Factors explaining variation in the fecundity of female Baltic salmon (*Salmo salar*)
– the influence of length, body condition and growth rate at sea

Ulrika Tollerz Bratteby

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Abstract

Understanding factors influencing variation in fecundity is crucial to manage Atlantic salmon (*Salmo salar*) populations in the Baltic Sea. Larger individuals usually have a higher size-specific reproductive investment than smaller individuals, thus leading to a higher fecundity. Still, fecundity varies a lot among equally sized individuals and there is little known about what is causing this variation. In this study, I consider the effects of body length, condition and growth rate at sea on fecundity in Atlantic salmon females in the Baltic Sea. I collected fecundity data and data on growth rate history at sea in salmon originating from river Dalälven, which returned to spawn in mid-July to September 2004-2018, after spending two years at sea. I used scales to analyze marine growth patterns of the salmon. My results show that length is the factor that has the greatest influence on Atlantic salmon fecundity. Nevertheless, the relationship between fecundity, length and body condition varies among these years. In addition, there is a declining trend of how much of the variation in fecundity that can be explained by the interactive effect of length and body condition at the time of return to the river for spawning. Using circuli formation rate and inter-circuli distance as proxies for body growth, I show that growth rate during the first and second year at sea does not add to explain fecundity variation, after accounting for length and body condition. Still, being the factor determining body length, growth rate evidently has a great indirect effect on the fecundity of female Atlantic salmon. Individuals that grew poorly during their first year at sea did not compensate for their poor growth by growing faster during their second year at sea. In addition, the two growth estimates proved not to be related, which indicates that they are in fact independent factors of marine growth rate.

Though it may be other factors than marine growth patterns that are causing variation in the fecundity of same-sized female Atlantic salmon in the Baltic Sea, limitations to my dataset on growth rate at sea means it is still relevant to contemplate this as an independent factor possibly affecting fecundity. Furthermore, I conclude that it is important to include the rate at which circuli are formed in addition to the inter-circuli distance when using this method to similar or other studies in the future.

Keywords: Atlantic salmon, *Salmo salar*, Baltic Sea, fecundity, body size, body condition, growth rate, scale reading.

Sammanfattning

För att förvalta och bevara populationerna av atlantlax (*Salmo salar*) som finns i Östersjön är det viktigt att förstå vilka parametrar som påverkar deras fekunditet. Det är välkänt att stora och tjocka honor har högre fekunditet, med bland annat större eller fler ägg. Men vad orsakar variationen i fekunditet hos individer som är lika stora? I denna studie har jag beaktat effekterna av kroppsstorlek, kondition och tillväxtmönster till havs på fekunditet hos laxhonor i Östersjön. Jag samlade fekunditetsdata och data över tillväxtmönster under tiden till havs från honor som härstammade från Dalälven och som återvände för att leka i mitten av juli fram till september 2004-2018. För att studera honornas tillväxtmönster till havs använde jag laxfjäll från individer som fångades under sensommaren 2018, vilka återvände till Dalälven efter att ha spenderat två år till havs. Mina resultat visar att kroppslängden när honorna återvänder för att leka är den faktor som förklarar det mesta av variationen i fekunditet mellan år. Under 2004-2018 varierade förhållandet mellan fekunditet, kroppslängd och kondition och det blev allt mindre av variationen i fekunditet som kunde förklaras av dessa parametrar och av interaktionen mellan dem. Genom att använda hastigheten för bildandet av fjällets så kallade strior samt avståndet mellan dessa för att uppskatta tillväxthastigheten till havs visar jag att tillväxtmönster under det första och andra året som laxhonorna spenderar i Östersjön inte har någon direkt effekt på deras fekunditet. Men, eftersom den totala tillväxten till havs är det som avgör kroppslängden när laxarna återvänder för att leka har den ändå en stor indirekt effekt på honornas fekunditet. Individer som växte långsamt under sitt första år till havs växte dåligt även under det andra året, vilket innebär att det inte sker någon kompensatorisk tillväxt. Dessutom visade det sig att hastigheten med vilken det bildas strior och avståndet mellan striorna är oberoende av varandra och således inte indikerar samma sak vad gäller tillväxtmönster till havs.

Även om det kan finnas andra faktorer som förklarar varför det finns skillnader i fekunditet hos atlantlax som är lika stora och som lever i Östersjön finns det begränsningar i min data som innebär att fortfarande är relevant att fortsätta studera tillväxtmönster till havs i detta avseende. Utifrån mina resultat drar jag även slutsatsen att det är viktigt att använda bägge tillväxtmått inte enbart titta på avståndet mellan striorna, när denna metod används för liknande eller för andra syften i framtiden.

Nyckelord: Atlantlax, *Salmo salar*, Östersjön, fekunditet, kroppslängd, kondition, tillväxthastighet, tillväxtmönster, fjäll.

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1   Introduction

In most fishes, including Atlantic salmon (*Salmo salar*), there is a positive relationship between female body size and the number and size of eggs produced (Fleming 1996; Marteinsdottir & Begg 2002; Barneche *et al.* 2018). One of the reasons for this is that the size-specific reproductive investment is higher in larger individuals than smaller individuals (Jonsson *et al.* 1991b, 1997). To better understand variation in female fecundity, it is therefore important to consider variation in adult body size. Still, even though the fitness advantages of a big old fat fecund female fish are well known both in general (Hixon *et al.* 2014) and for salmonids specifically (Fleming 1996; Dickerson *et al.* 2002; Reid & Chaput 2012), less is known about what is causing variation in fecundity of equally sized individuals (Thorpe *et al.* 1984; Dickerson *et al.* 2002; Quinn *et al.* 2011). The environment experienced at sea, e.g. different prey communities, water currents and temperatures, could potentially affect the fecundity of Atlantic salmon females (Jonsson & Jonsson 2009; Keinänen *et al.* 2012, 2018) through favouring energy allocation into either somatic growth or energy storage (Fleming 1996). When considering the effects of growth patterns (i.e. the subsequent periods of high or low growth rates) at sea on fecundity for different salmonid species, previous research have been inconclusive, as studies have shown both positive (Quinn *et al.* 2004, 2011) and no (Jonsson *et al.* 1996) relationship between growth patterns at sea and fecundity. One potential reason for such varying relationships could be that these studies are made on different salmonid species and systems. Another could be that the authors used different methods for calculating growth at sea, e.g. using scale readings for comparing the size of adult fish to that of the time when the juvenile migrated out to sea with (Quinn *et al.* 2004) or without (Jonsson *et al.* 1996) considering the number of growth seasons the salmon spent at sea. Yet, given that growth at sea might influence fecundity of equally sized salmon and, since only one of these studies have investigated the direct effects of growth patterns at sea on Atlantic salmon fecundity, we still do not know how growth patterns at sea affect the fecundity of equally sized Atlantic salmon in other systems than River Imsa (Jonsson *et al.* 1996).

Most fish have indeterminate growth, meaning they continue to grow throughout their lives. Individual differences in growth rate causes variation in size-at-age of Atlantic salmon (Forseth *et al.* 2011) and it also influence the age or size at which an individual reaches sexual maturity (Wootton 1998). In addition, since individuals can grow at different rates during their life-span, individuals of the same age and size can vary in their growth histories (Dietrich & Cunjak 2007). For several anadromous salmonid species, growth varies depending on e.g. biotic factors such as food availability (Keeley & Grant 2001), age and body size (Forseth *et al.* 2011), and inter- or intraspecific interactions (Pyper & Peterman 1999; Chamberlin *et al.* 2017), or with abiotic factors such as water temperature (Handeland *et al.* 1998; Friedland 2000), salinity (Handeland *et al.* 1998), oxygen level (Brett 1952; Hosfeld *et al.* 2008) and photoperiod cycles (Björnsson 1997; Fjelldal *et al.* 2005). For Atlantic salmon in the Baltic Sea, there is great spatial variation in prey availability, prey quality, temperature and salinity, which could affect the growth potential of salmon depending on where it is feeding (Casini *et al.* 2014; Keinänen *et al.* 2017; Jacobson *et al.* 2018).

In seasonal environments, the growth of fish is higher during the warm compared to the cold seasons (Forseth *et al.* 2011). Such annual patterns, where a season with low growth rate follows one of fast growth, as well as when salmon undergo their ontogenetic habitat shift between fresh and salt water, can be traced by irregularities in calcified structures such as scales (Frost & Kipling 1959; Steinmetz & Müller 1991), otoliths (Tsukamoto & Kajihara 1987) and bones (Le Cren 1947; Frost & Kipling 1959). In salmon, fish scales are typically used for age determination and growth analyses (Fisher & Pearcy 1990; ICES 1998; Marco-Ruis *et al.* 2013). Similar to tree growth rings, scale circuli are deposited at the scale margin as fish grow (Wootton 1998). The scale circuli formation rate and the distance between successive pairs of scale growth rings (inter-circuli distance) of salmonids have been found to positively correlate with growth rate (Fisher & Pearcy 1990, 2005). Thus, variation in body growth patterns can be studied by calculating the number of circuli and the inter-circuli distance (Peyronnet *et al.* 2007) (Fig. 1). The faster the fish grows, the more circuli is formed per unit time and/or the wider is the spacing between circuli (Doyle *et al.* 1987; Fisher & Pearcy 1990).

In this study, I used scales to analyse the growth patterns at sea of female Atlantic salmon originating from the Swedish river Dalälven, which is connected to the Baltic Sea. In addition, I studied the relationship between fecundity and body length, body condition and growth at sea of returning salmon in Dalälven. I specifically ask if (1) the explanatory power of the relationship between length, condition and

salmon fecundity varies between years, (2) whether there is a relationship between growth during the first and second year at sea and (3) if variation in the fecundity of same-sized female salmon could be explained by differences in growth patterns at sea, after accounting for their length and body condition. I hypothesize that (i) the relationship between length, condition and salmon fecundity is constant between years, (ii) that growth during the second year at sea depends on the growth rate the year before, and consequently, that an individual that grow poorly during its first year at sea will compensate for this by growing faster during the next. Finally, I hypothesize that (iii) differences in marine growth pattern between individuals can explain variation in the fecundity of same-sized Atlantic salmon females.

2 Materials and Methods

2.1 Study species and system

In the Baltic Sea, there are distinct genetic populations of Atlantic salmon. Anthropogenic activities such as damming of rivers for hydropower and stream alterations for logging (e.g. channel widening and displacement of main-channel gravels) have negatively affected the overall ecological status of Baltic Sea rivers and as a consequence, degraded salmon reproduction areas and the life conditions of Baltic salmon (Johansen *et al.* 2001; HELCOM 2011). Because these modifications have decreased the reproduction potential for salmon, many populations in the Baltic Sea experienced a severe decline starting in the middle of the 19th century as they could not sustain themselves via natural reproduction (Karlsson & Karlström 1994; HELCOM 2018; ICES 2018). To compensate for the reduction in natural production, stocking of salmon has been widely practised. In 2017, 4.3 million salmon smolts were released into the Baltic Sea while the total wild production in all Baltic Sea rivers combined was 3.5 million smolts (ICES 2018).

Having an anadromous life history pattern, the Atlantic salmon hatch and develop as juveniles in the river, then migrating to the sea where they undergo most of their growth (McDowall 1997; Klemetsen *et al.* 2003). Once reaching maturation, they return to their natal river to spawn. Before leaving the river, juvenile salmon undergo the process of smoltification through which it undergoes changes to cope with life at sea (Hoar 1988). Emigrating Atlantic salmon post-smolts are assumed to shift to a piscivorous diet at the earliest possible occasion (Mitans 1970; Levings 1994; Sturlaugsson 1994), ultimately relating to the individual size of the juvenile salmon (Salminen *et al.* 2001). After smoltification, there is a key feeding period during the first few months at sea. During this time, the salmon experience a rapid increase in

growth, which reduces predation risk (Friedland & Haas 1996; Rikardsen & Dempson 2011), and they continue to grow and store energy until the onset of maturation. Some individuals become sexually mature after their first winter at sea (individuals referred to as one-sea winter, 1SW) while others reach maturation after spending several years at sea (multi-sea winter, MSW) (Vladić & Petersson 2015). The Atlantic salmon is iteroparous, meaning it can reproduce several times over its lifetime (Fleming 1996; Thorstad *et al.* 2011). However, most adults spawn only once before dying (Fleming & Reynolds 2004; Jonsson & Jonsson 2004). Due to its strong homing behaviour (Stabell 1984; Thorstad *et al.* 2011), the majority of the Atlantic salmon individuals usually find their natal river after reaching sexual maturation, where they will migrate upstream to spawn in the area they left as smolts. Given that Atlantic salmon do not feed during the time between reaching their natal river (May-July) and the actual spawning event (November-December), they rely on the energy storage they have accumulated while feeding at sea to survive the upstream migration, develop gonads and to successfully spawn (Fleming 1996; Siira *et al.* 2009; Whitlock *et al.* 2018).

I conducted this study on one of the Baltic populations of Atlantic salmon (henceforth referred to as Baltic salmon), which were reared at Älvkarleby Fisheries Research Station, situated in the river Dalälven in central Sweden. Because of the hydro-electric power plant built in Älvkarleby in 1915, anadromous fish are unable to migrate upstream beyond the first dam to reproduce. Due to this migration barrier, the salmon population in river Dalälven is dependent on compensatory releases of salmon smolt to compensate for the loss in natural production (Petersson *et al.* 1996). At the Fisheries Research Station in Älvkarleby, roe from spawning females is fertilized and the offspring are reared in tanks until smoltification, when the juveniles become silvery and start to swim with the current instead of against it in the rearing tanks. This usually happens after two years in the hatchery, at a size of 170 to 220 mm (ICES 1998). The research station releases approximately 140 000 hatchery reared salmon and trout each year (ICES 2018).

