tonnes of Atlantic salmon were exported annually.

Towards the end of the 19th century, the River Mandalselva was one of the best salmon rivers in Norway (Haraldstad and Hesthagen 2003), and for several years it was the highest-ranked river on the official catch statistic. During the first 60/70 years of the 20th century, acidification eradicated Atlantic salmon from the river. However, a liming program that used calcium carbonate ($CaCO_3$) to neutralize acid water was initiated in 1997. The Atlantic salmon population increased rapidly after liming, apparently due to the spawning of large number of wild strayers, and today it supports a self-sustaining population of Atlantic salmon (Haraldstad & Hesthagen 2003; Hesthagen et al. 2011). The annual salmon catch in the River Mandalselva is now more than five tonnes (Fig 2).

In addition to anadromous Atlantic salmon and brown trout (*Salmo trutta*), the river supports populations of freshwater resident brown trout, freshwater resident Artic charr (*Salvelinus alpinus*), three-spined stickleback (*Gasterosteus aculeatus*), perch (*Perca fluviatilis*), European eel (*Anguilla anguilla*), introduced brook charr (*Salvelinus fontinalis*), introduced rudd (*Scardinius erythrophthalmus*) and introduced European minnow (*Phoxinus phoxinus*) (Haraldstad & Hesthagen 2003).

3. Materials and methods

3.1 Bag net

Bag nets were first used in Norwegian fjords and coastal areas in 1844 (Dahl 1929). This form of fixed fishing gear is the only legal form of caching Atlantic salmon at sea in this part of Norway (Lovdata 2010). A bag net consists of two main parts; a leader net and a trap (Shearer 1992b). There may be one or two traps located on each side of the leader net, named single- or double-headed bag net. The trap itself consists of one or two sequential funnels, with the innermost leading to a catch chamber. In this study I used a single-headed bag net with one funnel (Fig 4).

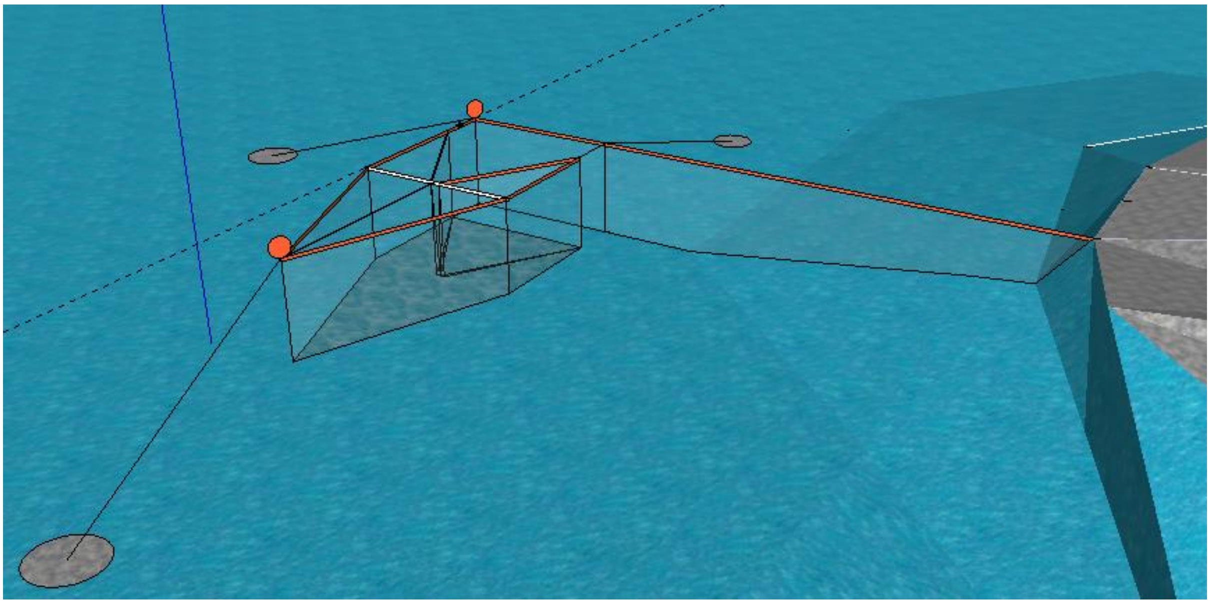

Fig 4 A Single-headed bag net with one funnel, attached to a leader-net that is moored to a post on the shoreline. The outer edge of the leader-net and trap is anchored on the seabed (grey circles). A series of floats (orange circles and lines) hold the trap and leader net in position.

Fish swimming parallel along the shore may be deflected and guided by the leader net towards a 30 cm opening in the trap. The mesh size of the leader net was 125 mm (bar-mesh) and it covered the whole water column. The net was moored to a post on a rock, and jutted perpendicularly to the shoreline. The outer end of the leader-net was anchored on the seabed. The trap was mounted in a right angle to the leader net, and was held in place by another anchor on the seabed. A bar that floated on the surface outstretched the trap. The trap was approximately 15 meters long, five meters wide and three meters deep, with 63 mm bar-mesh-size. A series of floats and weights held the trap and leader net in position.

Atlantic salmon were sampled during the fishing seasons 2004-2010. The Norwegian environmental authorities set regulations for the duration of the bag-net fishing period, which varied among years: During 2004-2008 the legal fishing period was from 1 June to 5 August, in 2008-2009 it was from 15 June to 20 July, and in 2010 from 20 June to 16 July. During these periods, it was allowed to fish from Monday 06.00 p.m. to Friday 06.00 p.m.

The bag net was emptied twice a day, in the morning and in the afternoon. Fish lengths (to nearest 0.5 cm) and wet weight (to nearest 100 grams) were recorded for all individuals. Scales were taken from the area above the lateral line, from the posterior edge of the dorsal fin to the anterior edge of the anal fin (Dannevig & Høst 1931), and stored dry in envelopes (Shearer 1992a). Sex was registered for all fish sampled in 2010.

3.2 Scale reading

Age and growth of the fish were determined by scale reading. Approximately 50 to 100 scales per individual were collected. Ten scales with small central plates were used for the analysis (Jonsson & Stenseth 1976). The scales were cleaned in a Petri dish with soap water and rubbed clean between two fingers (Shearer 1992a), and thereafter placed between two object glasses and dried over night. Impression of each scale was pressed onto a cellulose acetate slide by a scale press. A stereoscopic microscope (Leica MS5, 16x magnification) with mounted digital camera (Leica DFC320, 0.63x magnification) was used to record an image of each scale impression. Using the program Adobe Photoshop Elements 2.0 (Copyright© 1990-2002) the quality of the pictures were improved. The measurements on each scale were carried out in the program Image pro express 6.3 (Copyright© 1993-2008). All distances were measured in pixels.

All measurements were made along the longest axes of the scale, from the focus to the end of the scale (Fig 5) (Shearer 1992a). Four scales were measured for each fish.

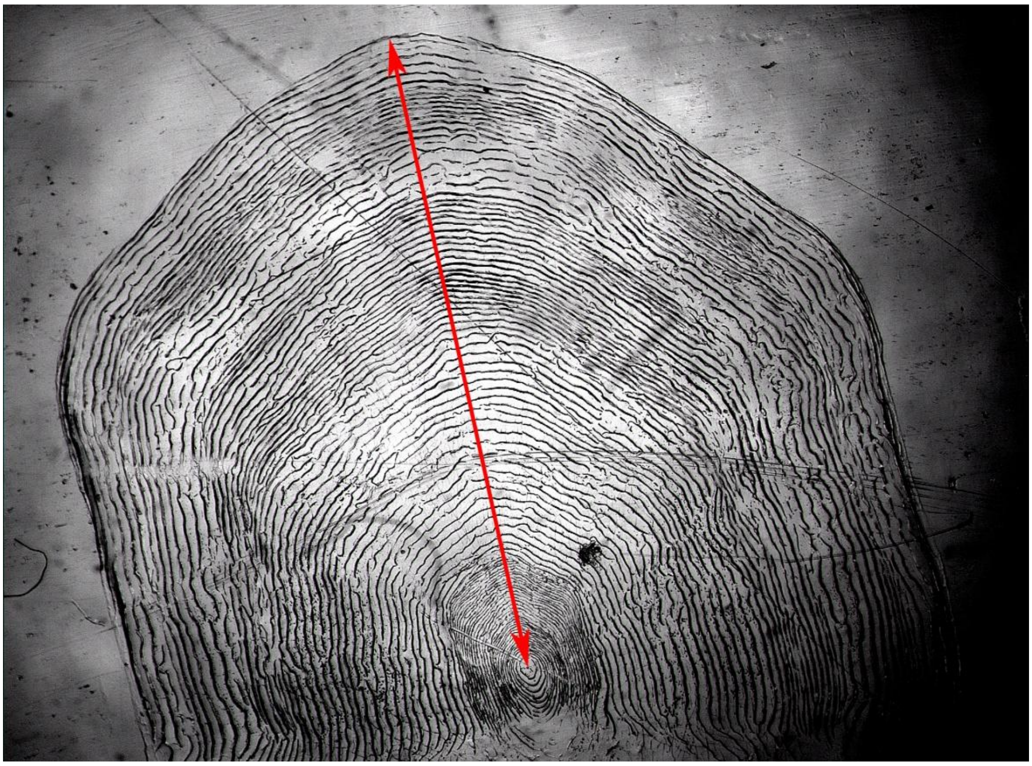

Fig 5 Scale from Atlantic salmon caught at Stumpodden. The longest axes of the scale, from the focus to the edge of the scale are illustrated (red line).

The freshwater annuli were identified by the short distances between the circuli, and forking of the circuli (Fig. 6) (Dahl 1910). The end of the fresh water growth zone was identified by increased inter-circuli distances. “Plus growth”, following the last freshwater winter zone and before the fish entered seawater, a period of intermediate growth was frequently identified (Shearer 1992a).

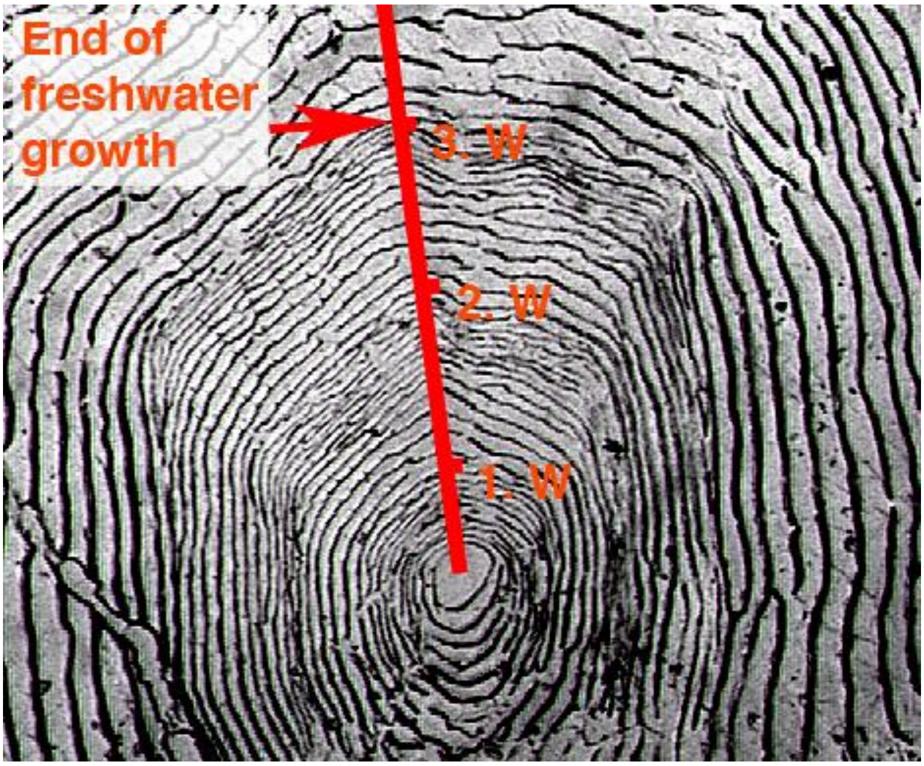

Fig 6 A section of Atlantic salmon scale illustrating; freshwater annuli (1-3 W) and end of freshwater growth zone (red arrow).

The sea-winter bands were identified by short inter-circuli distances and sometimes forking of the circuli (Fig 7) (Dahl 1910). The annual zone is a theoretical line running between the last of the narrow spaced circuli of a winter band and the first of the wide spaced circuli of the following summer band (Shearer 1992a). This indicate that one year of growth is completed. The annual growth zone was identified by the first continuous circulus cutting over the narrow spaced, incomplete circulus or/and the first widely spaced circulus after the winter band.

