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Why have the eggs in Baltic salmon (*Salmo salar* L.) become larger?

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Abstract

The size of the eggs in fish long been regarded as an important parameter in comparative ichthyology, as it has been linked to fitness related traits such as the survival and competitive ability of the offspring. However, very few studies exist where variation in egg-size within a population has been investigated over long time. In this thesis, I have analyzed the size of the eggs in 1126 returning female Baltic salmon (*Salmo salar* L.) caught in a breeding fishery in river Ume, Northern Sweden between 1974 to 2016. My main goal was to investigate how condition factor or egg number affected the egg-size in salmon, and whether any trend in egg-size existed over time. Independently of the body size and yearly effect, mean egg size of the hatchery (6.01899 mm) and wild (6.004838 mm) reared females didn't have any statistical significant difference (p value > 0.05). Larger females produced significantly bigger (diameter) and more eggs. When the sample was fragmented with 7 length classes (70-75, 75.1-80, 80.1-85, 85.1-90, 90.1-95, 95.1-100 and 100.1-105 cm), females showed increasing egg size trend over the years. But the females didn't tend to increase producing more eggs over time which can be the evolutionary price they paid to achieve larger egg size. Condition factor of the fishes didn't increase significantly over the years. But larger fish length groups with better condition factor laid larger and more eggs. Several hypotheses were discussed to explain the observed egg size variation, but no clear cut explanation could be found to the somewhat contradictory results except for a clue to have an indirect relationship with the sprat population in the Baltic which is a major food for salmon.

Key words: Baltic salmon, egg size, egg numbers, length,

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Introduction

Natural selection tends to maximize the fitness of the animal by working on life history traits (Wootton, 1993). Parents invest in the reproduction to increase their own fitness and that of their offsprings (Smith and Fretwell, 1974). For oviparous organisms, this investment can be in the form of modifying egg size (Quinn et al., 1995) and the number of laid eggs (Barnett, 1955, Lloyd, 1987). Egg size is known to have fitness consequences upon survival and size at subsequent life stages in many species of fish, including salmonids (Einum and Fleming, 2000), while the number of eggs laid may have fitness consequences either through pure numerical advantages (probability to get as many copies of your genes into the next generation), or via more complex competitive trade-offs acting on fish larvae (Jonsson and Jonsson, 1999, Lasne et al., 2018). It is often assumed that there exists a trade-off between egg-size and egg-number, i.e a female can either produce large but few eggs or many but small eggs, but not large and many eggs (Elgar, 1990). Both egg-size and egg-number is correlated to the growth and size of the female (Blueweiss et al., 1978, Fox and Heath, 2003b); which in turn is a reflection of environmental and genetic constraints (Wootton, 2012). Independent of female size, environmental conditions may affect the investment and energy allocation in gonadal development (Healey, 2001). Hence, it is important to understand the dynamics and reasons behind variation in egg-size in a population, and to investigate if there are any long time trends.

Egg size is a very highly varied trait within and among fish species (Sargent et al., 1987, Einum and Fleming, 2002, Bagenal, 1971, Elgar, 1990, Chambers and Leggett, 1996). In general, egg size will vary depending on amount of maternal yolk reserves allotted per offspring (Sargent et al., 1987). There is a multitude of factors that may potentially effect egg size in fish, and when trying to understand the ultimate and proximate mechanism behind variation in egg-size, it's important to distinguish between factors

that are related to difference in life-history between species and those that may create egg-size variation within a species.

Fitness implications of egg-size variation in salmonids

Egg-size have been found to vary both within and between cohorts and years (Chambers and Leggett, 1996, Kinnison et al., 2001). Assuming differences in egg-size entails different levels of maternal investment as well as fitness, then the variation in egg-size may be driven by selection. Studies have since long shown a positive relationship between the size of the egg and the size of the offspring, both within species and populations. For example, egg size was found positively correlated with fry size in brown trout (*Salmo trutta* L.) already 100 years ago (Dahl, 1919). Larger fry may be more competitive and have more energy reserves than smaller fry, and hence have higher survival both before and after emergence. Growth and fitness of juveniles from larger eggs were advantaged over the juveniles from relatively smaller eggs (Einum and Fleming, 1999, Heath et al., 2003). *Salmo salar* offspring from bigger eggs take longer time to absorb the yolk sacs and develop as juveniles (Privo'Nev, 1960). Bagenal (1969) reported that at constant temperature, large brown trout fry from large eggs survive longer without food than smaller fry from smaller eggs.