2.2   Fish growth and aging fish

To study the growth rates experienced by the Baltic salmon during its time at sea, I used fish scales. Most fishes in the Baltic Sea grow considerably slower during winter (Diana 1979). When growth rate increases due to favourable conditions, as it does e.g. when the Baltic salmon smolts migrate from their natal river out to sea, it is visible in the scale as more circuli (visible as circular ridges, Fig. 1a) are being

formed per unit time (Doyle *et al.* 1987) and the circuli spacing, i.e. the distance between circuli, becomes wider (Fisher & Pearcy 1990) (Fig. 1b). Consequently, the end of the freshwater growth zone i.e. the time of sea migration can be visually identified by a substantial increase in inter-circuli distances (Wootton 1998). I identified this transition zone, i.e. the beginning of the marine growth zone, as in ICES (2011) (Fig. 1b). During winter, inter-circuli distances are short (Wootton 1998). In accordance to Shearer (1992), I considered one year of marine growth to be complete where the last of the narrow spaced circuli of the winter band transitioned into the first of the wide-spaced circuli of the following summer band (ICES 2011) (Fig. 1b). I defined the start of the second year at sea as being equal to the end of the first. I used two parameters as estimates of fish growth rate: inter-circuli distance and number of circuli (Fig. 1a).
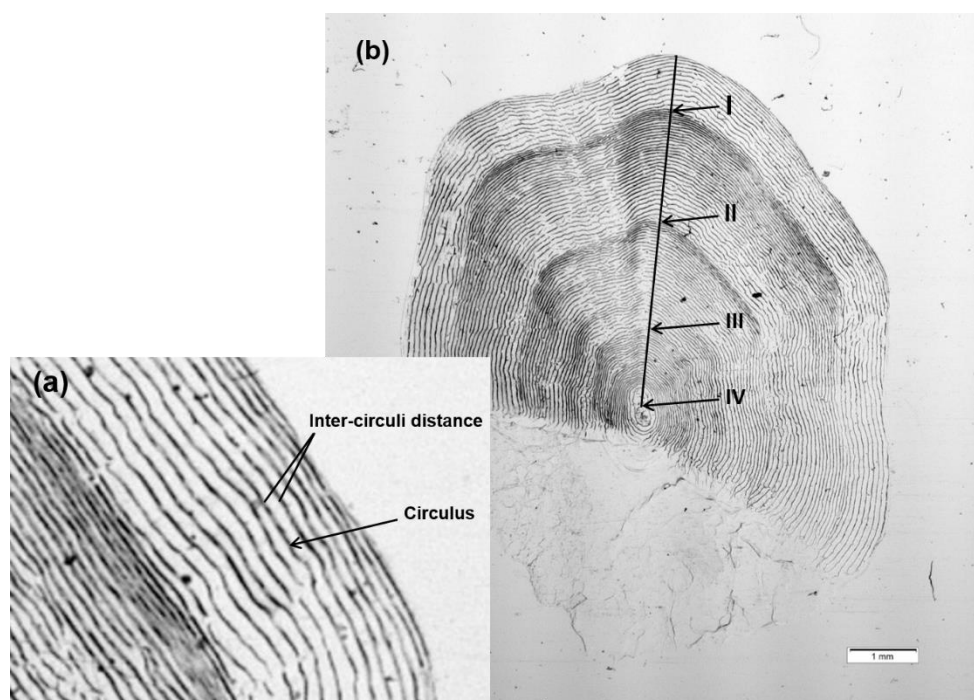

Figure 1. Scale impression of a 2SW female salmon caught in river Dalälven 2018. (a) The proxies for growth rate used in this study include the number of circuli formed during one growth season and the inter-circuli distances. (b) Scale features also include (I) the focus, (II) the beginning of the marine growth zone and the end of (III) the first and (IV) second sea winter.

2.3   Fecundity data

In 2004-2018, Baltic salmon migrating upstream to spawn in river Dalälven were caught in a fish trap located at the first dam. When the fish are caught, in mid-July to September, all individuals are tagged, weighted and length-measured. Females

and males are kept in separate tanks until the spawning event, which usually stretches from mid-October to late November. The fish are continuously monitored, and their health condition and reproductive status are supervised when approaching the time for spawning. When ready to spawn, the female salmon are sedated, weighted, measured and stripped of roe, and then weighted again (Table 1). Data collected on female fecundity include total egg biomass, volume, size, and colour. I used total egg biomass as the estimate of fecundity. This was given by subtracting the female's weight after being stripped for roe from the weight measured before. I used Fulton's K (Ricker 1975) as a measurement of body condition, following Eq. 1:

$$K = \frac{100W}{L^3}$$ (Eq. 1.)

where W is fish wet weight in grams, and L is body length in centimetres, with both measurements taken on the returning salmon at catch.

Table 1. *Number of individuals (n) sampled from river Dalälven for data collection on fecundity.*

Year	Sample size (n)	Size-range (cm)
2004	151	65-110
2005	132	62-108
2006	95	78-113
2007	108	64-110
2008	130	72-107
2009	137	68-113
2010	129	66-105
2011	111	67-105
2012	121	68-115
2013	105	73-106
2014	85	68-107
2015	98	72-108
2016	92	75-108
2017	97	67-115
2018	117 (104)*	70-106 (70-100)*

*Not*e: Subsample of 2SW female Baltic salmon.

2.4   Scale preparation and growth rate analysis

Scales were sampled from a restricted area close to the adipose fin and above the lateral line in females caught in 2017-2018. In 2017, scales were collected at the time of spawning (late fall). In 2018, scales were taken already when the fish were caught in the trap during summer. The scales were stored in paper envelopes until I prepared them for growth analyses. This process included making an impression of each scale by pressing them onto an acetate slide by a jewellery roller (Salsea-Merge 2008). I used a stereoscopic microscope (Olympus SZX9 with 16x magnification) with a digital camera (Olympus DFPL with 0.5x magnification) to record an image of each scale impression, with a calibrated scale bar for reference (Fig. 1b). For each image, measurements of marine growth rate were made using the open source processing program ImageJ, version 1.52i (ICES 2013; Rueden *et al.* 2017), applying the macro "Tree rings" in plugin ObjectJ, version 1.04q (Vischer & Nastase 2009). All distances, measured in millimetre, started at the centre of the focus, or in the case of so called replacement scales (where the original scale has been lost): from the middle of the central region, to the scale margin (Fig. 1b). The software marks circuli automatically by analysing the contrast between the dark circuli and the light spacing and it also calculates the inter-circuli distances (Fig. 2 and Appendix 2). Still, to make sure the software did not exclude or added circuli, I checked and if necessary corrected circuli markings for each scale image manually. I used a subset of two scales per female and made two separate readings for each scale to minimize sampling variation (Haraldstad *et al.* 2016). Based on these readings, I obtained a mean value of the number of individual circuli and the mean inter-circuli for each scale and individual. Given the poor condition of the scales collected in 2017, most likely because of sampling close to the spawning event before which the scales start to degrade (ICES 2011), these were not included in the analyses.

2.5   Statistical analysis

I statistically tested if (1) the explanatory power of the relationship between length and condition on salmon fecundity varies between years, (2) whether there is a relationship between growth during the first and second year at sea in females caught in 2018 and (3) if variation in the fecundity of the 2018 same-sized female salmon can be explained by differences in growth during the first and second year at sea, after accounting for their length and body condition. I used linear regression models to analyse the relationship between female fecundity (total egg mass) and length and body condition (Fulton's K) at the time of return to river, including the interaction between length and body condition. I conducted model selection based on the

Akaike Information Criterion (AIC), of which I selected the model(s) with the lowest AIC value (+ 2 units). This allowed me to study which models that were the most parsimonious.

I applied model selection for analysing growth-related effects on length, body condition and fecundity. For this purpose, I used a subset of the scale data so that it only consisted of the females that had spent two winters at sea (here forth referred to as "2SW"), collected in 2018 (Table 1), since there were no 1SW individuals and because the sample size of individuals older than 2SW were too small (n = 13) to be used in any statistical analyses. I used linear regression to assess the relationship between growth rate during the first and second year spent at sea. To asses if individual variation in growth rate varied between the first and second year, I compared the coefficient of variation (CV) for each growth season. Using Pearson's product moment correlation, I also examined if there was a correlation between the two different estimates of growth rate at sea; scale inter-circuli spacing and the number of circuli deposited. Lastly, I tested whether growth rate at sea, both during the first and second year, affects fecundity after accounting for the effect of body size and
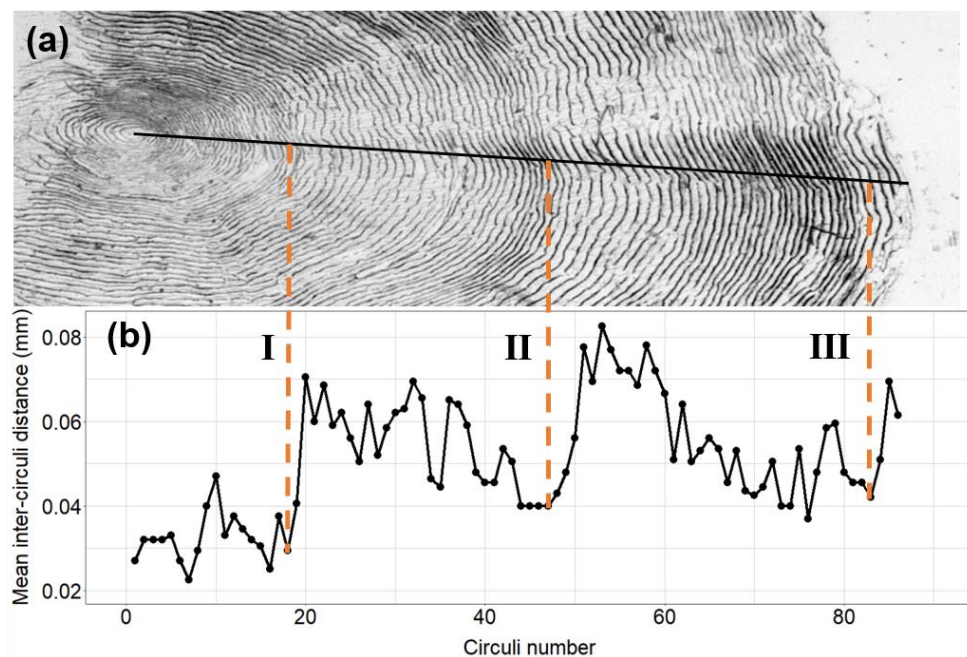

Figure 2. From the scale image (a) of a 2SW Baltic salmon female, circuli is automatically marked by ImageJ plugin ObjectJ along the black line, which provides a growth rate profile (b) of the mean inter-circuli distances. From the profile, it is possible to visually identify the start of the marine growth phase (I), the first (II) and the second (III) winter at sea.

condition. This was done by fitting a linear regression model using the growth proxies inter-circuli distance and number of circuli to the residuals obtained from the linear regression model including interactive effect of body length and condition on female fecundity. I used adjusted R^2 as the coefficient of determination and I conducted all statistical analysis using the software R, version 3.5.2 (R Core Team 2018). P-values of 0.05 or less were considered as significant.

3 Results

3.1 Variation in length, body condition and fecundity

During 2004-2018, the mean length of female salmon at return to river Dalälven varied between 84.4-93.0 cm and the mean body condition (Fulton's K) at catch varied between 0.97-1.16 (Fig. 3a, b). There was a positive relationship between female fecundity (i.e. total egg biomass) and body length ($F_{1,1708} = 3979$, $R^2 = 0.70$, $P < 0.001$) (Fig. 4a) and condition ($F_{1,1708} = 75.80$, $R^2 = 0.04$, $P < 0.001$) (Fig. 4b) at return to river Dalälven, for all years combined. Four outliers were identified (condition factor >1.6) (Fig. 4b), but these had no major influence on the above relationship ($F_{1,1704} = 85.47$, $R^2 = 0.05$, $P < 0.001$). Length, rather than body condition, was the variable explaining most of the variation in fecundity (Table 2) while the most parsimonious model explaining fecundity, in addition to length, included the interaction between length and body condition (Table 2). However, there was large variation in the explanatory power of this interaction among years (R^2 ranging between 0.66-0.90) and it declined during the study period ($F_{1,13} = 9.98$, $R^2 = 0.39$, $P < 0.0075$) (Fig. 5).