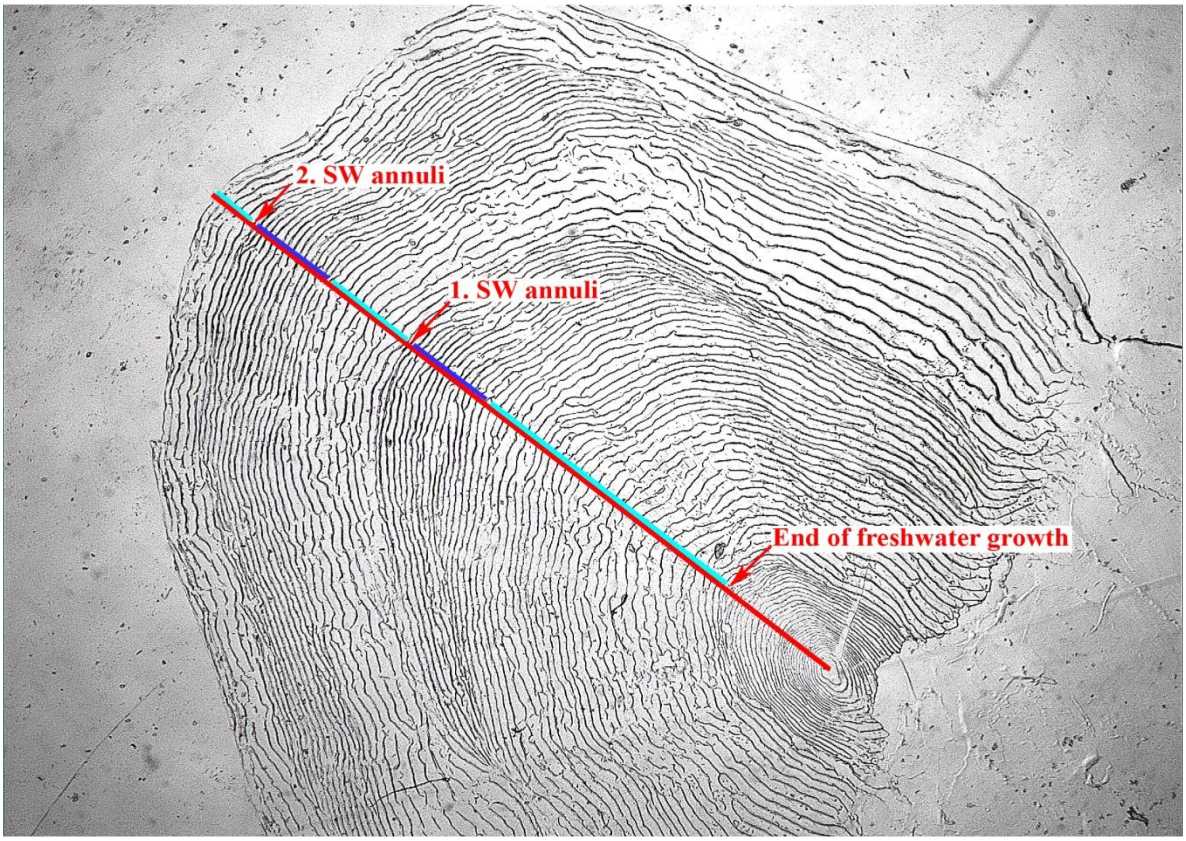

Fig 7 Scale from Atlantic salmon caught at Stumpodden illustrating; the scales annual zones during sea growth (red arrows), end of freshwater growth (red arrow), summer band (light blue) and winter band (dark blue).

As growth is reduced during homeward migration, narrow inter-circuli distances may be formed at the edge of the scale (Fig 8) (Shearer 1992a). Accordingly, closing at the end of the scale was not regarded as a sea-winter. The date of capture is important with regards to closing at the end of the scale. The edge of the scale and the winter-band may stick together for fish caught early in the season, while fish caught late may generate wider inter-circuli distances between the winter-band and the edge of the scale.

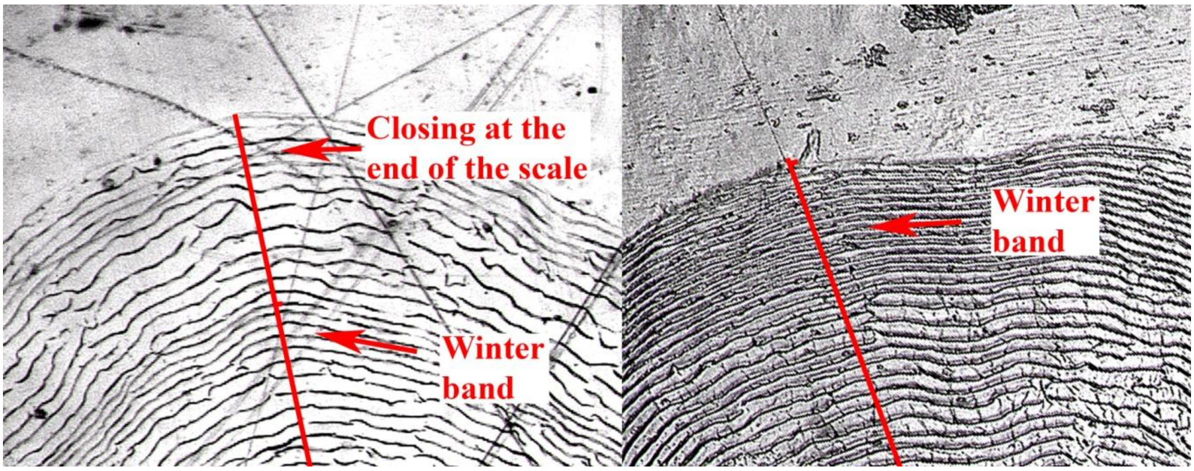

Fig 8 Scale from Atlantic salmon caught at Stumpodden illustrating; Atlantic salmon caught late in the season (left) (where the winter band and the closing at the end of the scale are separated) and Atlantic salmon caught early in the season (right)(where the winter band and the closing at the end of the scale sticks together).

A proportion of the sampled fish consisted of previous spawners. These fish were identified by eroded circuli on the side edge of the scale (Fig 9) (Dahl 1910; Maxwell 1913) and/or continuous bands at the posterior (exposed) part of the scale (B. Jonsson pers comm.). Atlantic salmon use approximately 50-60 % of their total energy during spawning (Jonsson et al. 1991; Jonsson et al. 1997; Jonsson & Jonsson 2003). After spawning salmon may stay in fresh water as kelts (Jonsson et al. 1990), and these periods may cause erosion on the scale margin and surface (Shearer 1992a). Since sea-winter annuli may be completely eroded, it may be difficult to age previous spawners. Previous spawners were therefore regarded as a group separate from the maiden fish.

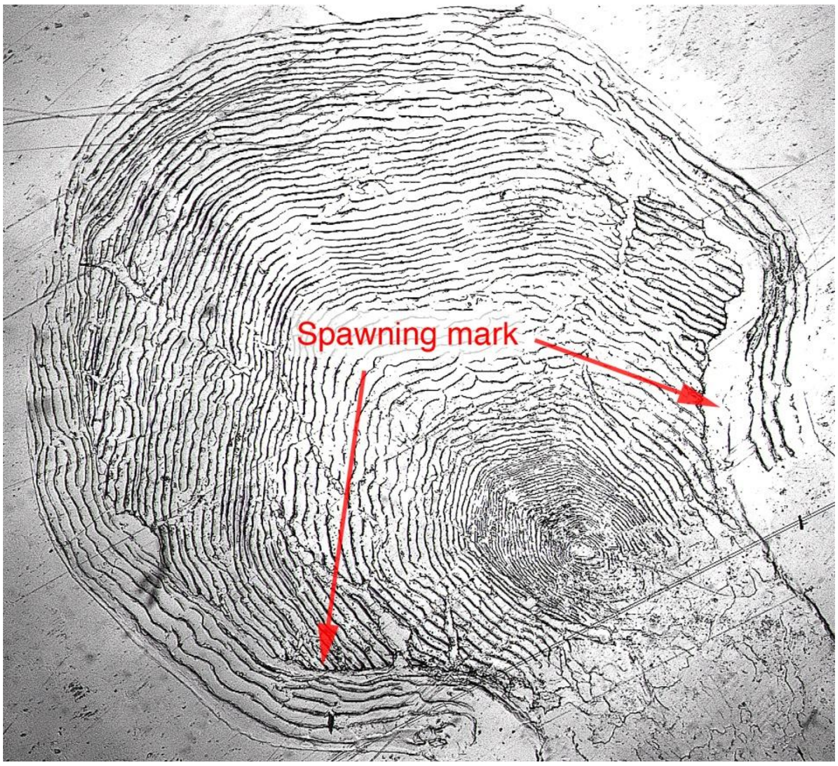

Fig 9 Scale from Atlantic salmon caught at Stumpodden illustrating; spawning marks on the scale side edges (red arrows).

Escaped farmed salmon were identified by recognition of specific morphological- and scale characteristics (Lund et al. 1989). The following on the site identification of morphological characteristics indicated farmed salmon; deformed fins, rounded tail lobes, shortened gill covers and snout/jaw deformation (Lund et al. 1989). The following scale characteristics indicated farmed salmon; a back-calculated smolt size which is larger than the upper limit for 95% variation in the local population, presence of estuary growth, presence of growth check at sea, and a large proportion of replacement scales (Fig 10) (Lund et al. 1989). Atlantic salmon classified as having farm origin were regarded as a separate group, and not included in the various sea-age groups of wild fish.

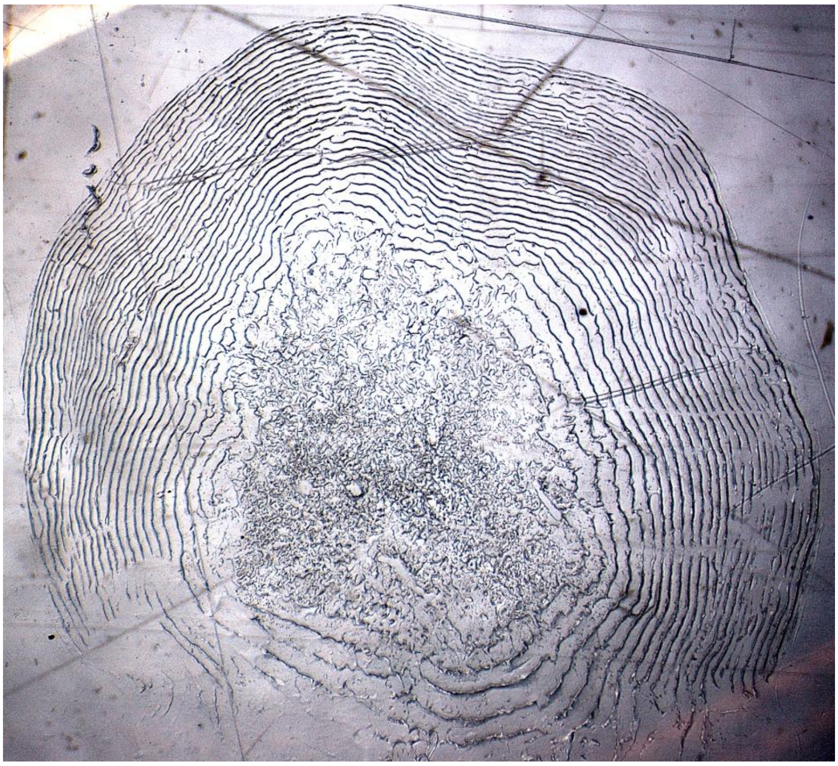

Fig 10 Replacement scale from escaped farmed Atlantic salmon caught at Stumpodden. The scale is replaced in the post-smolt period.

To examine growth more closely, the inter-circuli distances were measured. The inter-circuli distances of the last four circuli in the fresh water growth zone and all inter-circuli distances circuli in the marine phase were measured. The software Image Pro Express 6.3 (Copyright© 1993-2008) recognized the inter-circuli distances by analysing the contrast between the dark circuli and the light spacing. All scales were controlled manually, and incorrect identifications by the program were adjusted. The total number of circuli deposited during the years at sea was counted.

Using linear-back-calculation based on size-at-capture, the length at smoltification and the length at different years at sea were calculated (Dahl 1910; Lea 1910). Growth rates and specific growth rates were determined by using back-calculated lengths.

3.3 Measurement errors and sampling error from the scale readings

Two measurements were made along the longest axis of the scale, one from the focus to the edge of the freshwater growth zone and one from the focus to the edge of the scale (Fig 11). The material for measurement error consisted of ten randomly selected scales. All ten scales were measured 20 times in random order. The two transects were used separately in the analysis of measurement error. The material for sampling error comprised 36 individuals that were randomly selected. For each individual ten randomly selected scales were measured. The ratio between the freshwater growth zone and the total scale length was used in the analysis.