The effect of female size on egg-size

In salmonids, positive relationships (i.e egg size increased with female size) have been found for chinook salmon (*Oncorhynchus tshawytscha*) (Kinnison et al. (2001) and Atlantic salmon (Jonsson et al., 1996, Beacham and Murray, 1985), but not for sockeye salmon (Kaeriyama et al., 1997). When the offsprings evolve from smaller eggs with small amount of yolk sac reserve, the time of first feeding is short which affects further survival (Marteinsdóttir and Steinarsson, 1998). Higher survival of eggs from large females may however not only be a direct effect of the eggs being larger than smaller females, but may also be an indirect effect of the larger females being more competitive and able to offer better habitat (even before

hatching by competing for the better incubation habitat) for the eggs and juveniles (Hendry et al., 2001). So, fitness could theoretically be equally good for small eggs if they were to hatch in the same good habitat provided by large females.

The effect of environment on egg-size

Several studies have investigated the relationship between egg-size and various environmental factors. The results from Einum and Fleming (1999) supported the assumption that, with decreasing environmental quality, optimal egg size increases. Results by Taranger and Hansen (1993) indicated that high water temperature constrains salmon egg ovulation leaving negative effect on the gamete quality. The review study by Pauly and Pullin (1988) reported that eggs reared at lower temperature was larger than those reared in higher temperatures.

Beacham and Murray (1993) suggested that egg size tends to be smaller in northern populations of some pacific salmon species due to increased fecundity, older ages at maturity and limited energy that can be spent on egg production. Growth conditions, as well as an individual's propensity to grow (genetics), may effect egg-size. Atlantic salmon (*Salmo salar* L.) adult females who had rapid growth in freshwater produced more (in number) and smaller eggs than the slow growing ones at a given body size (Thorpe et al., 1984).

Trade-off between egg number and egg size

As both larger eggs and more eggs are assumed to increase the fitness of the female, and as investment to produce larger or more eggs is assumed to be costly, it is hypothesized that there exists a trade-off between egg number and egg size. Heath et al. (2003) found negative linear relationship between egg size and relative fecundity (eggs/kg) in captive chinook salmon, supporting the existence of such trade-off. Beacham and Murray (1993) revealed an effect of the distance of freshwater spawning migration on the

relationship between egg-number and egg weight in North American Pacific salmon (*Oncorhynchus*), in where the Chinook salmon that migrated the furthest had more but smaller eggs than fish that migrated shorter distance. Fleming and Gross (1989) found an effect of breeding competition in coho salmon, where both egg-size and egg-number decreased with increased competition.

Baltic salmon

The wild Baltic Sea populations of Atlantic Salmon is among the most threatened in the world due to years of excessive over fishing, hydropower development of rivers, pollution, habitat destruction and vitamin-B deficiency leading to reproductive failure (a symptom called M74) (Amcoff et al., 2002, Börjeson et al., 1996, Norrgren et al., 1993).

The Baltic Sea has been severely impacted by anthropomorphic activity the last 50 years, leading to large disturbances of the natural ecosystem. Large part of the sea bed is today anoxic as a result of eutrophication, temperature increase and less influx of salinity (Kabel et al., 2012). The composition of the marine fish community has been radically altered following over harvesting of top predators, such as cod. As a consequence, the feeding conditions for the salmon at sea has been shifting from a dominance of herring (*Clupea harengus*) in the diet, to a higher proportion of sprat (*Sprattus sprattus*), a diet-shift that has been correlated to M74 (Hansson et al., 2001, Karlsson et al., 1999).

Here I examine the relationship between body size (length) and egg size. I also investigated the impact of length and condition factor on egg size of the females. Overall, I studied if over the years, egg size of Baltic salmon (*Salmo salar*) showed any evolutionary trend or not considering the life history trait of more eggs or larger eggs argument. I also attempted to discuss the possible factors those might have influenced the plausible trend.

Methodology

Analytical overview

I analyzed data on egg size and egg-number of Baltic salmon from 1974 to 2016. The data set was examined to see if there was any trend in egg size or egg-number over time. I also tested the hypothesis that female size and condition affected egg-size and egg-number. I also tested the effect of number of sea winters spent by each female on egg-size and egg-number. In total, the dataset contained 1126 females (525 wild, 595 hatchery originated and origin was unknown for 6 individuals) for which egg-size, egg-number, weight, length, origin (wild/hatchery) and year-of-capture had been recorded.