Table 2. *Variables, coefficients and the corresponding AIC values of the linear regression models of fecundity in female Baltic salmon collected in Dalälven 2004-2018. Fecundity is measured as total egg biomass per individual. Body length and condition factor (Fulton's K) were measured at return to the river. The model with the lowest AIC value is highlighted in bold.*

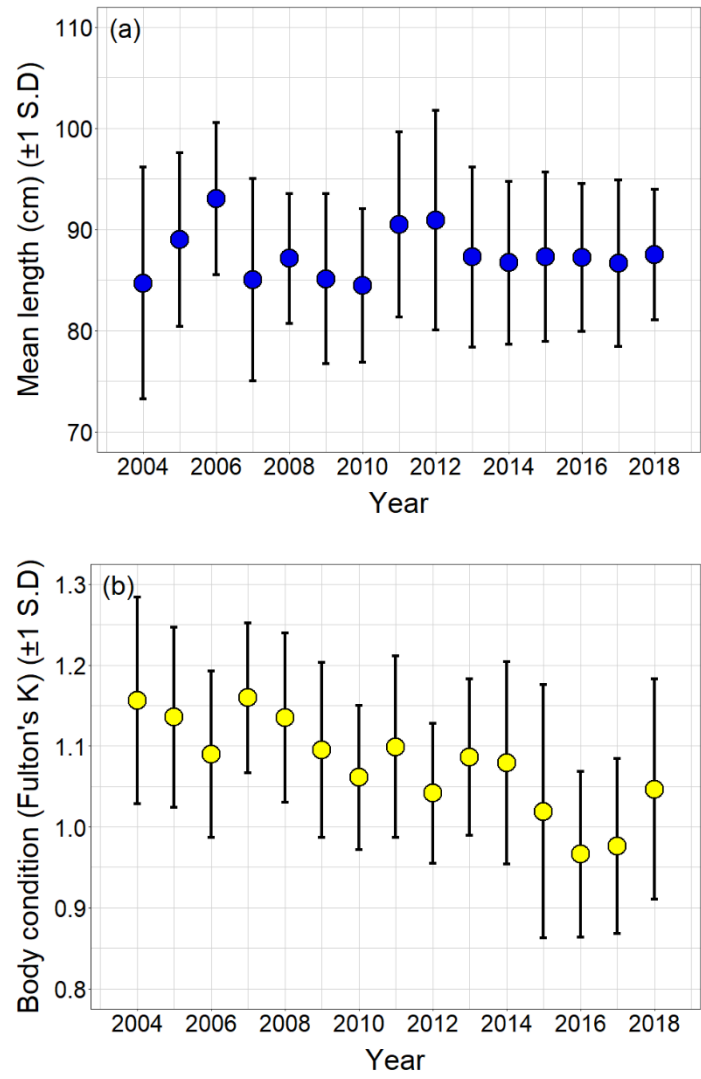| Model parameters	AIC	F(df)		R^2	P
Length x Condition	**378**	**2381.00**	**(3,1706)**	**0.81**	**< 0.001**
Length + Condition	408	3491.00	(2,1707)	0.80	< 0.001
Length	1132	3979.00	(1,1708)	0.70	< 0.001
Condition	3114	75.80	(1,1708)	0.04	< 0.001

Note: AIC, Akaike Information Criterion.

Figure 3. (a) Mean length (cm, ±1 standard deviation, S.D), and (b) mean body condition (±1 S.D), calculated as Fulton's K, of female Baltic salmon at return for spawning in river Dalälven for the years 2004-2018.
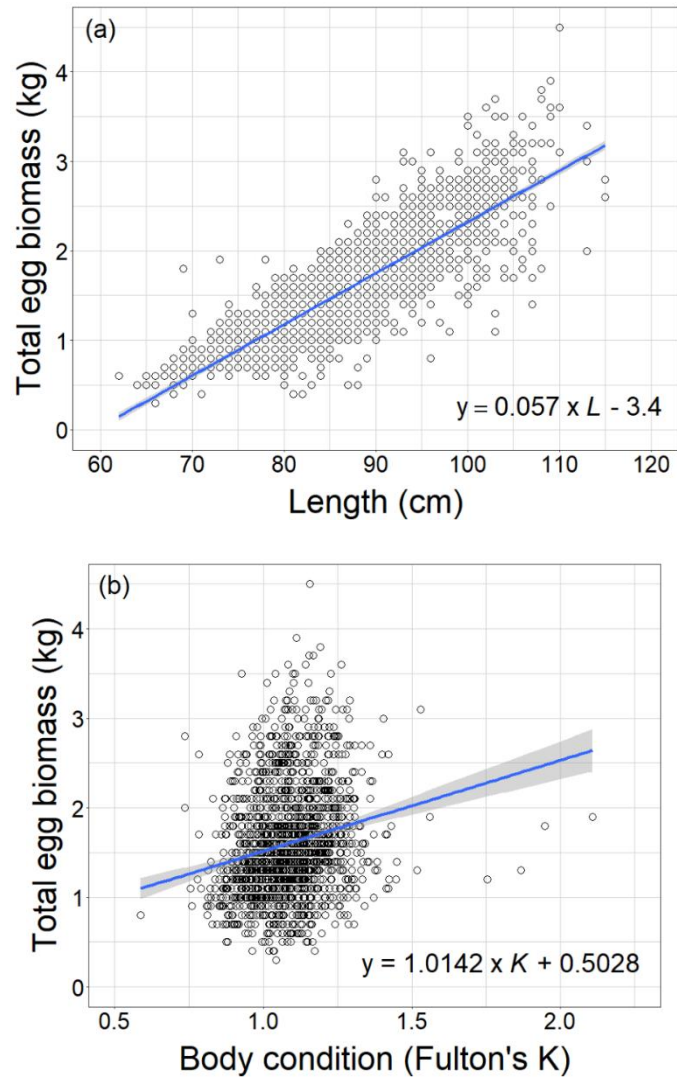
Figure 4. The relationships between (a) length (cm), (b) body condition (Fulton's K, at return to river) and total egg biomass (per individual) of salmon in river Dalälven 2004-2018. Solid lines represent significant relationships.
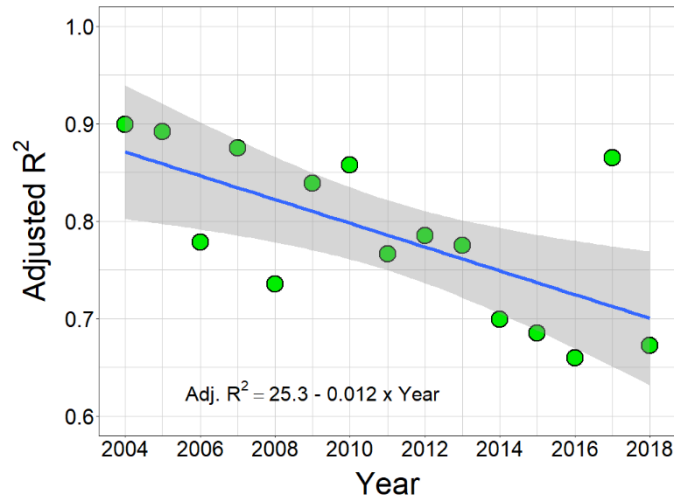
Figure 5. Annual variation in explanatory power (adjusted R^2) of the regression model explaining produced egg biomass (i.e. fecundity) per individual for the years 2004-2018 as a function of length (cm) and body condition (Fulton's K, at return to river Dalälven) and their interaction.

3.2 Variation in and consequences of early and late growth rate at sea

Salmon body size, at the time of return to river, had a significant and positive relationship to the number of circuli, but showed no relationship to inter-circuli distance (Table 3 and Appendix 1). Neither of the two growth estimates could add to explain variation in condition (Table 4 and Appendix 1). In 2018, growth rate (measured as inter-circuli distance and number of circuli) varied substantially among individuals, but more so during the first year at sea than during the second (Fig. 6a-d). There was no correlation between the two growth measurements, inter-circuli distance and the number of circuli (R = 0.00, P = 0.73). However, there was a positive relationship between indicators of marine growth rate during the first and second year at sea, both when measured as inter-circuli distance ($F_{1,88}$ = 18.27, R^2 = 0.16, P < 0.001) (Fig. 7a) and as number of circuli deposited ($F_{1,88}$= 5.49, R^2= 0.05, P < 0.02) (Fig. 7b).

Tabell 3. *Variables, coefficients and the corresponding AIC-values of the linear regression models explaining length at return to the river in 2SW female Baltic salmon (collected in Dalälven 2018). 0+ refers to the first year spent at sea and 1+ to the second. The model(s) with the lowest AIC value is highlighted in bold.*

Model parameters	AIC	F(df)		R^2	P
Mean inter-circuli distance 1+	**555**	**0.05**	**(1,88)**	**-0.01**	**0.82**
Mean inter-circuli distance 0+ + 1+	**556**	**0.72**	**(2,87)**	**-0.01**	**0.49**
Mean inter-circuli distance 0+ x 1+	558	0.48	(3,86)	-0.02	0.70
Mean inter-circuli distance 0+	632	1.14	(1,100)	0.00	0.29
Mean number of circuli 0+ x 1+	**534**	**9.00**	**(3,86)**	**0.21**	**< 0.001**
Mean number of circuli 1+	539	17,59	(1,88)	0.16	< 0.001
Mean number of circuli 0+ + 1+	540	9.12	(2.87)	0.15	< 0.001
Mean number of circuli 0+	623	10.20	(1,100)	0.08	< 0.01

Note: AIC, Akaike Information Criterion.

Tabell 4. *Variables, coefficients and the corresponding AIC-values of the linear regression models explaining condition at return to the river in 2SW female Baltic salmon (collected in Dalälven 2018). 0+ refers to the first year spent at sea and 1+ the second. The model(s) with the lowest AIC value is highlighted in bold.*

| Model parameters	AIC	F(df)		R^2	P
Mean inter-circuli distance 0+	**-116**	**0.20**	**(1,100)**	**-0.01**	**0.66**
Mean inter-circuli distance 1+	-99	0.00	(1,88)	-0.01	0.95
Mean inter-circuli distance 0+ + 1+	-98	0.09	(2,87)	-0.02	0.91
Mean inter-circuli distance 0+ x 1+	-97	0.67	(3,86)	-0.01	0.57
Mean number of circuli 0+	**-119**	**2.73**	**(1,100)**	**0.02**	**0.10**
Mean number of circuli 0+ + 1+	-102	2.30	(2,87)	0.03	0.11
Mean number of circuli 1+	-100	0.64	(1,88)	0.00	0.43
Mean number of circuli 0+ x 1+	-100	1.52	(3,86)	0.02	0.22

Note: AIC, Akaike Information Criterion.
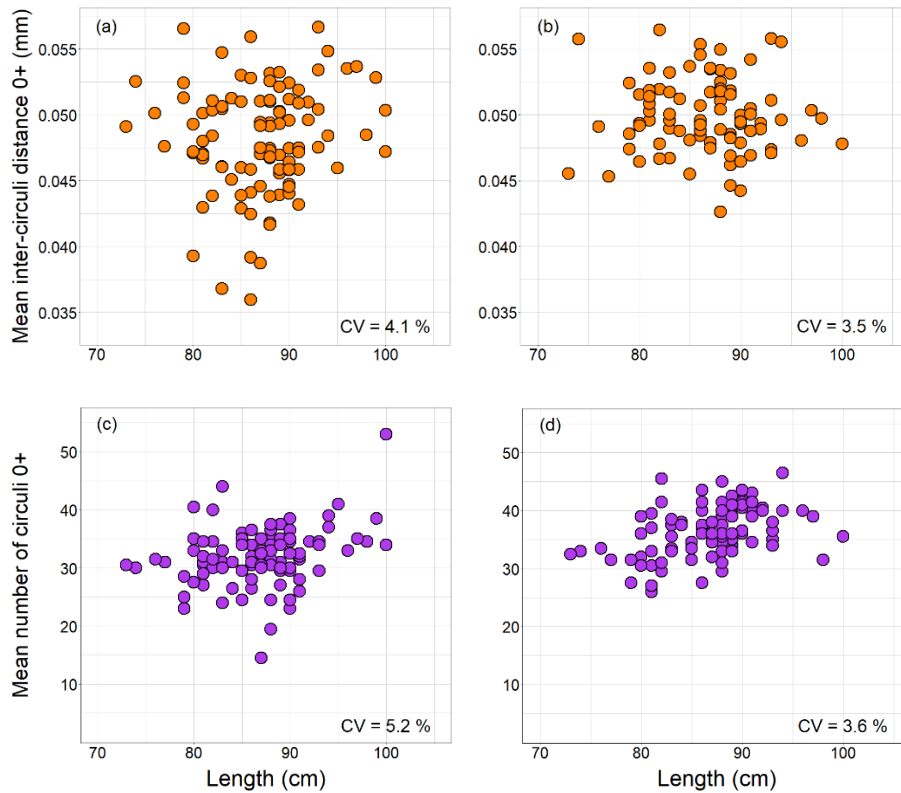
Figure 6. The variation in each of the two growth estimates for all female 2SW individuals caught in river Dalälven 2018: mean inter-circuli distance (mm) in 2SW female salmon during (a) the first (0+) and (b) second (1+) year at sea, and mean number of circuli in 2SW female salmon during (c) the first (0+) and (d) second (1+) year at sea. Each point represents one individual.