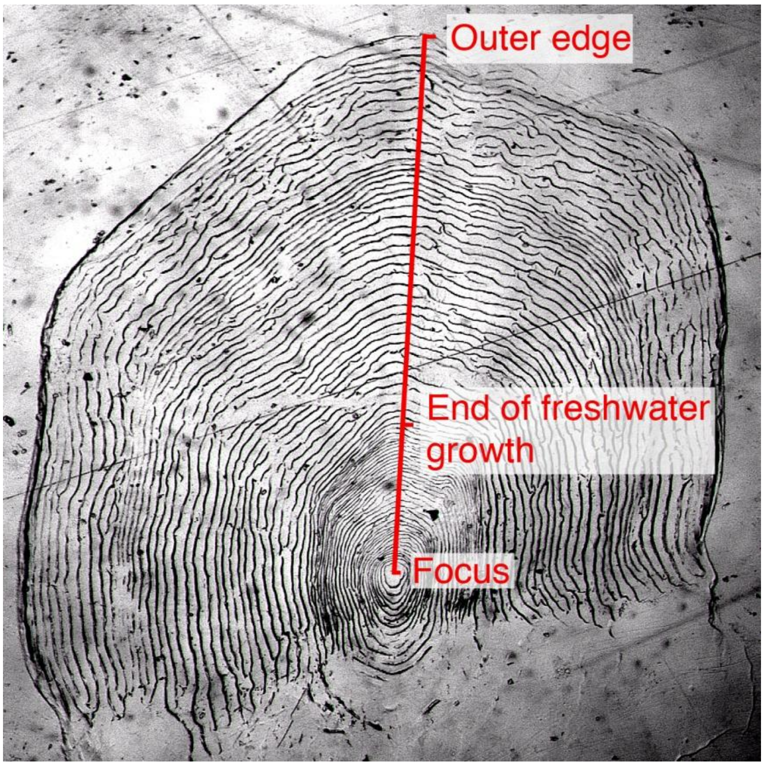

Fig 11 Scale from Atlantic salmon caught at Stumpodden illustrating; focus, end of freshwater growth and the outer edge of the scale.

3.4 Temperature data

Sea-surface temperature (SST) from the North Sea was obtained from two oil platforms, Gullfaks C (61°20´N; 2°27´Ø) and Sleipner A (58°40´N; 1°90´Ø) (Fig 12). The SST from the Norwegian Sea was obtained from oil platform, Heidrun (65°30´N; 7°30´Ø), and weather station, Mike (66°00´N; 2°00´Ø). The SST on the Skagerrak coast was obtained from the lighthouse at Lindesnes (57°98´N; 7°05´Ø). These stations were used because they probably represent the temperature conditions experienced by the Atlantic salmon during the growth years at sea. All SST data were obtained from the weather service eKlima (available at http://www.eklima.no). A common trend in the SST was estimated from a Dynamic Factor Analysis (DFA) using the R-based Brodgar software (http://www.brodgar.com).

Fig 12 The North Sea, Norwegian Sea and Skagerrak Sea with locations of oil platforms, weather station and lighthouse (red dots), all of which log sea-surface temperature (Statkart).

3.5 Statistics

The statistical tests were carried out in R (R version 2.11.1 and 2.12.0 (2010-05-31)). The data from the measurement error were re-sampled 1000 times using a non-parametric bootstrapping routine (Manly 1997). The bias was used to determine the accuracy of measurements in proportion to the number of scales measured. The coefficient of variance was used to estimate the measurement error compared with the numbers of repetitive measurements. The individual ID was used as a random factor in all further analysis, accounting for among-scales within individual variance. In order to predict fish length from scale radius I used linear regression based on ln-transformed fish length and scale radius. I used linear mixed-effects model (LME) to predict the number of circuli deposited related to specific growth rate. Since there was only one growth rate measurement per individual and four scale measurements it was not possible to use ID as random factor in this LME. I therefore used the mean number of circuli per individual and weighted by the inverse of the variance for the four scales measured per individual. To estimate growth patterns related to circuli spacing a generalized additive mixed model (GAMM) was used.

Throughout this thesis, model selection was based on Akaike's Information Criterion (AIC) following recommendations in Zuur et al. (2009). Technically, it is possible to calculate R^2 for mixed models (Orelien & Edwards 2008), but the validity of the value is much discussed (Venables 2000). Nevertheless, in order to assess the level of explained variance/deviance, R^2 values will be provided for the mixed models.

In the analysis in R, I used nlme-, mgcv-, ape-, lme4-, lattice-, Hmisc-, boot- and plotrix library.

3.6 Bag net catches

The bag net catches from Stumpodden were sorted by length- and age-classes (Fig 13). The total body length of Atlantic salmon varied between 520mm and 970mm. The length distribution of the 2SW fish overlapped partly with those of 1SW and 3SW salmon, while the 1SW class and the 3SW class were completely separated by length. Previous spawners exhibited the widest distribution in lengths, because it consisted of several age- groups. The dominant age-group in the catches was 2SW Atlantic salmon. The mean body weight for Atlantic salmon caught at Stumpodden varied between 3.3 kg and 4.3 kg in the years 2004-

2010. Previous spawners were caught every year. The portion of previous spawners was as high as 19.2% in the total catches. Escaped farmed Atlantic salmon were caught in three years: 2005, 2007 and 2008 (Table 1), but the portion of escaped farmed Atlantic salmon in the total catch, as revealed by morphology and scales, was as low as 1.2%.

Table 1 Bag net catches of Atlantic salmon from Stumpodden sorted by catch year and sea-age.

Year	1SW	2SW	3SW	4SW	Previous spawners	Not aged	Escaped farmed salmon	Sum
2004	8	24	2		6	1		41
2005	7	25			12		1	45
2006	4	31	1		14			50
2007	1	40	2	1	7	1	1	53
2008		24			2	1	1	28
2009		11	1		5			17
2010	2	6	1		1	1		11
Sum	22	161	7	1	47	4	3	245

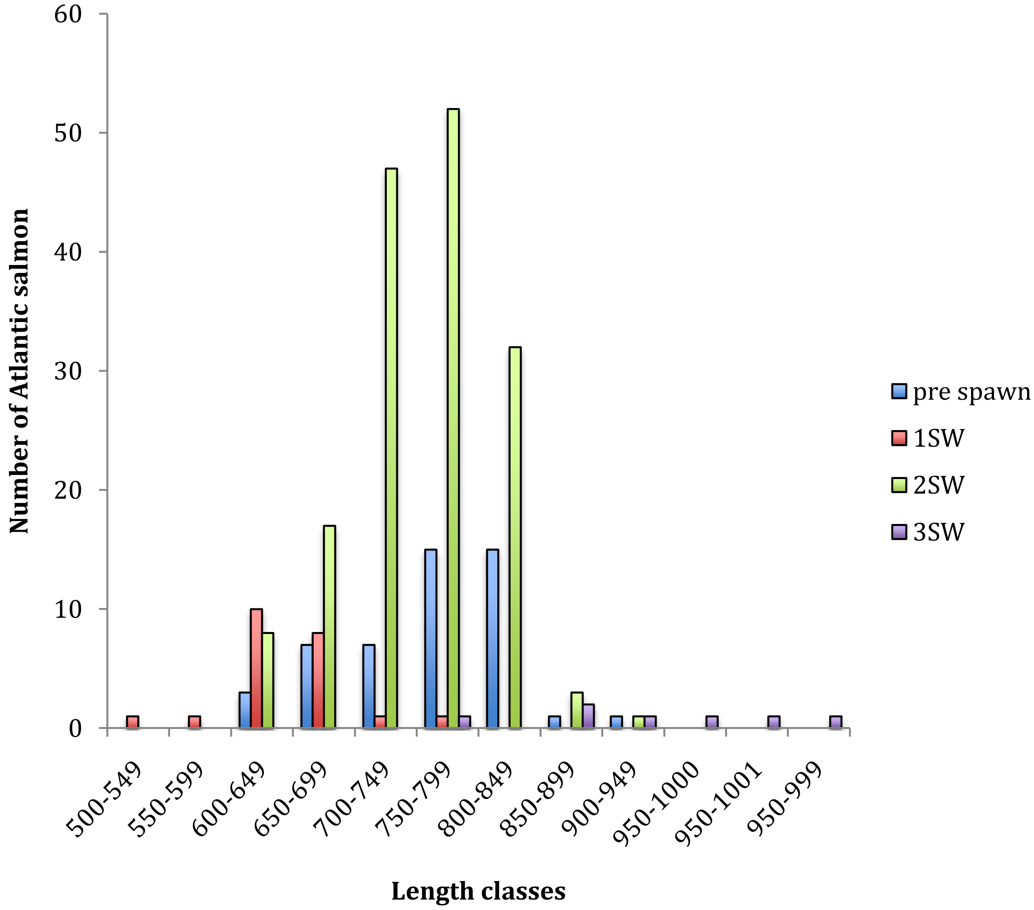

Fig 13 Number of Atlantic salmon caught at Stumpodden, sorted by length classes and sea-age in the years 2004-2010.

4. Results

4.1 Measurement errors and sampling error from the scale readings

The scale measurement errors were low, respectively 0.12% ±0.03% (SD) for the total scale radius and 0.61% ±0.15% (SD) for the scale radius at smoltification (Fig 14). The slopes of the lines declined as more readings were carried out, but stabilized after ten readings. The measurement errors were higher for the smolt radius than for the total scale radius. There was no relationship between the scale size and the measurement error (R^2=0.058, $p=0.50$). The sampling error declined when more scales were measured (Fig 15). Sampling error for ten scale measurements was 4.57% ±1.65% (SD). The slope of the line was highest from one scale measured to two scales measured. The modelled line reached the inflection point at four scales measured.

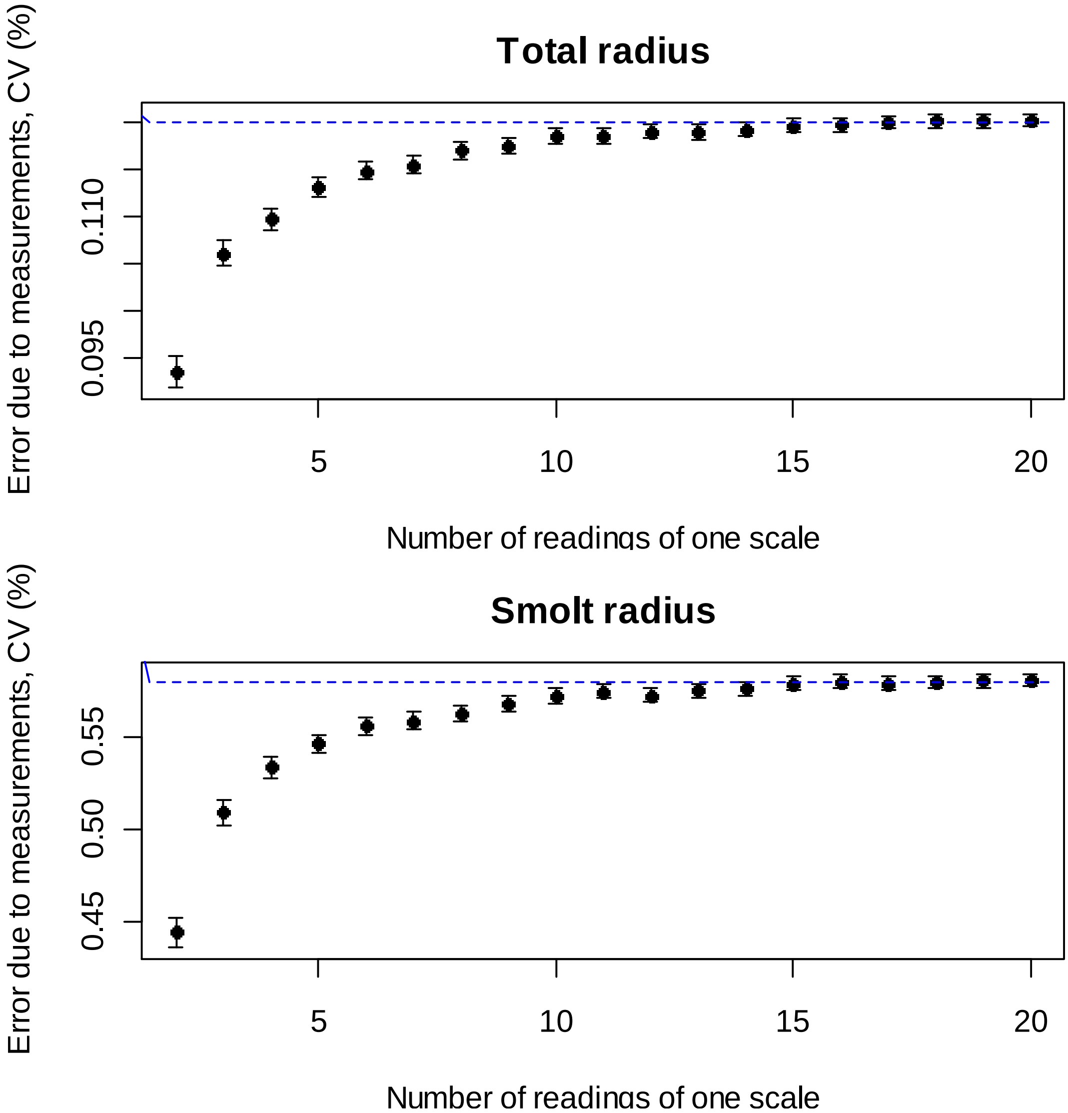

Fig 14 Error due to measurements (measurement error, CV%), as a function of number of times read for total scale radius (top) and smolt radius (bottom) of scales from Atlantic salmon captured at Stumpodden. Dashed blue lines resemble the expected measurement error for 20 scale readings.