Source of data

I received the data set from Norrfor's Fiskodlingen (fish hatchery), Umeå (63°53'00.3"N 20°01'19.1"E) which is a part smolt compensation program for hydroelectricity production of Vattenfall AB in Umeälven (Umeå river). As Norrfor's Fiskodlingen is a very old facility, it has long and extensive time-series on diverse biological attributes related to the salmon and sea trout being produced in the hatchery, as well as on the returning fish being caught in the fish ladder and used as breeders for the hatchery stock. The data used in this thesis was from the returning females that had been captured in the fish ladder at Stornorrfor's, and kept in the hatchery to be used as breeders. The specific variables that were collected from every year were: length of female (Fork length - FL), weight of female, number of eggs per female, average egg-size per female, origin of female (hatchery/wild, distinguished by the absence of adipose fin of the hatchery fish) and sprat population abundance in the Baltic sea from International Council for the Exploration of the Sea (ICES).

The data set has three time windows; 1974-1988, 2005-2007 and 2014-2016. I have not incorporated data from 1986 in my analysis, as I didn't have adequate amount of female body size and egg size data for that year in the original data. Data sets for 1974-1988 series was available in different paper binders. I transferred them manually from paper to electronic version (Microsoft Excel). The other two data segments were already in digital format. After I merged the data into Microsoft excel, I cleaned the data set by cross checking all inputs for obvious outliers. To check if the number of total eggs per female were reliable, I first calculated the theoretical number of eggs per female by using swelled number of eggs in liter and number of eggs per 25 cm values. I then calculated the deviation between the theoretical number and the recorded number, and where the deviation was large (above 1.00), I went through the data binders and corrected obvious misprints. Based on the fish length and weight (before stripping of eggs), I calculated the Fulton condition factor of each female with eq. 1 (Froese, 2006).

$$K=100*(W/L^3) \text{ -----eq. 1}$$

Here K is the Fulton's condition factor that is calculated by W= whole body weight (gram), L= fork length (cm) and 100 is used to bring it close to 1. Stevenson and Woods Jr (2006) mentioned condition indices as an important tool for conservation biology due to its capacity to provide information on habitat quality and reproductive output.

The egg size data was derived based on the number of eggs per 25 cm, a scale known as Brofeldt's scale (Stead and Laird, 2002). In this scale, bigger number means smaller eggs as more eggs fit into 25 cm scale. By dividing the number with 250, I got the egg size in mm (Stead and Laird, 2002). Although here in my data set, I used egg diameter in mm to quantify egg size, it can also be signified by yolk diameters in mm, egg volume in mm³ or egg dry weight in mg (Chambers and Leggett, 1996).

The total number eggs in the 1974 to 1988 data window was estimated by the hatchery managers by using counting boards, which will give a precision within ± 100 eggs. The next two data series (2005-2007 and 2014-2016) constituted the actual counted number of individual eggs in each individual. The variation in the total number of eggs per female was considerable (lowest=2400, highest=24627) with the mean value of 8677.

Analysis

An initial analysis revealed strong positive correlation between weight and length (Linear regression, $y=3.934*x+61.904$, $r^2=0.7557$), and subsequent tests on the effect of female size on egg-size and egg-number hence only focused on fish length. Egg-size and egg-number were linearly regressed against length to investigate if there was any significant relationship. I concur that the weight-length relationship is not linear, especially over a large size range. This is important to acknowledge when wanting to estimate e.g weight from length. In this case however, I only wanted to check for high correlation between length and weight in a pure statistical sense. I argue that if both length and weight have strong correlation then they will explain the same variance in my response-variable (i.e egg-size and egg-number). This is why I did not incorporate both length and weight in a model, and I therefore choose to use only length. A quadratic polynomial model was also fitted and compared to the non-polynomial model using Akaike information criteria (AIC).

To investigate trends in egg-size and egg-number over time (years), I first divided all females into distinct length-classes based on 5cm intervals starting from the minimum length up to the maximum length. This resulted in 9 length-classes (70-75, 75.1-80, 80.1-85, 85.1-90, 90.1-95, 95.1-100, 100.1-105, and 105.1-110). This subset of the data was made to adjust for the potential influence of length on egg-size and egg-number. Within each size-class I linearly regressed egg-size and egg-number against year to see if any trend was present.