3.3 Growth rate at sea affecting fecundity

There was no relationship between growth estimates during the first or second year at sea and fecundity in 2SW female salmon 2018, in addition to what was already explained by the interaction of length and body condition (for which $F_{3,100} = 51.05$, $R^2 = 0.59$, $P < 0.001$). This held true for both estimates of growth; neither the inter-circuli distance during the first ($F_{1,100} = 1.75$, $R^2 = 0.01$, $P = 0.19$; Fig. 8a) or second ($F_{1,88} = 0.14$, adjusted $R^2 = -0.01$, $P = 0.71$; Fig. 8b) year at sea nor the number of circuli during these sea years (first year: $F_{1,100} = 3.31$, $R^2 = 0.02$, $P = 0.07$; second year: $F_{1,88} = 0.00$, $R^2 = -0.01$, $P = 0.98$; Fig. 8c, d) could provide any additional explanation to variation in fecundity after accounting for that explained by length, body condition and their interaction at return to the river.
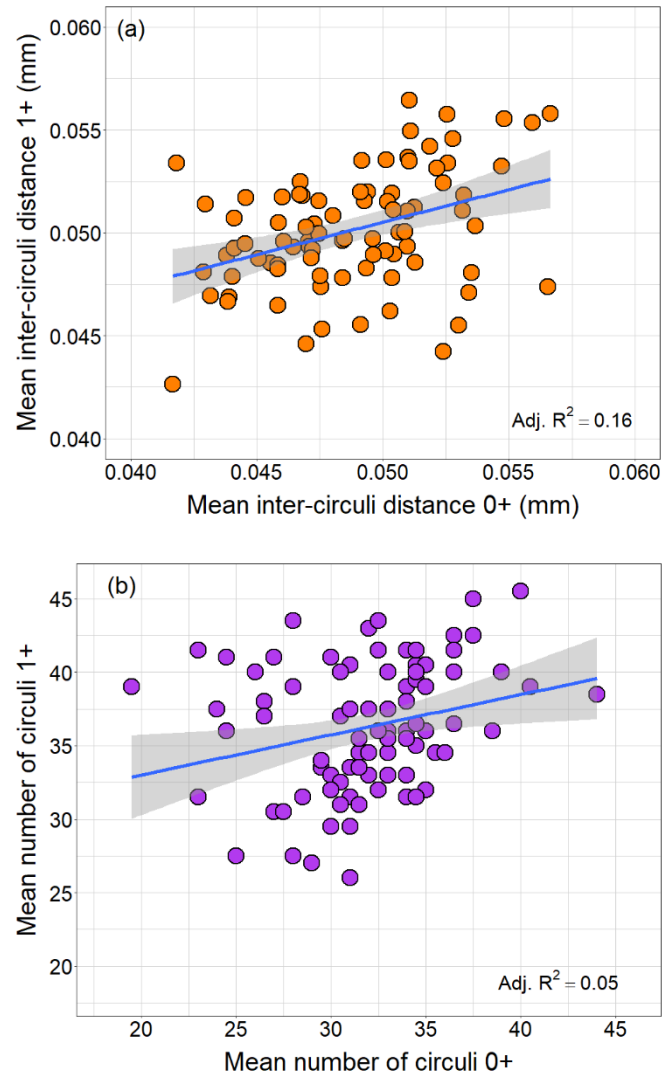
Figure 7. Relationships between the first and second year growth rate in female Baltic salmon at sea, based on (a) mean inter-circuli distance (mm) and (b) mean number of circuli. Solid lines represent significant relationships.
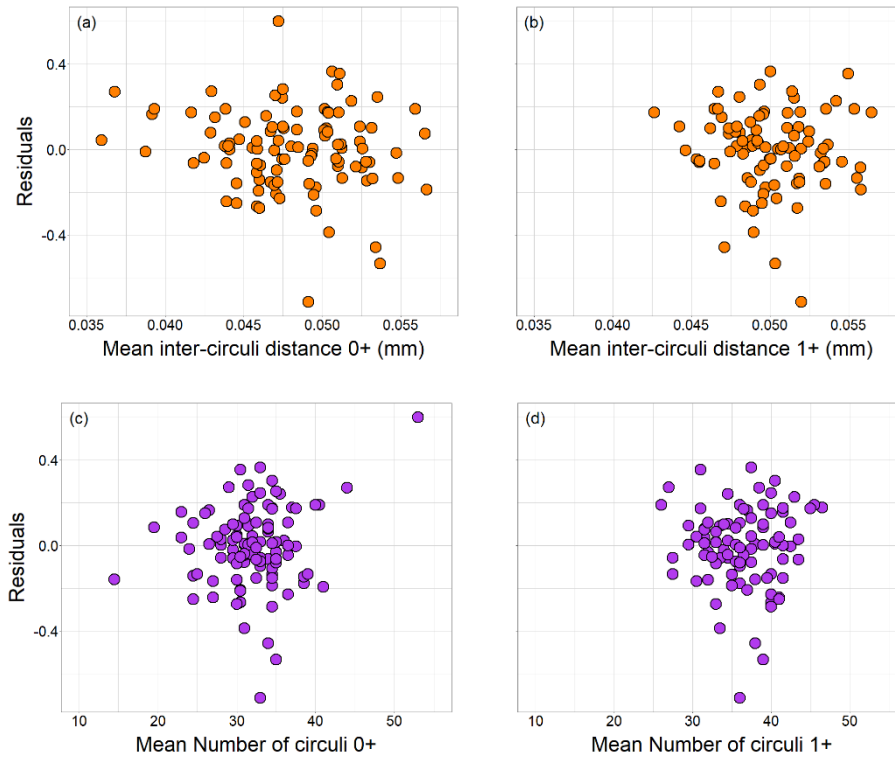
Figure 8. Relationship between the residuals obtained from the regression model explaining fecundity (total egg biomass) as a function of body length, condition and their interaction, at return to river Dalälven, and growth at sea (measured as mean inter-circuli distance) during (a) the first and (b) second year at sea. Also, the relationship between the residuals and growth at sea (measured as mean number of circuli) during (c) the first and (d) second year at sea.

4   Discussion

In this study, I show that there is year-to-year variation in the length and body condition of female Baltic salmon at the time of return to river Dalälven. Even though fecundity as expected was closely related to body size, I found that there was a decline over time in how much of the variation in fecundity that could be explained by female length and body condition. By using scale readings to determine salmon growth rate at sea, I show that individual variation in growth arises already during the first year at sea. In addition, high growth rates during the first year at sea meant high growth rates during the second year at sea. Thus, there is no evidence of compensatory growth, meaning that individuals do not compensate for poor growth during the first year at sea by growing faster during the second. I also find that female growth history at sea do not provide any additional explanation to why there is variation in fecundity, beyond the effects of length and body condition.

Fecundity evidently increases with female body size and condition, as has been confirmed in numerous studies on Atlantic salmon (Thorpe *et al.* 1984; Fleming 1996; Moffett *et al.* 2006; Reid & Chaput 2012; de Eyto *et al.* 2015). In accordance with my results, Moffett *et al.* (2006) identified length of Atlantic salmon to be the factor explaining the majority of the variation in fecundity (egg number). In addition to body length, Burton *et al.* (2013) found, similar to what is the case in my study, i.e. that an increase in body condition, for a given body size, led to an increase in fecundity. Still, I show that there are substantial differences in the extent to which variation in fecundity is explained by length and body condition (adjusted R^2 ranging between 0.66-0.90), and that the explanatory power of this interaction decreased in 2004-2018. This means that it at present is a lot of unexplained variation in fecundity (19 %) among female salmon in river Dalälven. There are several reasons why it is important to identify factors that can help predicting fecundity in Baltic salmon, including management of salmon populations in the Baltic Sea for conservation purposes and fisheries management. One factor that could add to explain the variation in fecundity other than length and condition, and which I have studied, is variation

in growth rate during the time spent at sea. However, using growth estimates from scales readings, I find that growth rate variation among female salmon adds little explanation to the remaining variation in fecundity after accounting for that explained by length and body condition. Nevertheless, since my study only included salmon which had matured after spending two years at sea, caught in 2018, it is also possible that the results would have been different if the study had included data collected over several years, multiple year-classes or if I had used a different methodology when measuring growth rate (e.g. studying the variation in growth during specific periods during the growth season).

Despite using different proxies for growth rate (i.e. calculating growth as the difference between adult body length and smolt length, divided by the number of growth seasons at sea), Jonsson *et al.* (1996) came to the same conclusion as I, i.e. that growth patterns at sea add little to explain variation in fecundity of Atlantic salmon, beyond the effect on body length at the time of return to river. Though using number of eggs and egg size as estimates of fecundity, two previous studies rather suggest that growth rate during the juvenile freshwater period affect Atlantic salmon fecundity, as higher growth rate during the time in freshwater led to more eggs but smaller egg size, independent of the effects of adult body size (Thorpe *et al.* 1984; Jonsson *et al.* 1996). Still, there are also studies on other anadromous salmonids suggesting that fecundity (e.g. number of eggs) differs depending on growth rate at sea, after controlling for body length (Quinn *et al.* 2004, 2011).

There are several reasons for why individuals can exhibit different grow rates at sea. These can include e.g. the effect of different "personal traits" such as risk taking behaviour when foraging (Biro *et al.* 2004) or differences in prey availability due to variation in the spatial distribution of Atlantic salmon in the Baltic Sea and thus, variation in feeding area (Kallio-Nyberg & Ikonen, 1992; Ikonen, 2006). Salmon prey species (Hansson *et al.* 2001; Vuorinen *et al.* 2014; Keinänen *et al.* 2018), size-specific prey availability (Jacobson *et al.* 2018) and prey quality (Keinänen *et al.* 2012, 2017; Casini *et al.* 2014) all varies spatially in the Baltic Sea. Interestingly, individuals form the same river (including my study system, river Dalälven) and born the same year feed in different areas of the Baltic Sea (Jacobson *et al.*, 2019, under review). How individuals behave when foraging and the differences in feeding areas and thus, food resources, may influence how much energy the individual can invest in somatic growth, therefore affecting the fecundity indirectly. However, based on my results it is likely that other factors than growth at sea influence the fecundity of salmon females in addition to final length and condition. Such factors could include e.g. variation in how much individuals invest in gonad development

(Alonso-Fernández *et al.* 2009). Also, the effects of variation in environmental conditions such as temperature, changes in prey quality and potentially the influence of environmental stressors such as toxins and diseases might not be visible in terms of affecting length or body condition, but may still influence fecundity. This could also be the reason why there is a decline in how much length and body condition to explain variation in fecundity among the years of this study.

Another possible factor causing variation in fecundity, not related to body growth rate at sea, is the influence of the conditions faced by the salmon when returning to the river to spawn. Salmon do not feed from the time that they leave the sea until the spawning event (Fleming 1996; Siira *et al.* 2009; Whitlock *et al.* 2018). Thus, while migrating upstream the river to reach their spawning grounds (in our study system, the dam is the first migration barrier), they rely on the energy that was stored during the time the salmon fed at sea. This energy is mainly allocated into three processes: metabolism, swimming and gonad development (Fleming 1996). As for other ectotherms, high temperatures increase the metabolic rate of fish. Thus, higher water temperatures could lead to a corresponding decrease in the amount of energy available for the salmon to invest in e.g. gonads (Jonsson *et al.* 1991a; Angilletta *et al.* 2002). Indeed, in a study by King *et al.* (2003), female Atlantic salmon that were exposed to elevated temperature during vitellogenesis (i.e. the phase of rapid ovarian growth which usually takes place during the summer and early autumn prior to the spawning event) experienced significant reduction in fecundity. Similarly, Pankhurst *et al.* (1996) found that in rainbow trout (*Oncorhynchus mykiss*), there were few fish that ovulated at elevated water temperatures and the fish that did had significantly lower egg production. The influence of river temperature on salmon fecundity was not studied here but would be an important factor to investigate in future studies aiming to explain variation in salmon fecundity in Dalälven and other rivers, especially between years.

Considering growth patterns at sea, my results show that salmon body size at the time of return to the river increased significantly with the formation rate of scale circuli (i.e. number of circuli), but not with inter-circuli distance. This result contrasts to some previous studies on salmonids, which have shown that both the rate at which circuli are deposited and the inter-circuli distance are positively correlated with body growth rate (and thus with length at return to the river) (Pearson 1966; Fisher & Pearcy 1990, 2005). Yet, inter-circuli distance is, to my knowledge, the proxy most commonly used for assessing salmon growth rate through scale readings (e.g. Friedland & Haas, 1996; Friedland & Reddin, 2000; Beamish *et al.*, 2004; Fisher & Pearcy, 2005; Hubley *et al.*, 2008; Soto *et al.*, 2018). Nevertheless, similar to the result of my study, Fisher and Pearcy (2005), when studying marine growth

rate in Coho salmon (*Oncorhynchus kisutch*), found that the circuli formation rate and inter-circuli distance were not correlated with each other. Also, studying Atlantic salmon body growth at sea, Peyronnet *et al.* (2007) found that the two growth estimates can suggest different patterns of growth. In fact, the authors concluded that estimates based on inter-circuli distance were more relevant during (and perhaps even restricted to) periods of poor growing conditions. These findings, as well as my own, indicate that the two growth rate-proxies: number of circuli and inter-circuli distance, are in fact independent estimates of growth rate. In addition, results from Fisher and Pearcy (1990) and Peyronnet *et al.* (2007) suggests that the rate at which circuli are formed or the inter-circuli distances could be related to several other factors besides growth rate, e.g. salmon age, size or environmental conditions. Thus, I find that when using scale readings for estimating salmon body growth at sea, it is important to use not only the inter-circuli distances as a proxy for growth rate but to also include the rate at which circuli are formed.

I found a positive relationship between growth rate during the first and second year at sea, i.e. the opposite of compensatory growth. As for fish in general, there are studies of salmonids, e.g. Atlantic salmon and Arctic charr (*Salvelinus alpinus*), that show that individuals usually experience accelerated body growth after periods of poor growth conditions (Johansen *et al.* 2001; Metcalfe & Monaghan 2001; Ali *et al.* 2003). Consequently, one would expect that an individual that grew poorly during its first year at sea would compensate for this by an increased growth rate during the following year, but this was not the case in my study. Accordingly, salmon growing poorly during their first year at sea are likely to be smaller at return to the river. This was confirmed by my results; at least when using the rate at which circuli are deposited as a proxy for growth, I found that individuals that formed less circuli during their first (and second) year at sea were smaller at the time of return to river Dalälven.