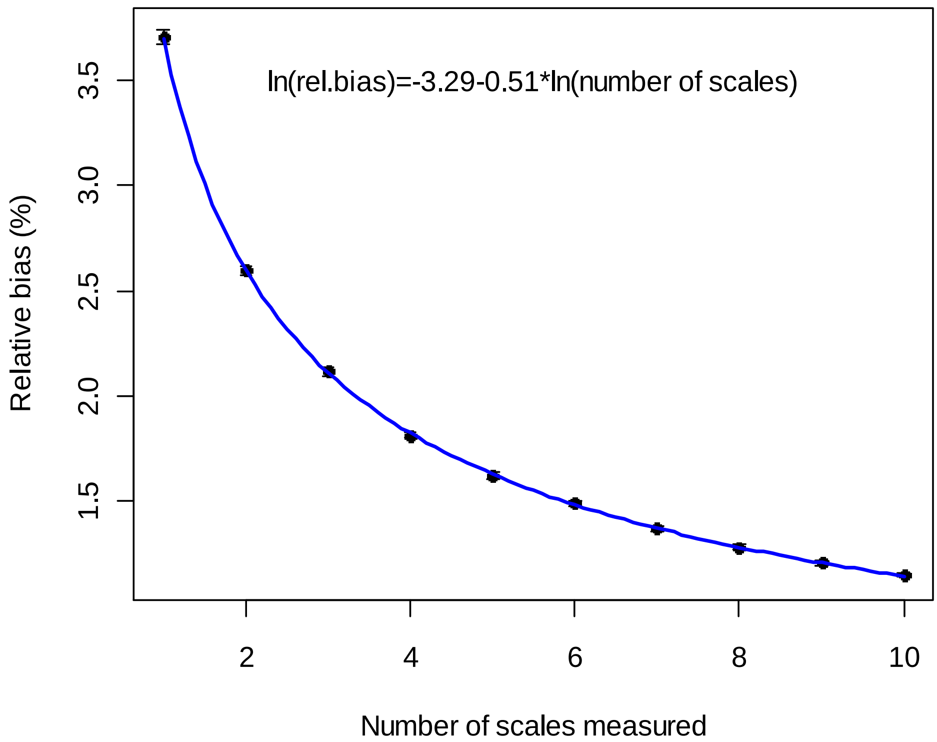

Fig 15 Sampling error (relative bias) as a function of number of scales measured per fish. All scales from Atlantic salmon captured at Stumpodden.

4.2 Scale size in relation to fish length

The total fish length of Atlantic salmon correlated positively with the scale radius (R^2=0.62, *p<0.00001*) (Fig 16, Table 2). The previous spawners displayed a slightly negative (but not significant) effect on the scale radius/fish length relationship (Table 3 and 4). I found no significant sea-age or catch-date effect on the scale radius/fish length relationship.

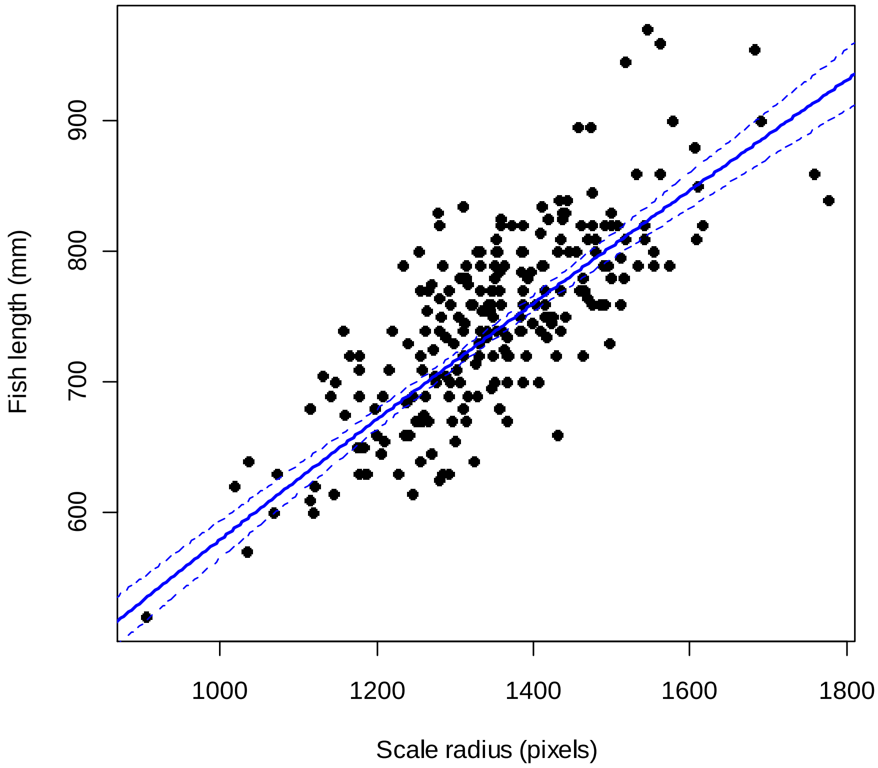

Fig 16 The linear relationship between total body length (mm) and scale radius (pixels) of Atlantic salmon captured at Stumpodden. Dashed lines give 95% confidence intervals of the predicted model (solid line).

Table 2 Parameter estimates for the linear relationship between fish length and total scale radius.

Parameter estimate

Parameter	Estimate	SE	p-value
Intercept	0.78843	0.29560	*0.00818*
Ln (Total scale radius)	0.80690	0.04104	*<0.00001*

Table 3 Model selection based on the effect of previous spawners on scale radius/fish length relationship.

Model	AIC	ΔAIC
Scale radius vs Fish length + Previous spawner	11552.75	
Scale radius vs Fish length * Previous spawner	11554.92	2.17
Scale radius vs Fish length	11560.24	7.49

Table 4 Parameter estimate and ANOVA table for the selected model including scale radius, fish length and previous spawner.

Parameter estimate

Parameter	Value	SE
Intercept	317.7896	57.02
Fish length	1.3840	0.07
Previous spawn	-21.4224	13.82

ANOVA

Test statistics

Term	df	F-value	p-value
Fish length	1	*330.19*	*<0.0001*
Pre Spawn	1	*2.40*	*0.1225*

4.3 Circuli formation rate

The specific growth rate of Atlantic salmon during the first year at sea was positively correlated with the number of circuli present at the end of the same period (R^2=0,667, Table 5, Fig 17). Based on the AIC level (Table 6), an additive model including sea-age and days after 1 January to the catch date (Day number) was used to predict the number of circuli deposited after the winter-band (R^2=0.87, Table 7, Fig 18). The number of circuli deposited after the winter-band related to the catch date varied between the see-age groups. 1SW fish deposed a higher number of circuli than the 2SW and 3SW fish.

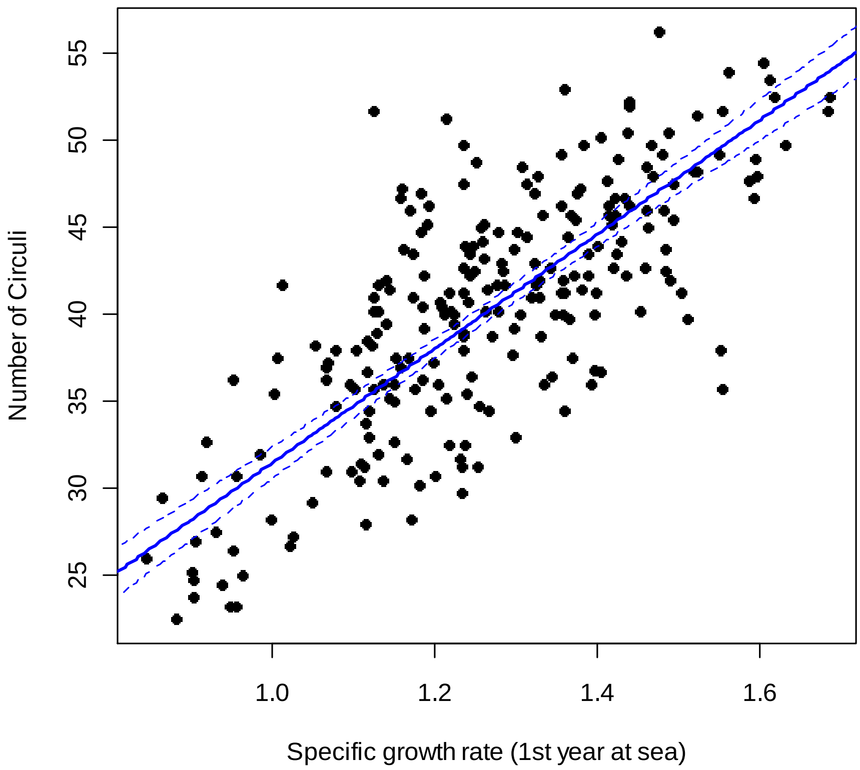

Fig 17 The linear relationship between number of scale circuli deposit during the first growth year at sea and specific growth rate of Atlantic salmon captured at Stumpodden. Dashed lines give 95% confidence intervals of the predicted model (solid line).

Table 5 Parameter estimate for the linear relationship between circuli number and specific growth rate.

Parameter estimate

Parameter	Estimate	SE	p-value
Intercept	-1.353	1.914	*0.48*
Specific growth rate (first year at sea)	32.833	1.516	<*0.00001*

Table 6 Model selection based on the effect of the number of circuli deposited after the last winter-band at sea.

Model	AIC	ΔAIC
Sea age + day number	3737.55	
Sea age * day number	3742.31	4.76
Sea age + number of days >7°C	3750.38	12.83
Sea age * number of days >7°C	3751.72	14.17
Sea age + number of days >8°C	3755.16	17.61
Sea age * number of days >8°C	3757.77	20.22

Table 7 Parameter estimate and ANOVA table of the selected model including sea age and day number.

Parameter estimate

Parameter	Value	SE
Intercept	-8.657	3.355
Sea age 2	-5.349	0.883
Sea age 3	-7.001	1.061
Sea age 4	-8.903	1.902
Day number	0.109	0.016

ANOVA

Test statistics

Term	df	F-value	p-value
Sea age	3	*28.2824*	*<0.0001*
Day number	1	*43.6639*	*<0.0001*

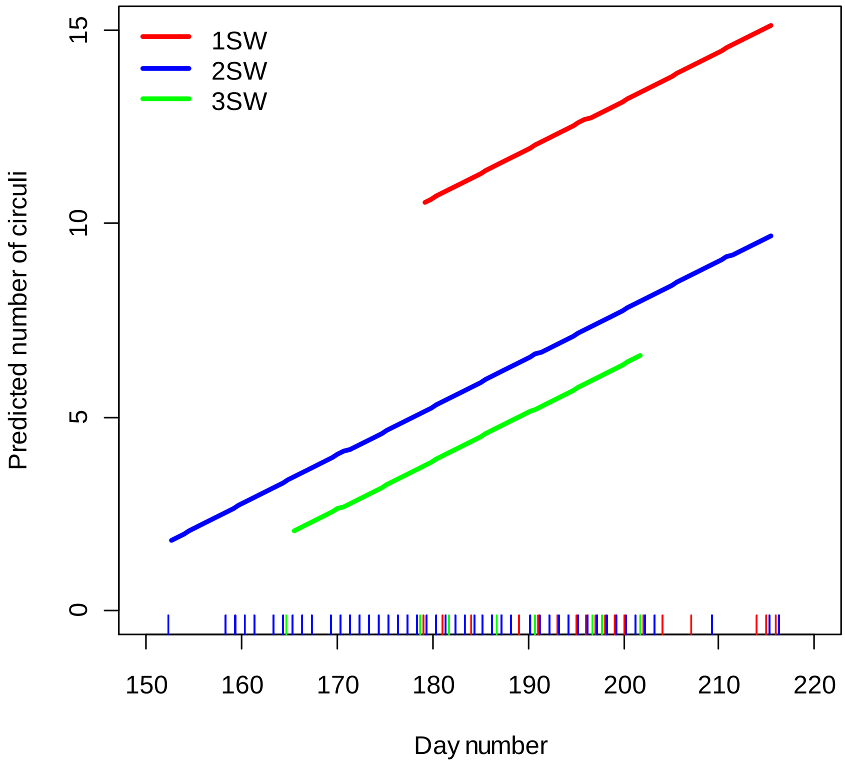

Fig 18 Predicted number of circuli deposited after the winter-band on scales of Atlantic salmon as a function of days after 1. January, to the catch date (day number). The coloured rug-markings on the x-axis represent observed catch days for Atlantic salmon at Stumpodden for the various sea-age groups.