Due to its importance from an economic, cultural and ecological viewpoint, with considerable efforts and resources spent to increase the population sizes of salmon in the Baltic Sea, it is critical to understand the parameters and mechanisms influencing fecundity. Yet, there is an increasing amount of unexplained variation in the fecundity of Baltic salmon from river Dalälven. In this study, I show that even though female size and body condition are key factors explaining fecundity of the Baltic salmon from river Dalälven, the explanatory power of these factors has declined during the last 14 years. My results show that growth patterns at sea do not have any direct effects that can add to explain variation in female fecundity. Still, growth rate at sea has great indirect influence on fecundity since it decides the body length of the returning salmon. In the future, when studying the effects of variation

in growth rate at sea on the fecundity of Atlantic salmon in the Baltic Sea, it would be advisable to replicate this study while including a time series of individuals of varying age at return. In addition, one should not only consider differences between growth seasons but also variation in growth during specific periods within growth seasons. It would also be relevant to study if the different patterns of marine growth have any effect on variation in fecundity in terms of differences in egg size or egg number.

Besides studying factors that are causing variation in the body size of returning salmon, I suggest that putting more emphasis into reviewing the potentially cryptic effects of the environment experienced at sea, as e.g. the effect of stressors such as dioxin and fungal infections (ICES 2018) or of variation in food choices that can cause e.g. thiamine deficiency (Keinänen *et al.* 2018). I believe this will help resolve the question about what is causing variation in fecundity of equally sized Baltic salmon. Finally, it would also be useful to consider the effects of fluctuation in environmental conditions in the river between years.

In this study, I have considered the previously poorly studied factor of marine growth patterns in an attempt of closing the knowledge gap to why there is variation in the fecundity of same-sized female Atlantic salmon in the Baltic Sea. I have also explored the method of using scale circuli as an estimate for growth rate, considering that this gives a more detailed picture of the growth pattern at sea rather than just considering differences in growth rate in terms of total body growth between the time the salmon migrate out to sea and the time they return to the river. Due to limitations of my dataset: the absence of a time series or differences in the age at which the salmon return to the river, I still believe it is relevant to consider the effect of marine growth patterns in the aim of explaining why there is variation in the fecundity of Baltic salmon in river Dalälven. I also consider my way of studying growth patterns to be relevant, and I have shown that when using this method in the future, it is important to include both the rate at which circuli are formed as well as the inter-circuli distance, because they are independent indicators of growth rate at sea.

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Appendix 1
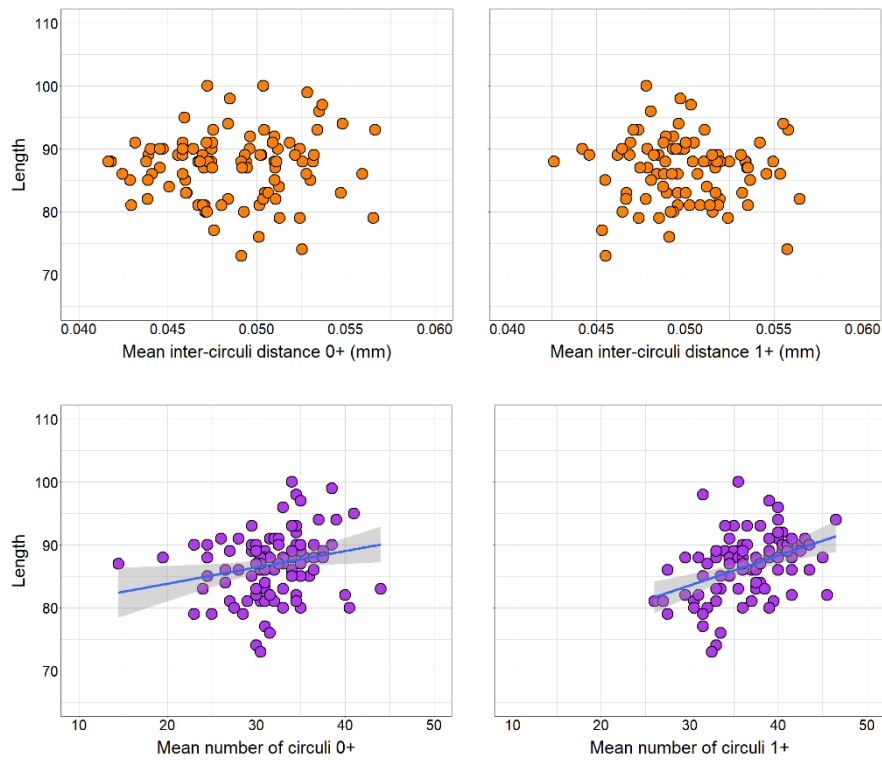
Figures describing the relationship between body length and growth in 2SW Atlantic salmon females at return to river Dalälven in 2018, during the first (0+) and second (1+) year at sea (Table 3). Solid lines represent significant relationships. The models are:

- Length ~ Mean inter-circuli distance 0+ (top left)
- Length ~ Mean inter-circuli distance 1+ (top right)
- Length ~ Mean number of circuli 0+ (bottom left)
- Length ~ Mean number of circuli 1+ (bottom right)
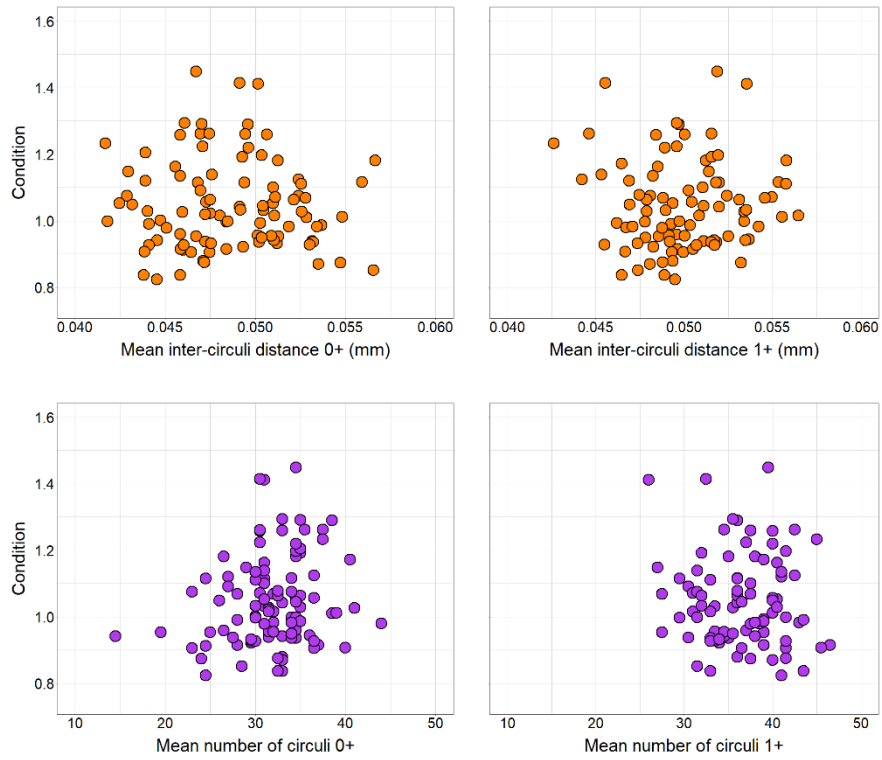
Figures describing the relationship between body condition (Fulton's K) and growth in 2SW Atlantic salmon females at return to river Dalälven in 2018, during the first (0+) and second (1+) year at sea (Table 4). The models are:

- Condition ~ Mean inter-circuli distance 0+ (top left)
- Condition ~ Mean inter-circuli distance 1+ (top right)
- Condition ~ Mean number of circuli 0+ (bottom left)
- Condition ~ Mean number of circuli 1+ (bottom right)

Appendix 2

Manual for how to use open source processing program ImageJ, version 1.52i
(ICES, 2013; Rueden et al., 2017), macro "Tree rings" in plugin ObjectJ, version
1.04q (Vischer & Nastase, 2009) for extracting measurements of Atlantic salmon
growth rate at sea.

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ObjectJ

Tree rings

1. Install ImageJ

Install ImageJ: https://imagej.nih.gov/ij/docs/install/windows.html

ImageJ User Guide:

https://imagej.net/docs/guide/146.html

Save the downloaded file in a folder on e.g. Disc (C:).

2. Install ObjectJ

- Guide for installing ObjectJ:

  https://sils.fnwi.uva.nl/bcb/objectj/2-Tutorial.html

1. Install ObjectJ

Download the latest version of objectj_.jar, put it into ImageJ's plugins folder, and restart ImageJ. Then choose menu Plugins>ObjectJ. Now you have an additional menu called ObjectJ.

(See next slide)

- Open ObjectJ in ImageJ.

(You'll have to do this every time you start up ImageJ.)
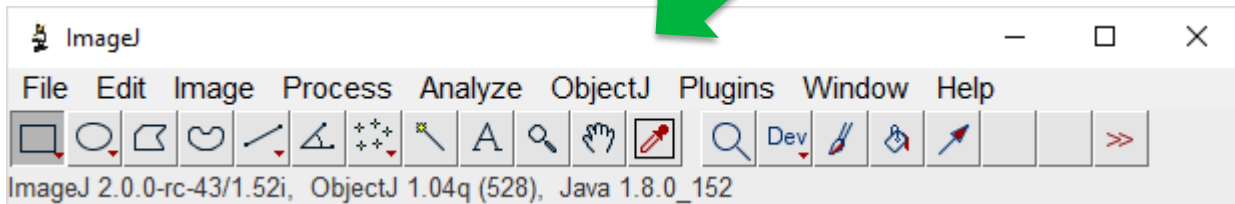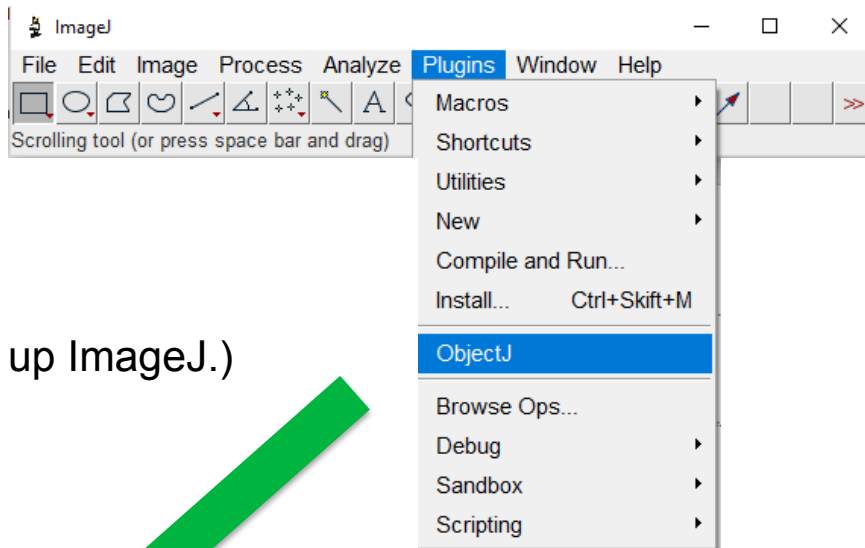
3. Start a project
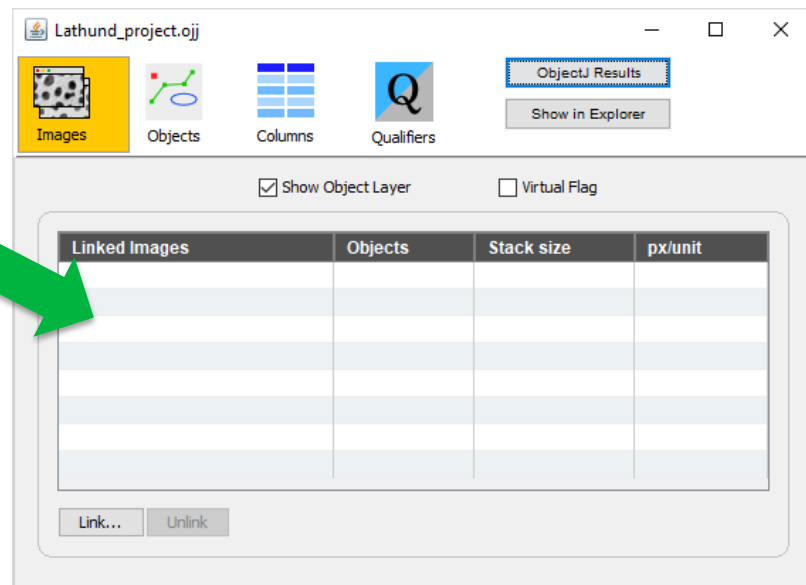
Start a new project, ObjectJ -> New Project.

Make sure you create an unique folder to put the project (and soon, pictures etc.) in.

- Following windows will open:
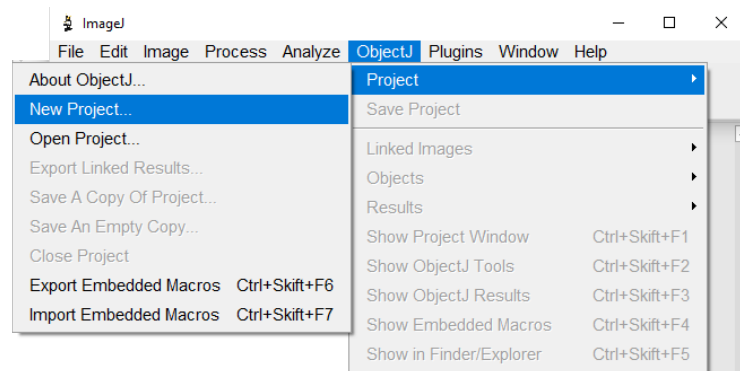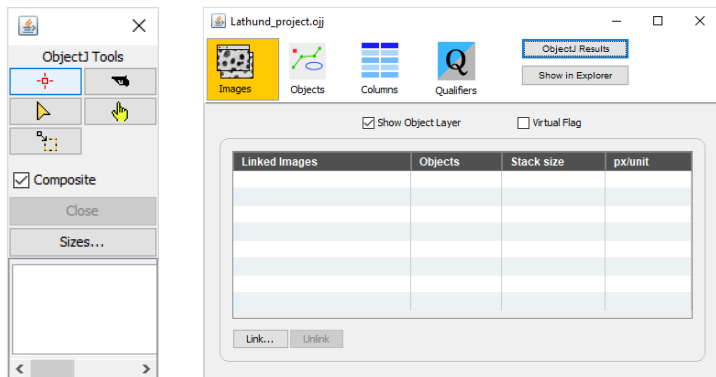
When added to the project, all your photos will be seen here:

Project window and tools are accessed here:
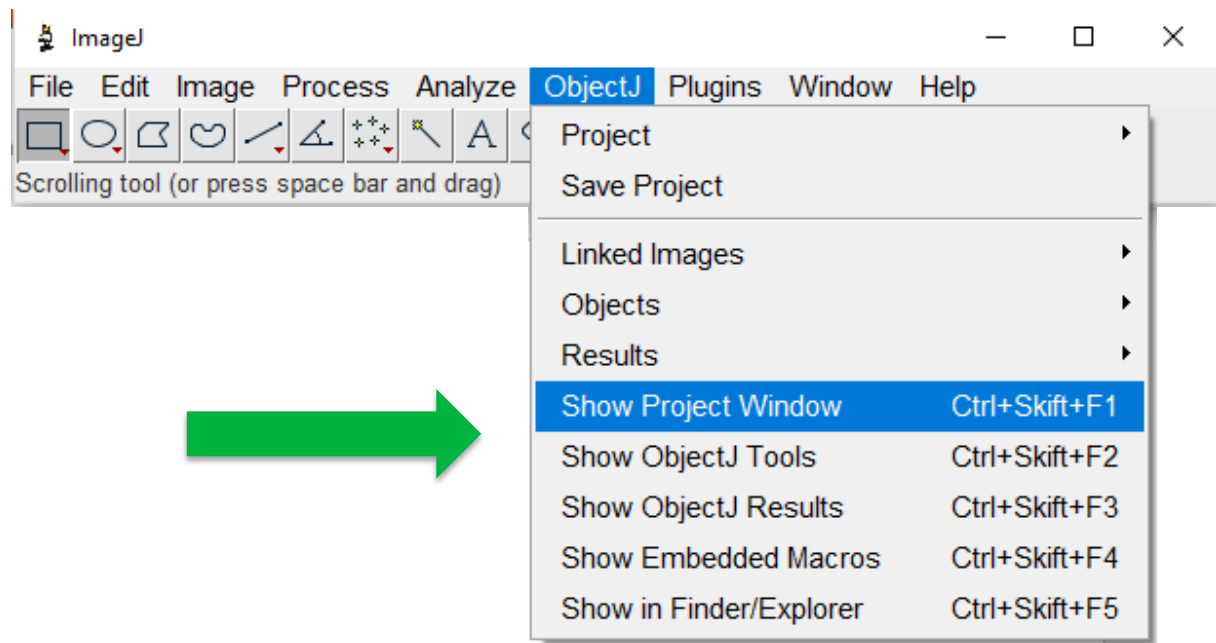
Now, **add the photos** you want to work with to the folder you created for your project.*

- Drag the photos into the Project Window.

- Double klick on the picture's name to open it.

- Go to File -> Save As in the ImageJ toolbar. Create a copy of the original file in the project folder (use the Tiff-format). Now, you can delete the original file saved in the project folder if you like. Save the file like this continously to be able to access the changes you will be makeing later. Also, save the project itself:

ObjectJ -> Save project.
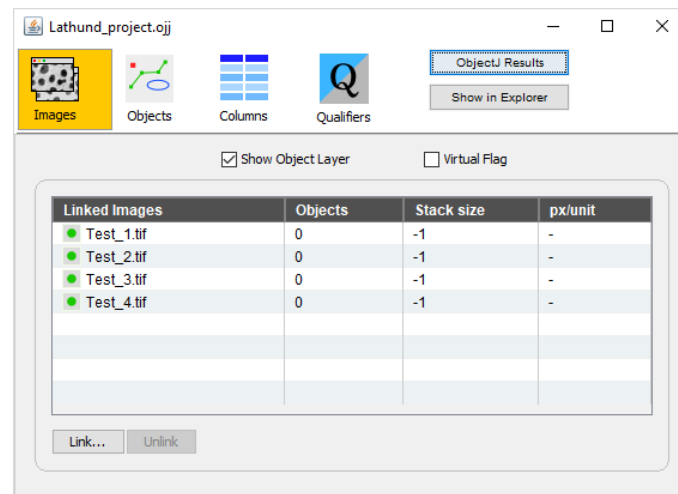
*If you change the location or re-name the folder, the project's photos will become unlinked (the green mark next to the file's name will turn red).

Now, we will **set the scale***. On the ImageJ toolbar, choose the straight line tool. Zoom in or out using "+" or "-". Use the scrolling tool (the hand) to move the picture.

Zoom in and draw a line where your scalebar/known distance is, while pressing the shift key. This will make the line go horizontal/straight. (See next slide.)
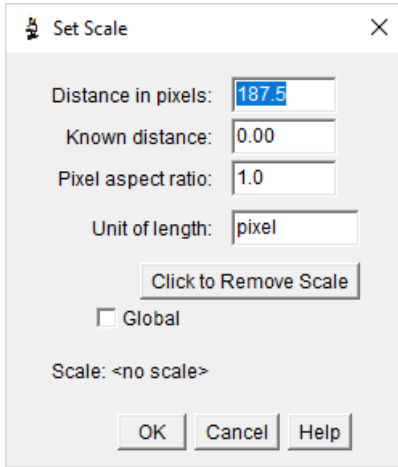
*You will probably need tp do this every time you re-open the project.
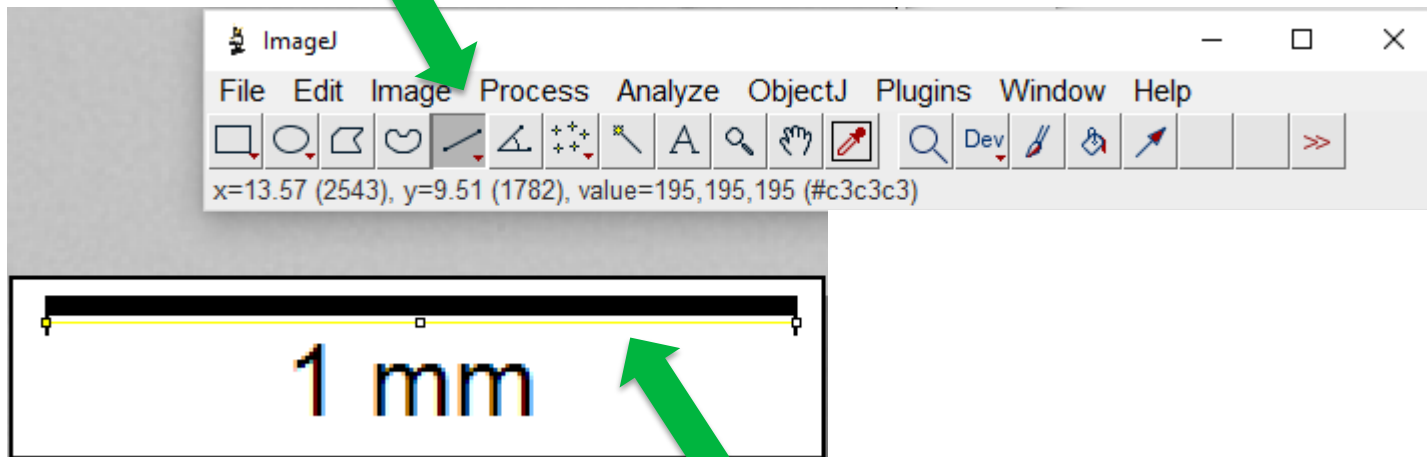
Go to Analyze -> Tools -> ROI Manager. Press "Add".

Rename the object (e.g. "Scale line"). Choose More -> Save and save the object in your project folder. To access the scale line, go to File -> Open, or Analyze -> Tools -> ROI Manager -> More -> Open.

To set the scale, choose Analyze -> Set Scale when the scale line is active.
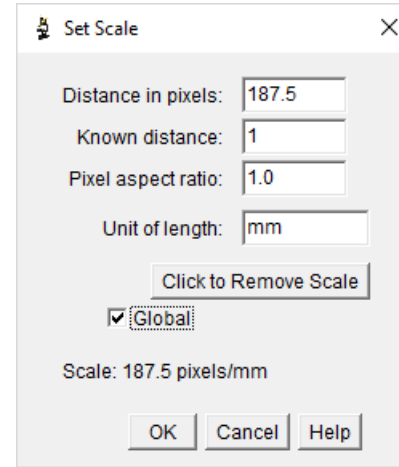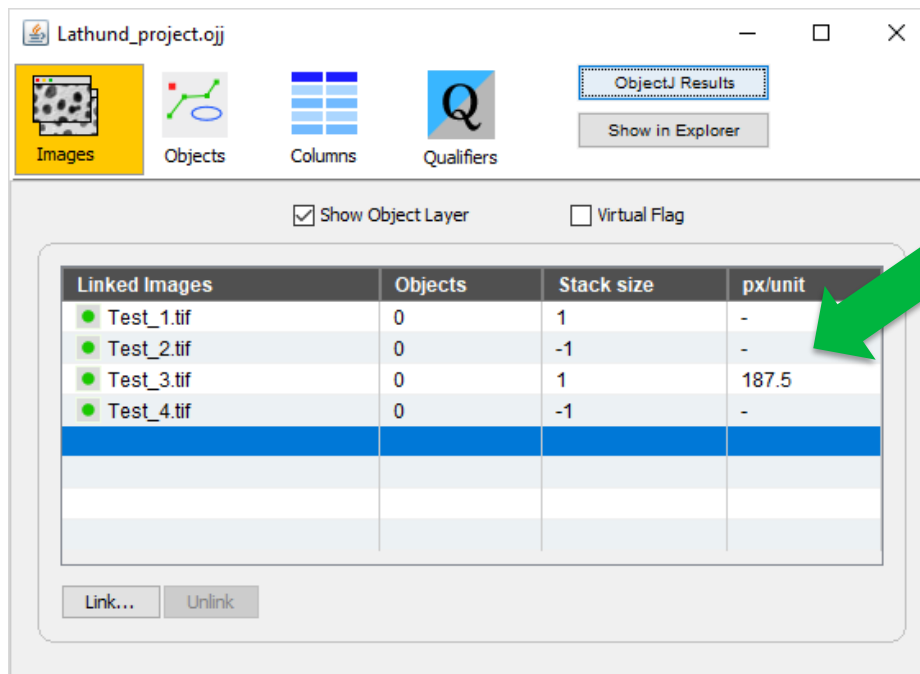
Choose unit and known distance. Check the "Global" box to apply this setting to all pictures by default. You can off cause change this at any time working on your project, depending on the picture.

Now, the scale setting can bee seen in the Project Window.
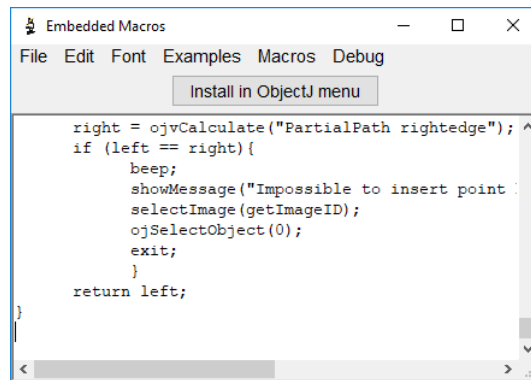
4. Install Tree rings' Macros

Choose ObjectJ -> Show Embedded Macros.

Copy and enter the code shown on the next slide (also added as a note to the next slide).
Press "Install in ObjectJ menu".