4.4 The relationship between circuli number and inter-circuli distances

The relationship between circuli number and mean inter-circuli distance for 1SW and MSW Atlantic salmon first growth year at sea were not strong (R^2=0.1013, Table 9, Fig 19). There was a slightly negative relationship between circuli number and mean inter-circuli distance for the MSW Atlantic salmon first growth year at sea. There was a slightly positive relationship between circuli number and mean inter-circuli distance for the MSW Atlantic salmon second growth year at sea (R^2=0.079, Table 10, Fig 20). The model selections were based on the AIC value (Table 8).

Table 8 Model selection based on the effect of mean inter-circuli distances on the maximum circuli number

Model	AIC	∆AIC
Mean inter-circuli distances ~ mean 1SW* maximum circuli number	746.28	
Mean inter-circuli distances~ mean 1SW+ maximum circuli number	747.20	0.92
Mean inter-circuli distances~ maximum circuli number	751.73	5,45

Table 9 Parameter estimate and ANOVA table of the selected model including mean inter-circuli distance, maximum circuli number and the relationship the two factors

Parameter estimate

Parameter	Value	SE
Intercept	16.912	1.228
Mean inter-circuli distances	1.567	1.308
Maximum circuli number	-0.007	0.026
Mean 1SW:Maximum circuli number	-0.048	0.028

ANOVA

Test statistics

Term	df	F-value	p-value
Mean inter-circuli distances	1	*3.1111*	*0.079*
Maximum circuli number	1	*24.0580*	*0.001*
Mean 1SW:Maximum circuli number	1	*2.8885*	*0.091*

Table 10 Parameter estimate and ANOVA table of the selected models for MSW second year at sea including maximum circuli number.

Parameter estimate

Parameter	Value	SE
Intercept	12.767	0.400
Maximum circuli number	0.068	0.016

ANOVA

Test statistics

Term	df	F-value	p-value
Maximum circuli number	1	19.416	*0.001*

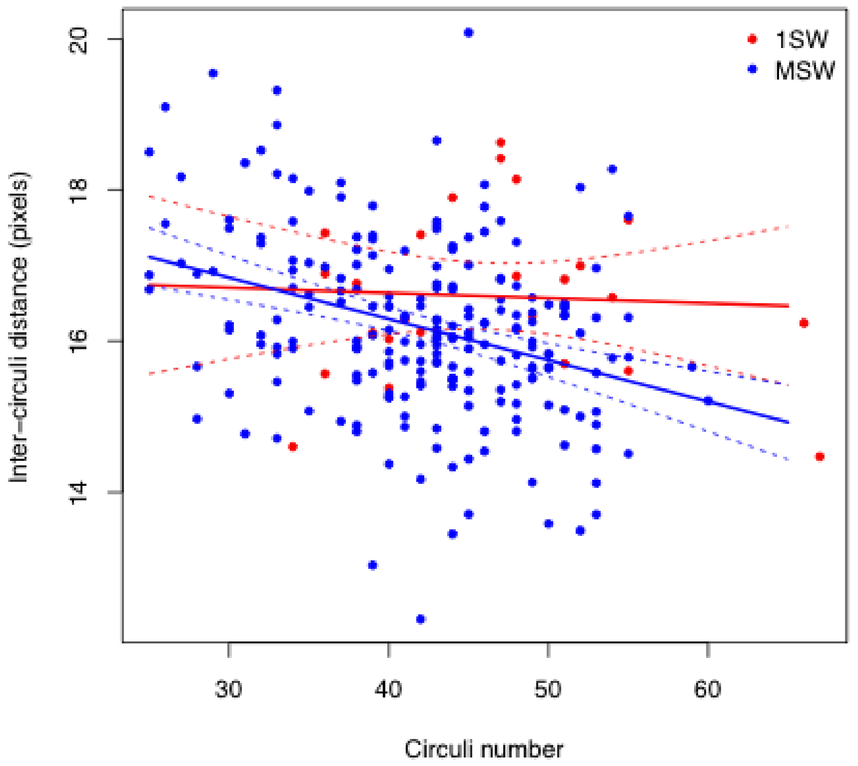

Fig 19 The relationship between mean inter-circuli distances (pixels) and circuli number for 1SW (red) and MSW (blue) Atlantic salmon during first growth year at sea. Dashed lines give 95% confidence intervals of the predicted models (solid lines). All scales are from Atlantic salmon captured at Stumpodden.

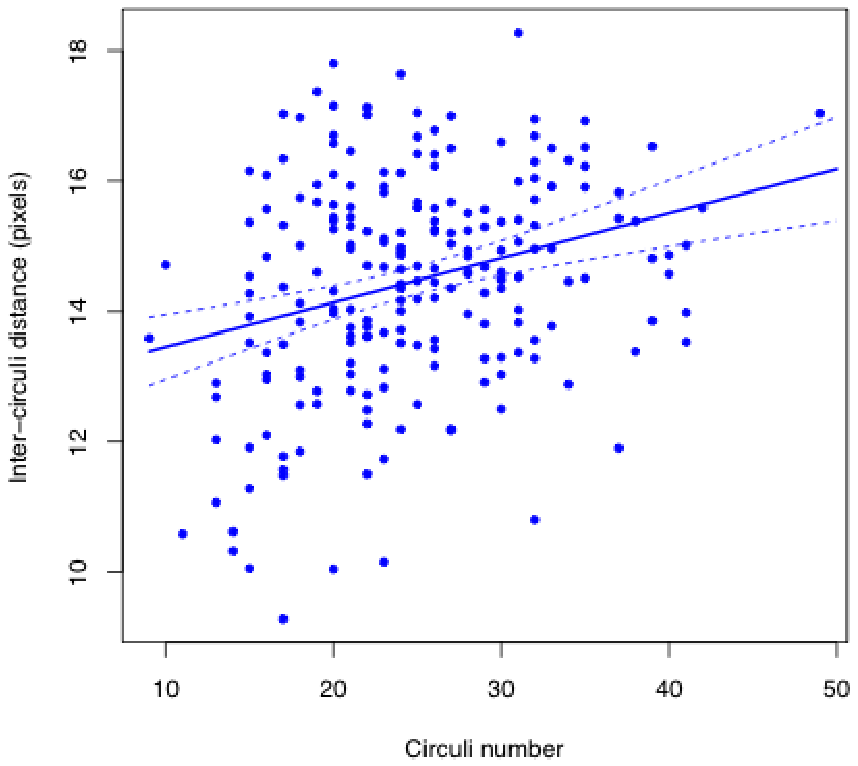

Fig 20 The relationship between mean inter-circuli distances (pixels) and circuli number for MSW Atlantic salmon (blue) during second growth year at sea. Dashed lines give 95% confidence intervals of the predicted models (solid lines). All scales are from Atlantic salmon captured at Stumpodden.

4.5 Atlantic salmon growth at sea

4.5.2 Post-smolt growth

To predict the inter-circuli distances prior to and after sea entrance the model combining smolt year and smolt age were used (R^2= 0.618, Table 12, Fig 21). This decision was based on the AIC value (Table 11). The same shapes of the inter-circuli distances curves were present in the years 2001-2008, but there were significant differences among years. The first four circuli represented fresh water inter-circuli distance prior to sea entry. At this point the inter-circuli distances were low. The distances were rapidly increasing after sea entry, but reached a point of inflection at circuli number six. The June SST at Lindesnes did not explain the difference in inter-circuli distances between years.

Table 11 Model selection based on the effect of inter-circuli distances for Atlantic salmon smolts prior and after sea entrance.

Model	AIC	ΔAIC
Circuli number (by) Smolt year + Smolt age	49462.29	
Circuli number + Smolt year	49529.26	66.97
Circuli number	49529.71	67.42
Circuli number (by) Smolt year	49532.47	70.18
Circuli number (by) Smolt year+ Total sea age	49534.19	71.90
Circuli number (by) Smolt age	50109.10	646.81
Circuli number (by) Total sea age + Smolt year	50610.46	1148.17

Table 12 Parameter estimate and ANOVA table of the selected model including circuli number, smolt year and smolt age.

Parameter estimate

Parameter	Estimate	SE
Intercept	12.439	0.8206
Smolt age 2	-1.291	0.8314
Smolt age 3	-0.678	0.8425
Smolt age 4	-0.891	0.1010

ANOVA

Test statistics

Term	Edf	df	F-value	p-value
Smolt age		3	*2.914*	*0.033*
Smolt year 2001	3.746		*225.50*	*<0.00001*
Smolt year 2002	3.928		*732.18*	*<0.00001*
Smolt year 2003	3.933		*840.78*	*<0.00001*
Smolt year 2004	3.949		*934.06*	*<0.00001*
Smolt year 2005	3.954		*1054.43*	*<0.00001*
Smolt year 2006	3.923		*600.11*	*<0.00001*
Smolt year 2007	3.735		*226.05*	*<0.00001*
Smolt year 2008	3.665		*65.93*	*<0.00001*

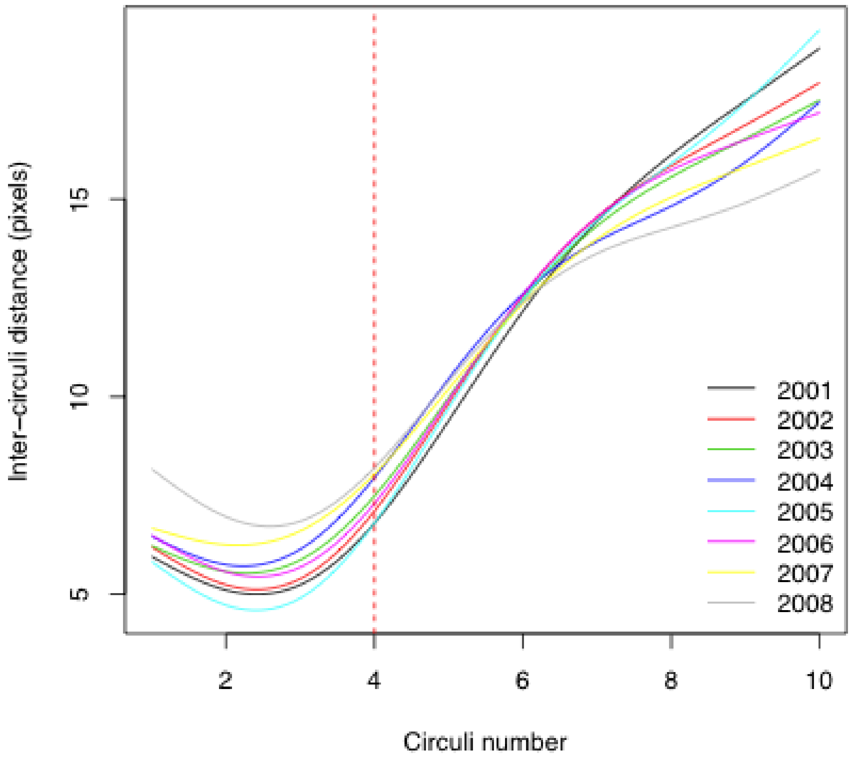

Fig 21 Inter-circuli distances (pixels) of Atlantic salmon captured at Stumpodden related to circuli number prior to and after smolting during the years 2001-2008, vertical line (Red dotted) illustrates sea entry.

4.5.2 Circuli number

The mean number of circuli deposited in the first growth year at sea varied around 40 circuli in the years 2001-2009, while around 20 circuli were deposited the second growth year at sea in the years 2002-2009 (Fig 22). There was a higher year-to-year variation the first growth year at sea compared with the second growth year at sea. But the year-to-year variations were significant different during both first- (ANOVA: $F_{8.936}=14.06, p<0.00001$) and second growth year at sea (ANOVA: $F_{2.857}=16.19, p<0.00001$). The 1SW Atlantic salmon deposited most circuli in 2004, while 2003 and 2005 are at a lower level. The circuli number in 2006 (n=1) and 2009 (n=2) are uncertain. The MSW Atlantic salmon deposited an increasing number of circuli from 2001–2004 the first growth year at sea, before the number dropped in 2005 and 2006. In 2007 and 2008 the variation in circuli number is higher.

The MSW Atlantic salmon deposited an increasing number of circuli from 2002–2004 the second growth year at sea, before the number dropped in 2005 (Fig 23). From 2006-2008 it stabilized on a higher level, before the number was lower in 2009.

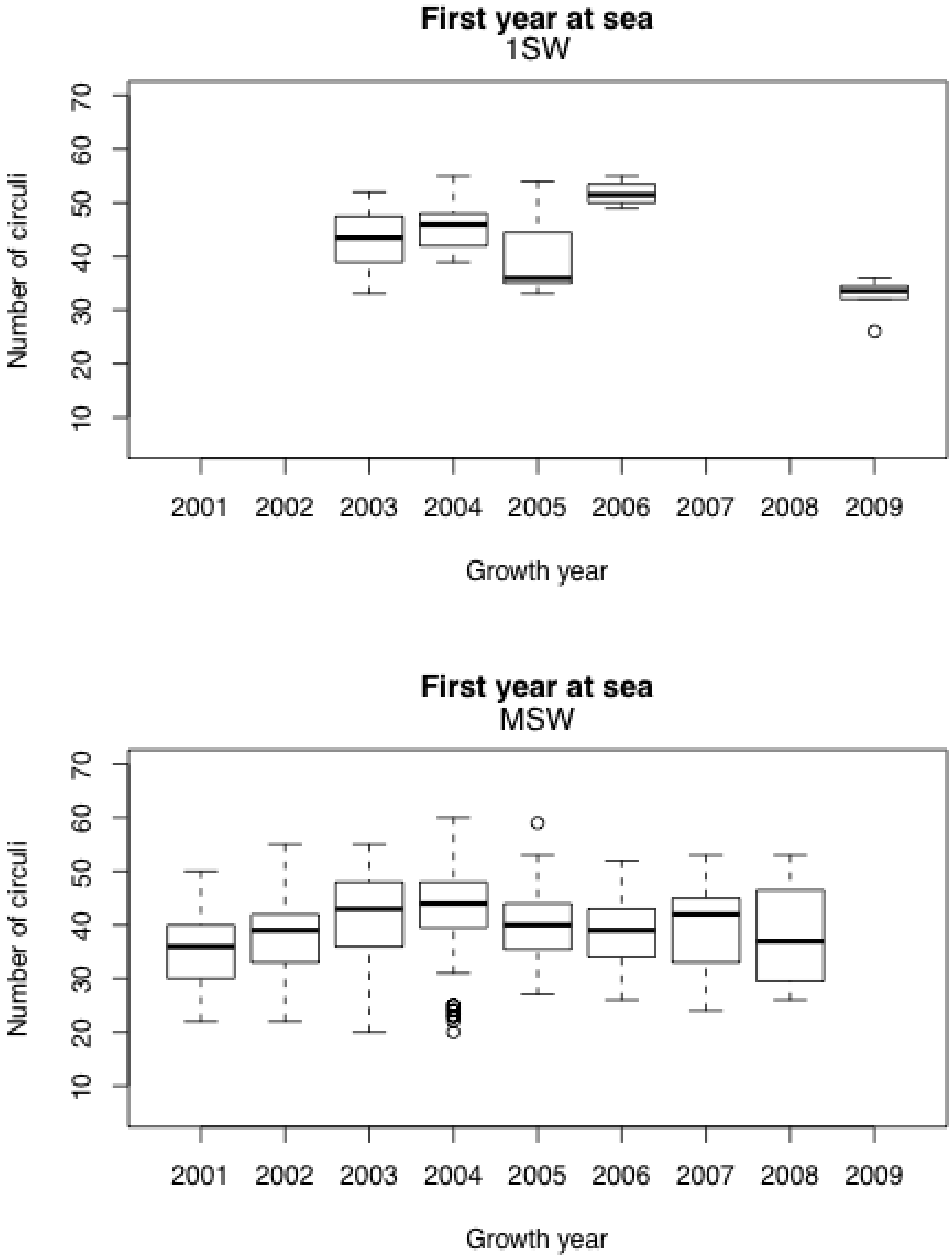

Fig 22 Mean number of circuli deposited on scales of Atlantic salmon during first growth year at sea for 1SW (top) and MSW (bottom) during 2003-2006, 2009 (1SW) and 2001-2008 (MSW). All scales are from Atlantic salmon captured at Stumpodden.

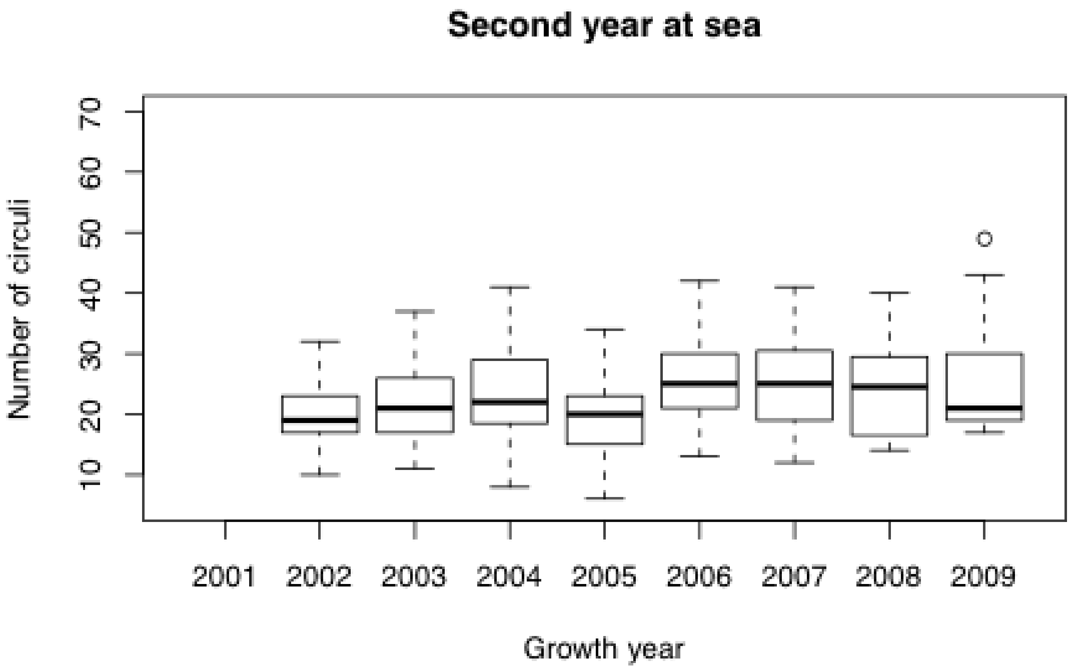

Fig 23 Mean number of circuli deposited on scales of Atlantic salmon second growth year at sea during 2002-2009. All scales are from Atlantic salmon captured at Stumpodden.

4.5.2 Inter-circuli distances

To predict the inter-circuli distances throughout the first growth year at sea for 1SW and MSW Atlantic salmon, the model grouping by age and growth year was used (R^2=0.38, Table 14, Fig 24). This decision was based on the AIC value (Table 13). The curves of the inter-circuli distances for the first growth year at sea for 1SW and MSW Atlantic salmon, exhibited a characteristic shape. Except for the 1SW fish in the years 2006 (n=1) and 2009 (n=2). There was a distinct increase in the inter-circuli distance after sea entrance, with a maximum at one third into the growth season. Thereafter, the distances declined. The overall shapes of inter-circuli distances throughout the years were similar for almost all years and age groups, but there were significant difference in inter-circuli distances between years and sea-age groups.

A variation in the peaks of maximum inter-circuli distance was observed between years. The peak of maximum inter-circuli distance for the 1SW Atlantic salmon first year at sea was high in 2003 and 2005, in 2004 it was at a lower level. For the MSW Atlantic salmon first year at sea the peaks of maximum inter-circuli distances declined yearly from 2001-2008.

To predict the inter-circuli distances throughout the second growth year at sea for MSW Atlantic salmon, the model grouping by growth year was used (R^2=0.203, Table 16, Fig 25). This decision was based on the AIC value (Table 15). The curves of the inter-circuli distances for the second growth year at sea for MSW Atlantic salmon, exhibited a characteristic shape. The inter-circuli distances starts of at a high level, with a maximum at one fourth into the growth season. Thereafter, the distances declined. The overall shapes of inter-circuli distances throughout the years were similar for all years, but there were significant variations between years and age groups.

Table 13 Model selection based on the effect of inter-circuli distances during the fist growth year at sea.

Model	AIC	ΔAIC
Rel. circuli no. (by) 1SW growth year	212163.5	
Rel. circuli no. (by) growth year + 1SW	212321.3	157.8
Rel. circuli no. (by) growth year	212322.3	158.8
Rel. circuli no. (by) growth year + sea age	212322.6	159.1
Rel. circuli no. + growth year	213147.0	983.5
Rel. circuli no. (by) 1SW + growth year	213150.3	986.8
Rel. circuli no.	213155.6	992.1

Table 14 Parameter estimate and test statistics of the selected model including relative circuli number and first growth year at sea.

Parameter estimate, test statistics

Term	Edf	SE	F-value	p-value
Intercept	16.215	0.076		*<0.001*
Growth year 2003, 1SW	3.983		*292.088*	*<0.001*
Growth year 2004, 1SW	3.975		*201.585*	*<0.001*
Growth year 2005, 1SW	3.946		*127.396*	*<0.001*
Growth year 2006, 1SW	2.188		*31.865*	*<0.001*
Growth year 2009, 1SW	3.690		*43.171*	*<0.001*
Growth year 2001, MSW	3.974		*354.644*	*<0.001*
Growth year 2002, MSW	3.991		*1219.332*	*<0.001*
Growth year 2003, MSW	3.993		*1068.354*	*<0.001*
Growth year 2004, MSW	3.996		*1278.198*	*<0.001*
Growth year 2005, MSW	3.993		*910.562*	*<0.001*
Growth year 2006, MSW	3.981		*549.912*	*<0.001*
Growth year 2007, MSW	3.971		*319.592*	*<0.001*
Growth year 2008, MSW	3.886		*98.676*	*<0.001*

Table 15 Model selection based on the effect of inter-circuli distances during the second growth year at sea.

Model	AIC	ΔAIC
Rel. circuli no. (by) 2SW growth year	82632.73	
Rel. circuli no. (by) 2SW growth year + sea age	82634.66	1.93
Rel. circuli no. (by) sea age + 2SW growth year	82688.93	56.2
Rel. circuli no.	82694.98	62.25
Rel. circuli no. + growth year	82705.84	73.11

Table 16 Parameter estimate and test statistics of the selected model including relative circuli number and second growth year at sea.

Parameter estimate, test statistics

Term	Edf	SE	F-value	p-value
Intercept	14.929	0.1013		*<0.001*
Growth year 2002	2.964		*15.63*	*<0.001*
Growth year 2003	3.731		*175.41*	*<0.001*
Growth year 2004	3.749		*194.74*	*<0.001*
Growth year 2005	3.507		*146.82*	*<0.001*
Growth year 2006	3.583		*391.80*	*<0.001*
Growth year 2007	3.862		*205.73*	*<0.001*
Growth year 2008	3.207		*113.71*	*<0.001*
Growth year 2009	3.391		*92.14*	*<0.001*