The code:

```
*/
var
minValley=8,   //minimum valley depth between two detected peaks
laneWidth = 20,  //lane width used for the peak detector
minOrMax = "min",// set peak at min or max value

x00 , y00, //starting point (zero if uninitialized)
yearArr, //year numbers belonging to ringWidthArr
ringWidthArr, //distances between subsequent tree rings
xxArr, yyArr, //contains Begin and Ring positions
xxAllArr, yyAllArr, //contains Begin, Link and Ring positions
markedImg = 0,
;

//
macro "Start a Sequence [F1]"{
        oiCloseObject();
```
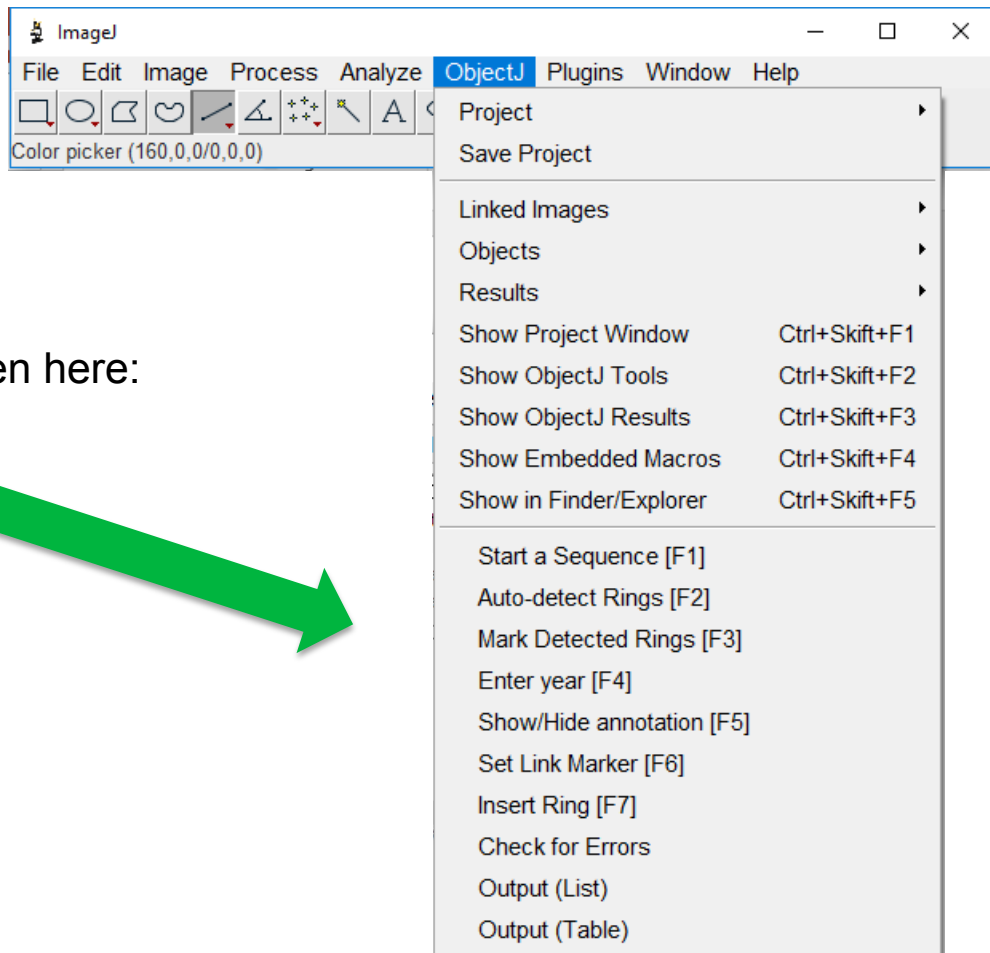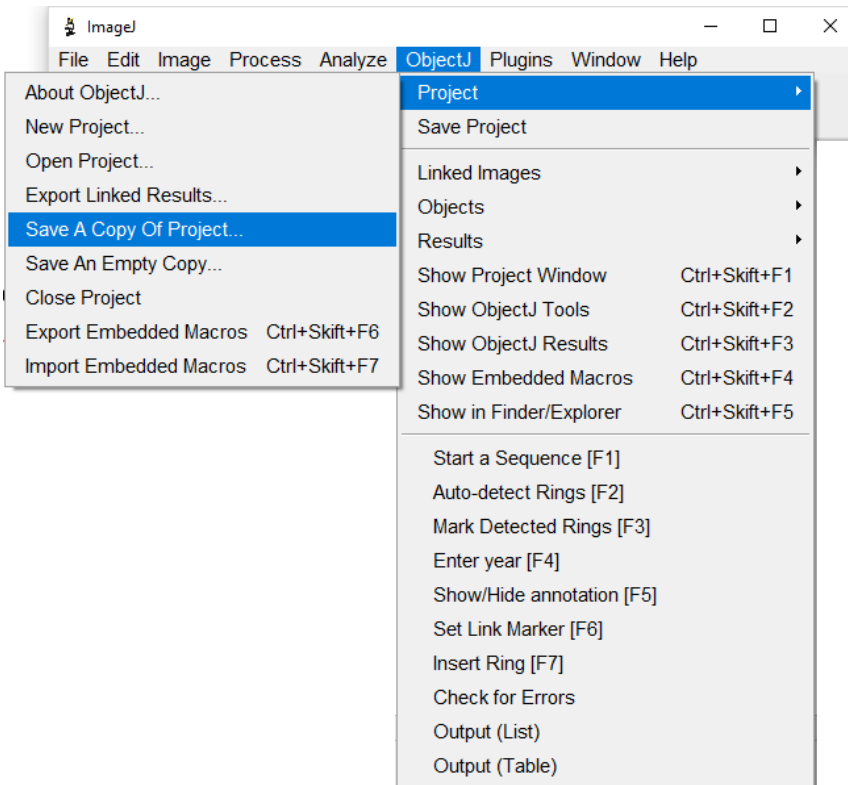
Now, the Tree ring macros can be seen here:
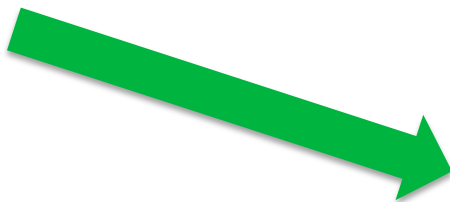
Save the project:
ObjectJ -> Save Project.

You can also save an extra copy, or an empty copy of your project - so that you don't have to set the macros etc. again.

5. Working on your photos

Open a photo that is added to your Project Window.

Go to ObjectJ -> Start a Sequence, or press F1*. A pink marker will appear. Place the starting point at the scale's focus** (see next slide). The starting point is an object, its object number shown next to the point. It can also be seen under "Objects" in the Project Window.

*Make sure your keyboard responds to your Fn-command and not e.g. sound or light settings – change by pressing Fn + Caps.
** Zoom in/out using +/- or use the scrolling tool (the hand) to move the picture.
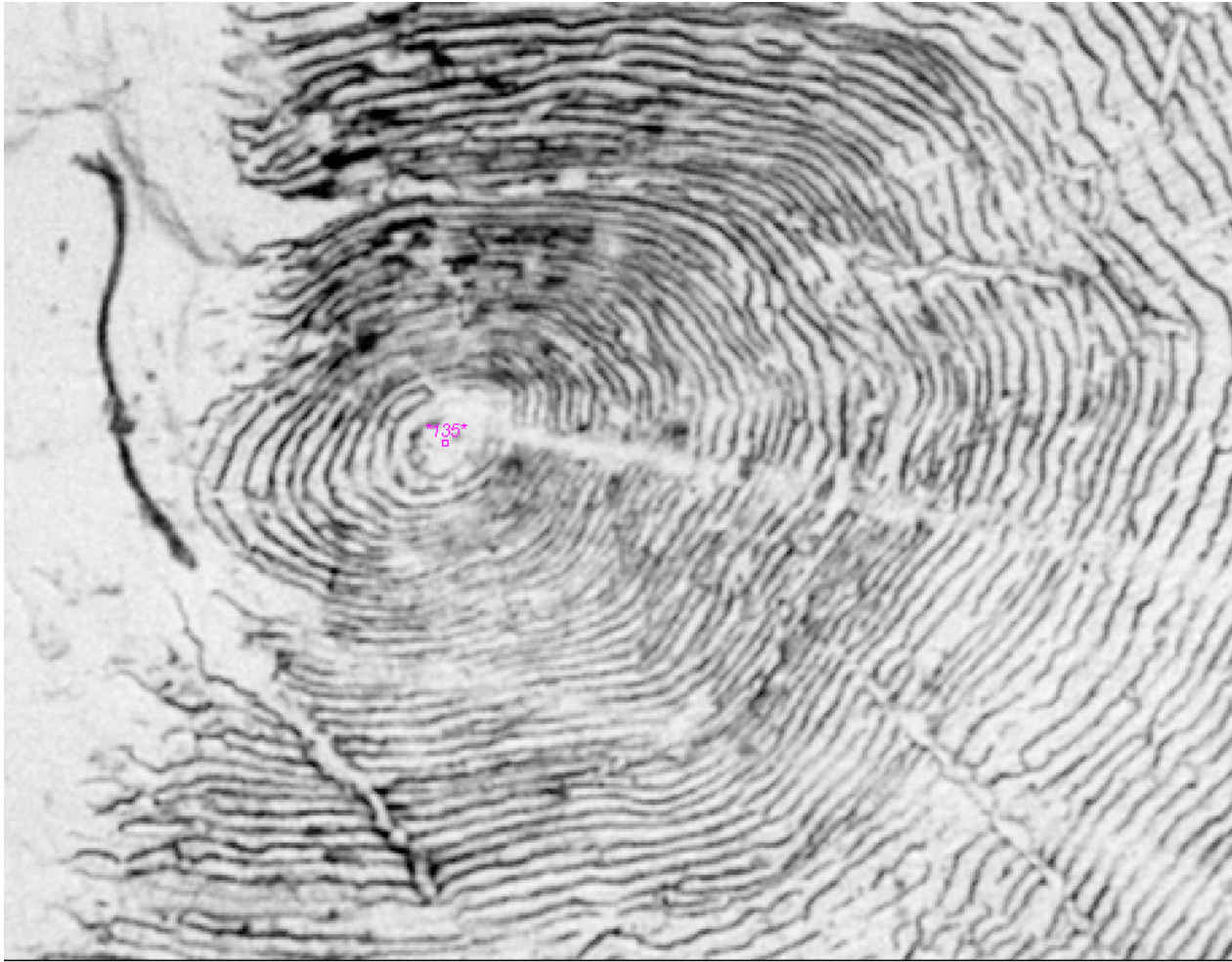
The pointer is now a blue marker.

Hold the marker where you want the line/markings to go, e.g. at the edge of the scale. Go to ObjectJ -> Auto Detect Rings, or press F2. A set of white points will appear. Redo this stage until you are happy with the positioning of the object, then choose ObjectJ -> Mark Detected Rings, or press F3. The object will now consist of the pink starting point (with number) and the blue points marking the rings/circuli (see next slide).
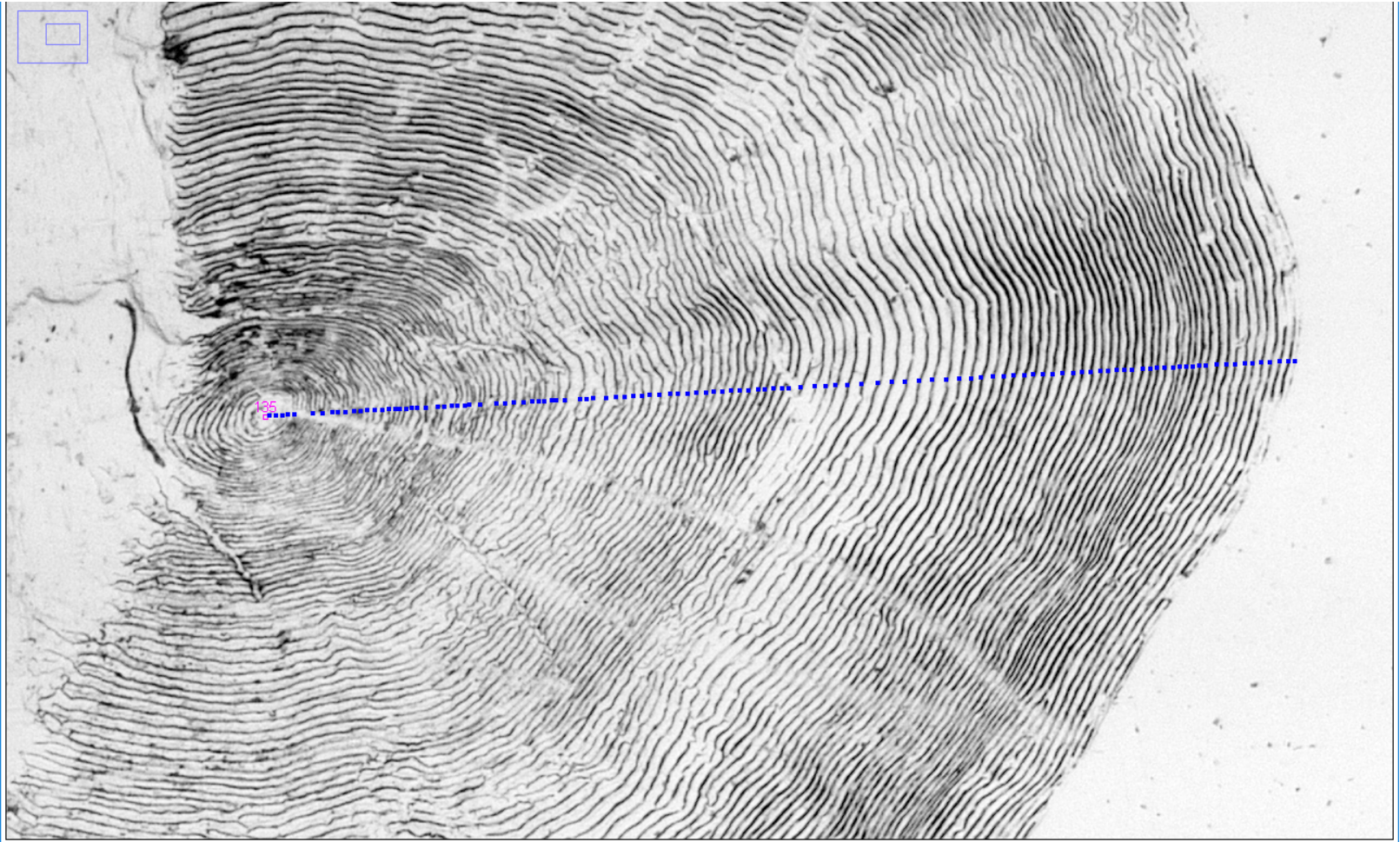
Now it's time to use the tools (OjectJ -> Show ObjectJ Tools).

Move tool
Moves all/single points.
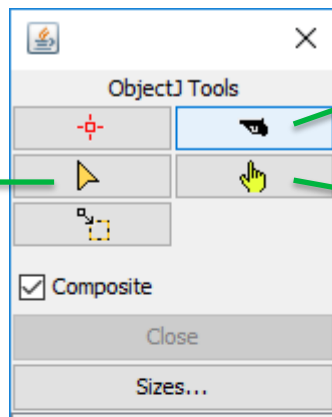
Pistol tool
Deletes all/single points.

Finger tool
Chooses an object.

Move and/or **delete** single points by choosing the corresponding tool, while pressing the Alt-key.

Add points by pressing F7 while using the finger tool. The point will appear where the pointer is. (The finger tool must have chosen/activated the object for it to be able to insert new points.)

Sometimes, a help line will appear, linking the markings. You can manage it through ObjectJ -> Show/Hide Annotation, or by pressing F5.

When you are happy with your object, choose ObjectJ -> Enter Year, or press F4. Enter a "starting year" (e.g. 1920). Remember, the program thinks it is working on tree rings ☺
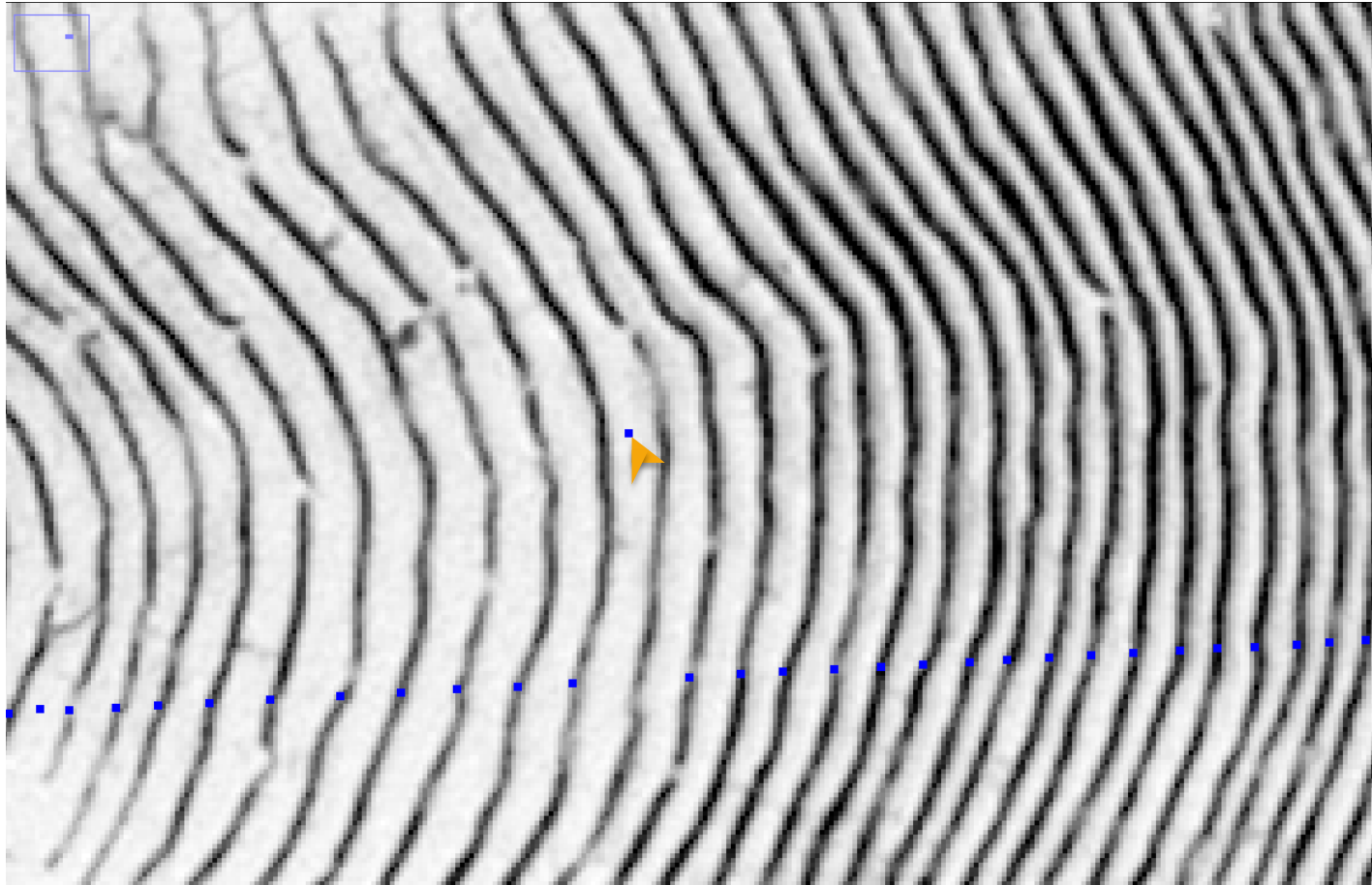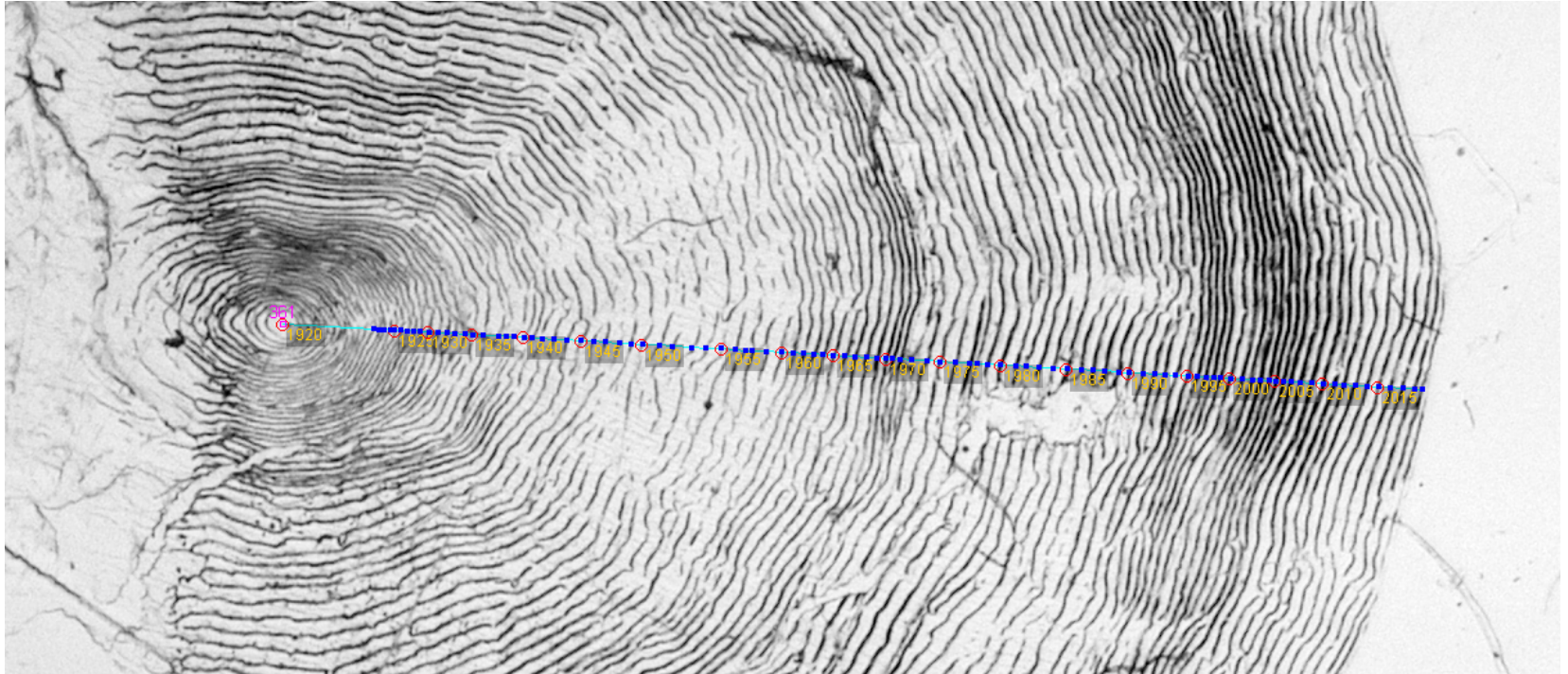
Note:

Ctrl + Z doesn't usually work…

(Unfortunally)

6. Output

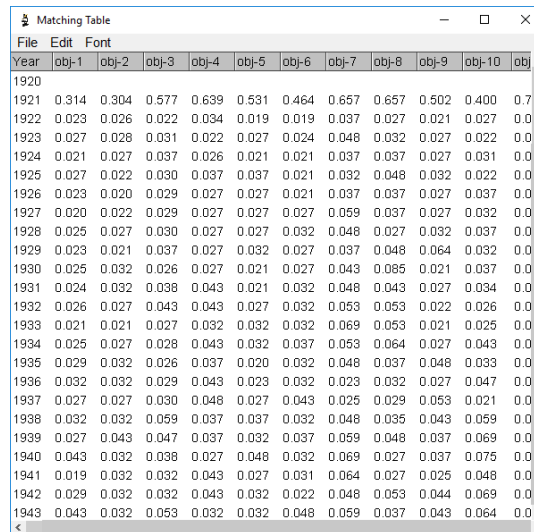To **calculate the distances** between the rings/circuli, go to ObjectJ -> Output (Table). Choose the window "Matching Table". Your table will be showing *all* the distances of *every* object in the project. Save by choosing File -> Save.

The file will be saved as a .csv.

Matching Table

Year	obj-1	obj-2	obj-3	obj-4	obj-5	obj-6	obj-7	obj-8	obj-9	obj-10	obj
1920											
1921	0.314	0.304	0.577	0.639	0.531	0.464	0.657	0.657	0.502	0.400	0.7
1922	0.023	0.026	0.022	0.034	0.019	0.019	0.037	0.027	0.021	0.027	0.0
1923	0.027	0.028	0.031	0.022	0.027	0.024	0.048	0.032	0.027	0.022	0.0
1924	0.021	0.027	0.037	0.026	0.021	0.021	0.037	0.037	0.027	0.031	0.0
1925	0.027	0.022	0.030	0.037	0.037	0.021	0.032	0.048	0.032	0.022	0.0
1926	0.023	0.020	0.029	0.027	0.027	0.021	0.037	0.037	0.027	0.037	0.0
1927	0.020	0.022	0.029	0.027	0.027	0.027	0.059	0.037	0.027	0.032	0.0
1928	0.025	0.027	0.030	0.027	0.027	0.032	0.048	0.027	0.032	0.037	0.0
1929	0.023	0.021	0.037	0.027	0.032	0.027	0.037	0.048	0.064	0.032	0.0
1930	0.025	0.032	0.026	0.027	0.021	0.027	0.043	0.085	0.021	0.037	0.0
1931	0.024	0.032	0.038	0.043	0.021	0.032	0.048	0.043	0.027	0.034	0.0
1932	0.026	0.027	0.043	0.043	0.027	0.032	0.053	0.053	0.022	0.026	0.0
1933	0.021	0.021	0.027	0.032	0.032	0.032	0.069	0.053	0.021	0.025	0.0
1934	0.025	0.027	0.028	0.043	0.032	0.037	0.053	0.064	0.027	0.043	0.0
1935	0.029	0.032	0.026	0.037	0.020	0.032	0.048	0.037	0.048	0.033	0.0
1936	0.032	0.032	0.029	0.043	0.023	0.032	0.023	0.032	0.027	0.047	0.0
1937	0.027	0.027	0.030	0.048	0.027	0.043	0.025	0.029	0.053	0.021	0.0
1938	0.032	0.032	0.059	0.037	0.037	0.032	0.048	0.035	0.043	0.059	0.0
1939	0.027	0.043	0.047	0.037	0.032	0.037	0.059	0.048	0.037	0.069	0.0
1940	0.043	0.032	0.038	0.027	0.048	0.032	0.069	0.027	0.037	0.075	0.0
1941	0.019	0.032	0.032	0.043	0.027	0.031	0.064	0.027	0.025	0.048	0.0
1942	0.029	0.032	0.032	0.043	0.032	0.022	0.048	0.053	0.044	0.069	0.0
1943	0.043	0.032	0.053	0.032	0.032	0.048	0.059	0.037	0.043	0.064	0.0

7. Useful links

- ObjectJ in general

https://sils.fnwi.uva.nl/bcb/objectj/3a-ManualMenu.html

- About Tree rings

https://sils.fnwi.uva.nl/bcb/objectj/examples/TreeRings/TreeRings-9.htm

- Manual of starting a new project

https://sils.fnwi.uva.nl/bcb/objectj/2-Tutorial.html

- Additional ImageJ manual

https://imagej.nih.gov/ij/macros/

- About plugins

https://imagej.net/docs/guide/146-16.html#toc-Section-16

- Concepts in ObjectJ

https://sils.fnwi.uva.nl/bcb/objectj/5-Concept.html

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Best of luck to you! /Ulrika