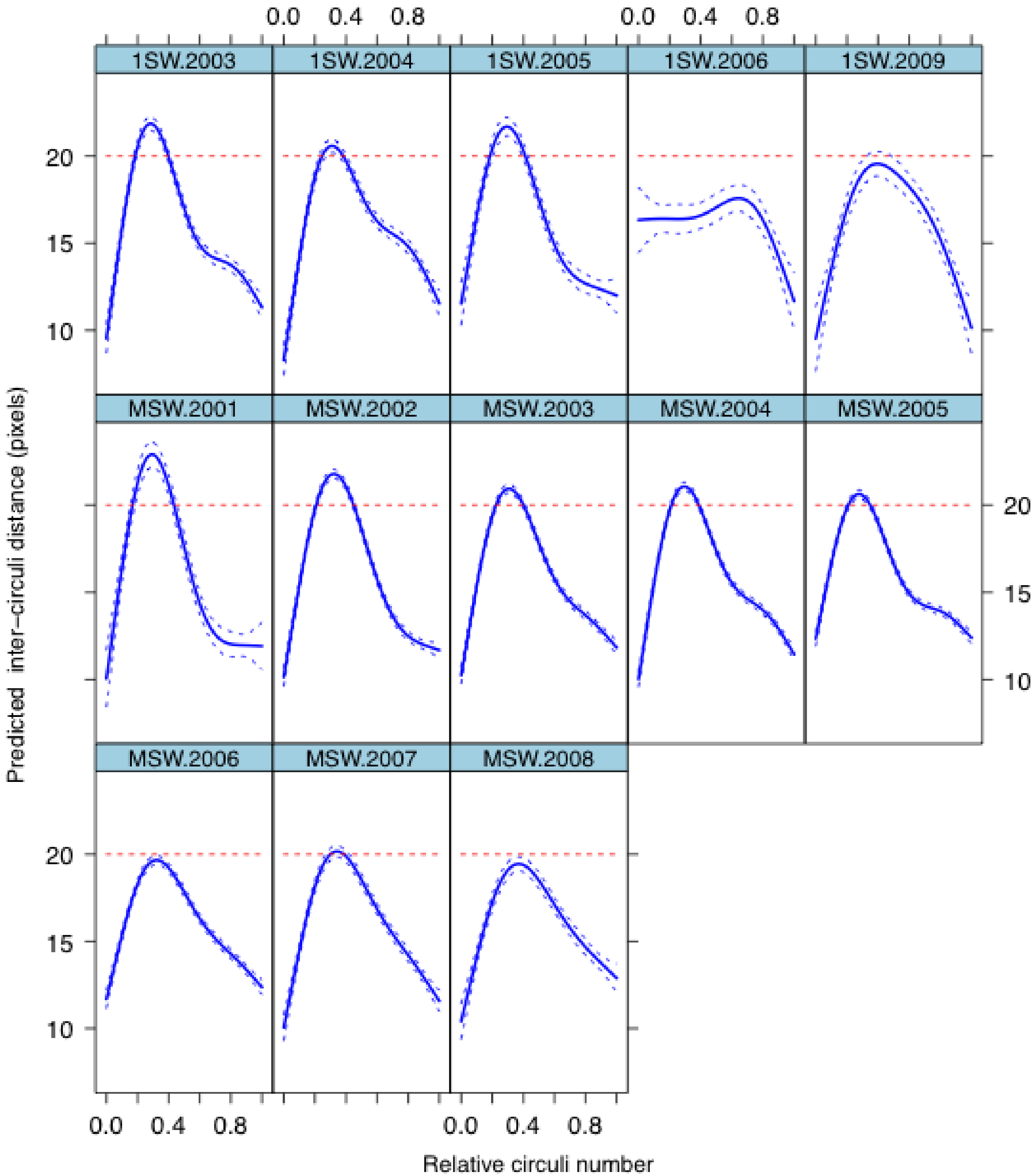

Fig 24 Inter-circuli distances (pixels) of Atlantic salmon caught at Stumpodden related to relative circuli number, for the first growth year at sea for 1SW and MSW during 2003-2006, 2009 (1SW) and 2001-2008 (MSW). A reference line is added at 20 pixels (red dotted).

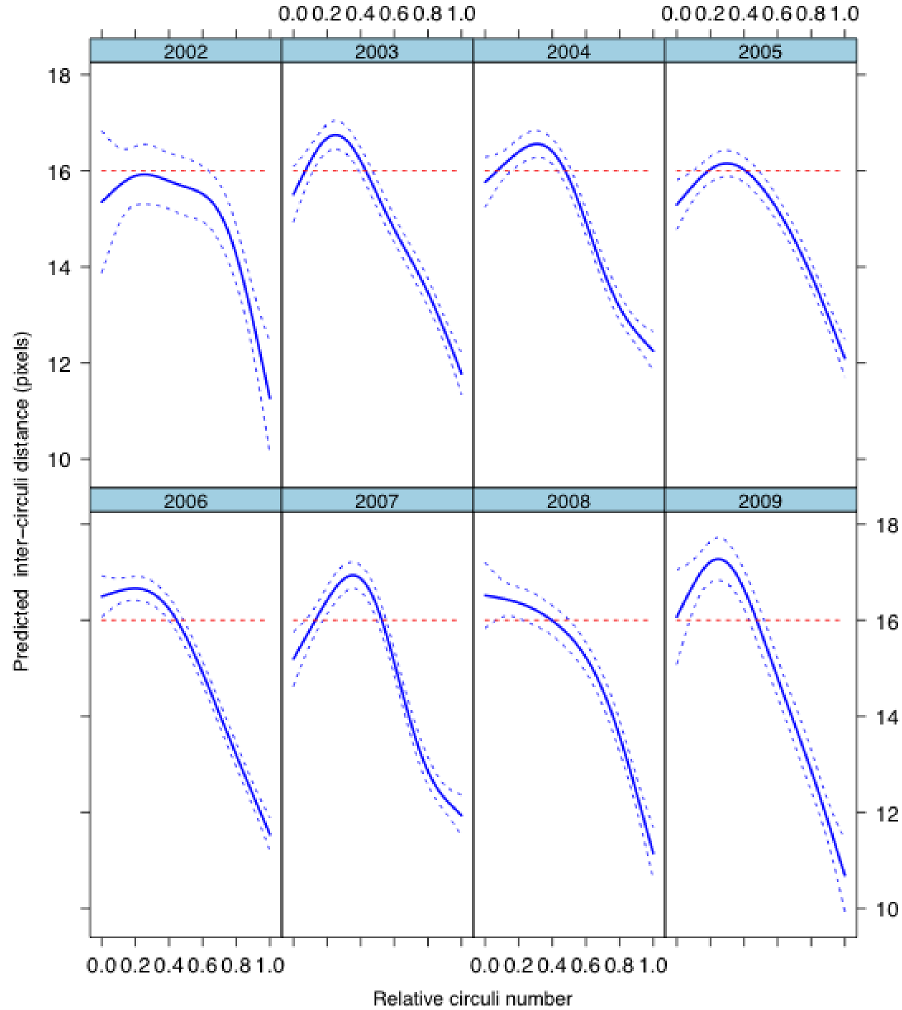

Fig 25 Inter-circuli distances (pixels) of Atlantic salmon caught at Stumpodden related to relative circuli number, for the second growth year at sea for MSW fishes during the years 2002-2009. A reference line is added at 16 pixels (red dotted).

4.5.3 Mean circuli number and mean inter-circuli distances during first growth year at sea

The total number of circuli deposited the first growth year at sea were significant different between the 1SW and MSW Atlantic salmon (ANOVA: $F_{1.239}$ =*7.01 p=0.008,* Fig 26). 1SW fish deposited a higher number of circuli than the MSW fishes. The mean inter-circuli distances during the first growth year at sea differ for the 1SW and MSW Atlantic salmon, but the difference is not significant (ANOVA: $F_{1.239}$ =*2.82 p=0.095,* Fig 27). The mean inter-circuli distances are higher for 1SW fish than the MSW fishes.

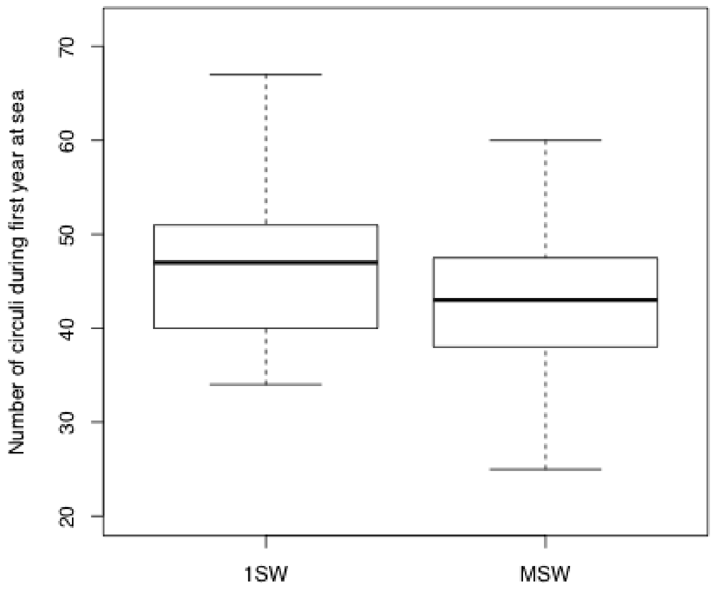

Fig 26 Mean number of circuli deposited on scales of 1SW and MSW Atlantic salmon during first growth year at sea. All scales are from Atlantic salmon captured at Stumpodden 2004-2010.

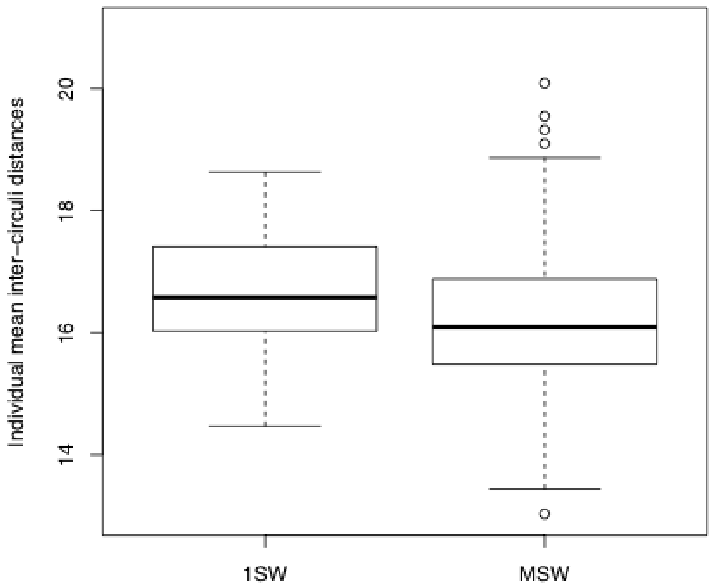

Fig 27 Individual mean inter-circuli distances (pixels) of 1SW and MSW Atlantic salmon first growth year at sea. All scales are from Atlantic salmon captured at Stumpodden 2004-2010.

4.6 Modelled sea-surface temperature

There was best support (AIC-based) for one common trend, which described the SST for the five sites (Fig 28). All sites loaded positively on the model (Fig 29). The site Lindesnes loaded the most, consequently generated highest amplitudes in SST during the period, 1999-2010.There was high variation in the peaks of summer SST observed between years. In the years 1999-2001 the summer peaks were at a low level. During 2002-2004 the summer peaks were high, before it dropped in 2005. The low point of winter SST varied between years, but at lower amplitudes than the summer peaks.

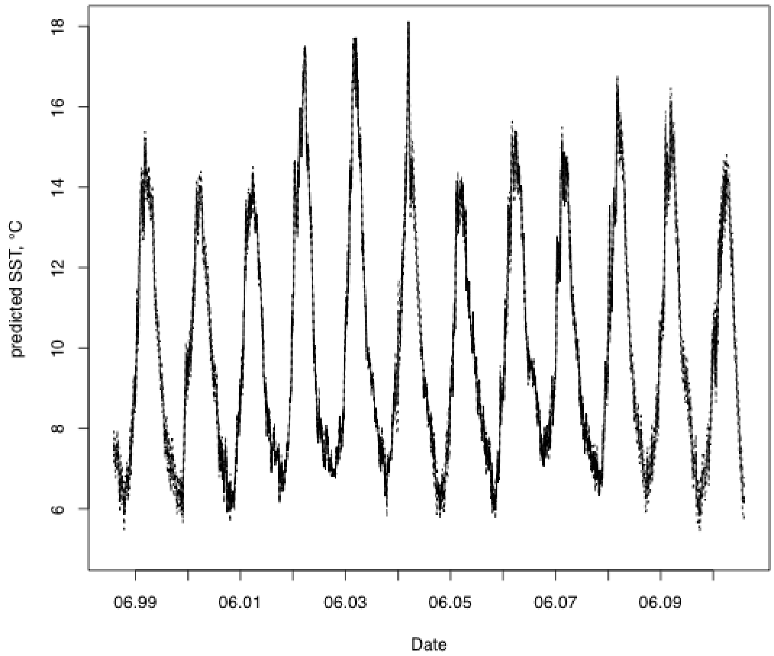

Fig 28 The DFA-predicted (common trend) sea-surface temperature (ºC) in the years 1999-2010. Temperature data were obtained from five localities in the North Sea, Norwegian Sea and Skagerrak coast

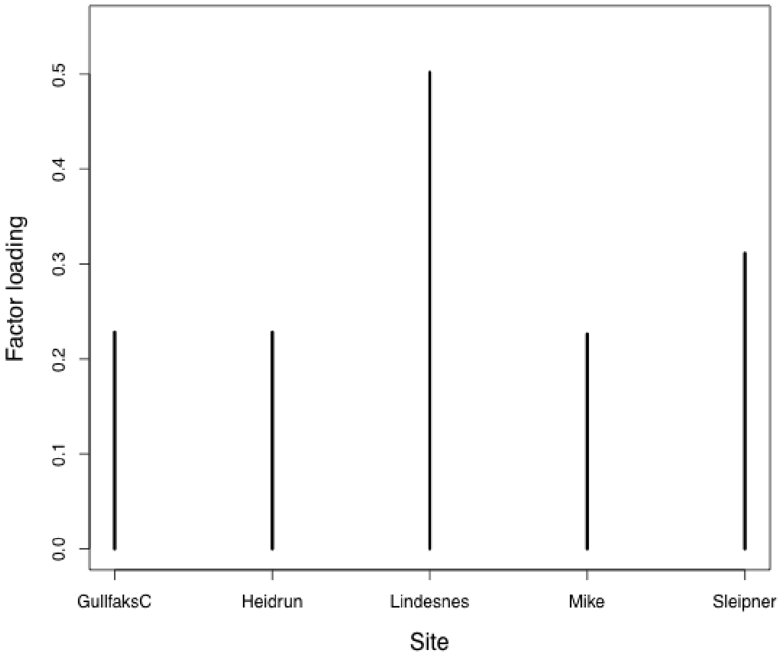

Fig 29 Factor loading on the DFA sea-surface temperature model for the various sites located in the North Sea (GullfaksC and Sleipner), Norwegian Sea (Heidrun and Mike) and on the Skagerrak coast (Lindesnes).

5. Discussion

Measurement errors and sampling error

The measurement errors from the scale readings in this study are low; consequently one reading of each scale was enough to obtain a precise measure. This finding illustrate that the scale measurement in my study are more accurate then the scale measurements obtained by Jonsson and Stenseth (1976).

Findings in this study demonstrate that as one includes more scale replicates in the analysis, the sampling error declines. This illustrates the problem with using only one scale per fish for retrospective growth analysis. When choosing the optimal number of scales for analysis one have to make a decision between the reduction in sampling error by including another scale and the time spent by reading scales. In this study I used four scales per fish, based on the mentioned factors and the inflection of the modelled line. These findings are in accordance with that of Jonsson and Stenseth (1976). In future scale analysis I recommend that more than one scale per fish is incorporated in the analysis, and that four scales seem to be a number that both take into account the amount of work and requirements for precision.

Atlantic salmon growth at sea

The inter-circuli distances rapidly increased after sea entry, indicating an increased growth rate when the smolts enter seawater. When experiencing starvation or reduced food quantity related to smolting, the Atlantic salmon post-smolt might put on a growth spurt above normal growth rates when food levels are restored (Maclean & Metcalfe 2001; Friedland et al. 2009b). This compensation is what we might see in the increasing inter-circuli distances after sea entry. When inter-circuli distances starts to level off at circuli number six, the compensation for the energy losses at smolting are probably restored, and a “normal” post-smolt growth is resumed. These findings are in accordance with the retrospective growth analysis of Atlantic salmon smolts entering the Gulf of St. Lawrence from the Miramichi River (Friedland et al. 2009b).

Another hypothesis explaining the inflection on the inter-circuli distance curve might be that there is a bottleneck for the growth and survival at this point. Reduced inter-circuli distance at circuli number six might be an indicator of post-smolts facing unfavourable conditions related to temperatures or food supply (McCarthy et al. 2008; Friedland et al. 2009b). One might expect to observe a marked reduction in the growth rate if there was a bottleneck. In this study, the reduction in the inter-circuli distances was not pronounced. Nevertheless Atlantic salmon captured at Stumpodden are fish, which have survived this potential bottleneck, and the post-smolt mortality at this point is thus not traceable in my data. There might however be high mortality in this period as documented in other studies (McCarthy et al. 2008; Friedland et al. 2009b).

There was a significant year-to-year variation in the Atlantic salmon post-smolts inter-circuli distances. This indicates that there was a variation in the growth rate between years, and this variation may be related to temperature and food supply (Friedland et al. 2000; Hvidsten et al. 2009). Results from River Orkla demonstrate that the thermal conditions experienced by post-smolts during their early sea migration may be crucial for the subsequent return rate of adults after one to three years at sea (Hvidsten et al. 2009). On the contrary, the June SST at Lindesnes did not explain the year-to-year variation in my data, and probably was the June SST at Lindesnes not a representative measure of the actual SST the post-smolt encountered during the first month after sea entry.

Another factor explaining year-to-year variation in the Atlantic salmon post-smolts inter-circuli distances may be the consequences of accumulated labile aluminium (LAl) in the gills of smolts before they entered seawater (Kroglund et al. 2007). Al in the gills of smolts inhibits gill NaK-ATPase activity, and thereby reducing hyposmoregulatory capacity and marine survival of post-smolt. Although River Mandalselva is limed, low concentration of LAl may still have a negative effect on the Atlantic salmon population (Kroglund et al. 2007). This might be a factor affecting both survival and growth of post-smolt from the rivers in southern Norway.

There was a reduction in the peaks of maximum inter-circuli distances for the MSW Atlantic salmon first growth year at sea over the entire study period, 2001-2008, indicating a reduction in growth during these years. The SST data obtained from my study does not indicate a general decline in the temperature. Although a general decline in the Atlantic salmon growth at sea over the last decades has been documented by other studies (Friedland et al. 1993; Friedland et al. 2000; Jonsson & Jonsson 2004; Friedland et al. 2005; Peyronnet et al. 2007;

McCarthy et al. 2008; Todd et al. 2008), and linked to variations in SST (Friedland et al. 1993; Friedland et al. 2000; Jonsson & Jonsson 2004; Todd et al. 2008).
The 1SW and MSW Atlantic salmon deposited an increasing number of circuli the first and second growth year at sea from 2003–2004 (2002-2004 for MSW). There was an overall drop in total circuli number in 2005. Since the drop was present for all sea-age groups both first and second year at sea one can exclude any effects during smolting, post-smolt migration and spawning migration, and thus, the drop may indicate a year with unfavourable conditions in the North Atlantic Ocean. The SST data used in my study exhibited high peaks in summer SST during the years 2002-2004, before the summer SST dropped in 2005. A high growth rate should be expected when the summer SST is high, and vice versa, a low growth rate when the summer SST is at a low level. A temperature related growth for Atlantic salmon at sea are documented in other studies (Friedland et al. 2000; Jonsson & Jonsson 2004).

There is a lower year-to-year variation in the total circuli number deposited the second year at sea compared with the first year at sea. In terms of feeding habits there is a significant difference between Atlantic salmon first and second year at sea (Jacobsen & Hansen 2000; Haugland et al. 2006). Several studies have documented that stomach contents of returning Atlantic salmon consisted entirely of fish (Jacobsen and Hansen 2000). In contrast, stomachs of Atlantic salmon during the first year at sea contained up to one third of crustacean prey (Jacobsen and Hansen 2000). The observed difference in variation in circuli number between Atlantic salmon first and second year at sea, may be due to the fluctuation in preferred pray abundances. Haugland et al. (2006) documented large year-to-year variation in the diet of Atlantic salmon during their first year in the Norwegian Sea. They found a positive relationship between the forage ratio of the Atlantic salmon during the first year at sea and the abundance of herring (*Clupea harengus*) recruits (Haugland et al. 2006). There may be a higher variation in abundance of suitable prey for the Atlantic salmon during their first year at sea compared with the second year at sea.

There was a significantly higher number of circuli deposited in scales of 1SW Atlantic salmon compared with the MSW fishes during the first growth year at sea, and a higher mean inter-circuli distances during the first growth year at sea for 1SW fish than the MSW fishes. This indicate that 1SW Atlantic salmon had a higher growth rate than the MSW fishes during their first year at sea. These findings are in contrast to Hutchings and Jones (1998) that found a positive among-population association between sea-age at maturity and growth rate at sea for

Atlantic salmon. Moreover, Norwegian MSW populations tend to grow faster than 1SW population (Jonsson et al. 1991).

The observed differences in growth rate between 1SW and MSW first year at sea indicate that a high growth rate may result in maturation after one year at sea. These findings are opposed to earlier findings and the general view of growth related maturation for Atlantic salmon at sea (Jonsson et al. 2003). Fish appear to delay maturation when the growth rate stays high, and attaining maturity when the growth rates starts to level off (Jonsson & Jonsson 1993). In contrast to Atlantic salmon parr that mature younger than slow growers and Pacific salmon slow growers at sea are associated with older age at maturity in those species with multiple ocean age groups (Jonsson et al. 2003). One might think that both increased and decreased growth rate may induce maturity (Jonsson & Jonsson 1993), and that Atlantic salmon with an intermediate growth rate during first year at sea become MSW fishes.

The observed difference in circuli number and inter-circuli distances between 1SW and MSW Atlantic salmon first year at sea may be intensified by the catch selectivity of the bag net. The number and length distribution of the 1SW Atlantic salmon group captured at Stumpodden may not be representative for the cohort, because only the upper size fraction of the 1SW fish is captured by the bag net and the main run of the 1SW is timed after the bag net fishing period (Jonsson et al.1990; Strand & Heggberget 1996; Jonsson et al. 2003). Hence is the 1SW Atlantic salmon captured at Stumpodden mainly large fast growing individuals.

When testing circuli formation rate related to catch date there was a significant relationship between catch date and number of circuli after the winter band. There was a significant difference in the circuli formation rate for the different age groups. Consequently, 1SW fish, with the most circuli, had a higher growth rate in the spring than the MSW fish. There is a high probability that the different age groups of Atlantic salmon occur in separate areas in the North Atlantic Ocean and that the MSW group is located further away from their home river than the 1SW fish (Jacobsen et al. 2001). The MSW fish may start their spawning migration earlier in the spring than the 1SW. Hence the 1SW may spend longer time in the feeding area before migrating to the home river to spawn. There might also be differences in temperature and food supply in the various feeding areas.

Another explanation of the difference in circuli number between 1SW and MSW Atlantic salmon after the last winter-band may be that the smaller 1SW Atlantic salmon have a higher specific growth rate than the lager MSW fish and hence more circuli. The specific growth rate is size dependent and decreases with fish size. The circuli formation rate is positively correlated to specific growth rate (Pearson 1966; Bilton & Robins 1971a; Bilton & Robins 1971b; Fisher & Pearcy 1990; Fisher & Pearcy 2005; Peyronnet et al. 2007). These correlations might intensify the observed differences in circuli number between the sea-age groups.

In this study I found no obvious relationships between mean inter-circuli distances and total circuli number during the first and second growth year at sea. Moreover, there were a miss mach between the levels of maximum peaks of inter-circuli distances and total circuli number during the years at sea. Circuli formation rate and inter-circuli distance appear to be partly independent indicators of growth rate. Inter-circuli distance and circuli formation rate both seem to increase with increasing growth rate, but they do not increase at the same pattern in one individual, in a group or year class of Atlantic salmon. High growth rate results in wide inter-circuli distances and/or higher total circuli number. Low growth rate results in narrow inter-circuli distances or/and low circuli formation rate. It may even result in no circuli deposition at all, or even absorption of existing circuli (Shearer 1992a). These findings highlight the importance of considering both circuli number and inter-circuli distance for describing Atlantic salmon growth rather than to only rely on inter-circuli distances (Peyronnet et al. 2007). Consequently, future retrospective growth analysis using scales should use both circuli formation rate and inter-circuli distances to document growth.

Findings in my study indicate that the same number of circuli will not be deposited at a given time throughout the growth year at sea. The growth rate is higher in the spring and summer than in the autumn and winter. Moreover, the individual variation in seasonal growth rate is high. Consequently, it is probably difficult to relate circuli number to a given date or month. Friedland et al. (1993) suggested that the circuli formation rate might be generalized for the Atlantic salmon first growth year at sea. They suggested that mean formation rate is approximately four circuli per month during the spring and summer period, and two circuli per month in the autumn and winter. By using this assumption in further studies they related circuli number to putative months at sea and measured inter-circuli distances as the only measure of growth (McCarthy et al. 2008; Friedland et al. 2009b). The growth recorded over these inter-circuli distances and putative months does not necessarily occur over comparable periods in different years, as indicated in my study. When the goal of a study is to trace variation in growth rate, the variation in circuli formation rate should not be omitted.

There may be ways to link circuli number to periods or months during the Atlantic salmon growth at sea. Peaks of maximum and minimum inter-circuli distances may be linked to the period when the growth is at the maximum and minimum, when the photoperiods are at a maximum and minimum level (Peyronnet et al. 2007). This may hold because the Atlantic salmon growth rates are controlled by photoperiod cycles in addition to endogenous rates, food availability and temperature (Fjelldal et al. 2005). Another way of describing growth as inter-circuli distances is to scale the circuli number, like I did in this study. If dividing each circulus on the total number of circuli deposited for that individual that year, then all circuli number are between zero and one. Then it is possible to compare individuals with different total circuli number. But one may not trace the variation in circuli formation rate during the growth year at sea using this method.

Conclusion

The increases in the inter-circuli distances during the weeks after the smolts have entered seawater might be a sign of compensatory growth, or there may be a bottleneck for Atlantic salmon survival and growth, as indicated by the inter-circuli distances starting to level off, probably caused by unfavourable environmental conditions.

The observed variations in growth during the years at sea are probably related to variation in temperature that might act on fish growth directly by affecting physical processes or indirectly by affecting changes in the ecosystem. My study indicates that high growth rate may result in earlier maturation, while an intermediate growth rate during first year at sea most likely gives delayed maturation and thus MSW fishes.

I found that circuli formation rate is positively correlated with fish growth, and these findings highlight the importance of considering both circuli number and inter-circuli distance for Atlantic salmon growth, rather than to rely on inter-circuli distances only. Consequently, future retrospective growth analysis using scales should use both circuli formation rate and inter-circuli distances to document growth.

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