The subset into size-classes was also made to investigate the relationship between condition factor and egg-size and egg-number. The rationale here was that the fulton condition factor is biased over large size-gradients, and hence only applicable for comparisons between fish within similar size-ranges. Within each size-class, egg-size and egg-number was regressed against condition-factor. Condition factor was also regressed against year within each size-class to investigate if there were any trend over time.

To investigate a potential trade-off between egg-size and egg-number, egg-size was linearly regressed against egg-number within each size-class. To examine the combined effect of year, condition factor and egg number on egg size, I conducted a multiple regression analysis. Pair test were done among Sprat population (three years' average), length, condition factor, egg size and number of eggs.

Data analysis package

To analyze the data, statistical analysis package R version 3.4.4 and RStudio version 1.1.442 were used. JMP was used for the pair test.

Results

Highest (1632.37 ± 229.37) mean relative fecundity (eggs per kg fish) was recorded in 2005 (Table 1). The mean length of the sampled females didn't show any regularity but highest mean length was recorded in 1974. In 2015 when the mean length was 84.29 ± 8.84 cm as lowest comparing with the other years but the condition factor was calculated to be 0.97 ± 0.06 which is same for the year 2007. But in 2007, mean fish length and weight were 88.96 ± 8.29 cm and 7.04 ± 2.08 kg (Table 1). Table 1 also reveals that relative fecundity were poorer in 1987 sample (990.14 ± 90.15) and 1988 sample (998.34 ± 23.64) compared to the other years.

Table 1: Yearly mean and standard deviation (in bracket) of weight (kg), length (cm), relative fecundity and condition factor.

Year	Weight(kg)	Length(cm)	Relative fecundity(egg/kg)	Condition Factor
1974	8.48(1.46)	94.57(5.91)	1181.92(177.55)	0.99(0.05)
1975	7.01(1.62)	88.20(7.59)	1238.09(203.87)	1.01(0.10)
1976	7.20(1.74)	91.20(7.90)	1277.62(205.36)	0.93(0.08)
1977	6.88(2.06)	88.49(8.94)	1209.26(224.17)	0.96(0.09)
1978	5.81(1.45)	84.84(7.02)	1263.44(268.27)	0.93(0.09)
1979	6.13(1.68)	86.34(8.56)	1276.71(278.88)	0.93(0.08)

1980	6.45(1.75)	88.14(8.79)	1333.06(215.04)	0.92(0.09)
1981	5.63(1.57)	85.54(9.05)	1384.80(282.90)	0.88(0.08)
1982	6.26(1.62)	86.64(7.47)	1338.08(308.99)	0.94(0.10)
1983	7.35(1.51)	92.23(6.30)	1517.48(434.81)	0.92(0.07)
1984	7.63(2.24)	92.05(8.22)	1255.11(240.23)	0.95(0.09)
1985	6.91(2.02)	89.35(7.93)	1286.27(263.93)	0.94(0.08)
1987	7.97(1.60)	93.31(5.27)	990.14(90.15)	0.97(0.10)
1988	7.47(2.02)	91.70(8.46)	998.34(23.64)	0.94(0.11)
2005	6.94(1.67)	88.62(6.98)	1632.37(229.37)	0.98(0.09)
2006	7.84(2.11)	92.94(8.04)	1601.43(279.05)	0.95(0.11)
2007	7.04(2.08)	88.96(8.29)	1599.70(282.37)	0.97(0.06)
2014	6.60(2.09)	88.03(8.82)	1188.72(225.23)	0.94(0.07)
2015	6.02(1.96)	84.29(8.84)	1299.64(231.51)	0.97(0.06)
2016	6.69(0.98)	87.31(3.85)	1315.22(200.71)	1.00(0.07)

The mean egg diameter went down from 1974 to 1976. From 1979 to 1982, the mean egg sizes were close to each other. Although, it increased again for the next two consecutive years (1983-1984), it dropped drastically in 1985. The egg size for 1987's and 1988 individuals were obscurely same within group but different among the groups (Figure 1). Figure 1 also shows irregular increase and decrease for data from 2005 to 2016.

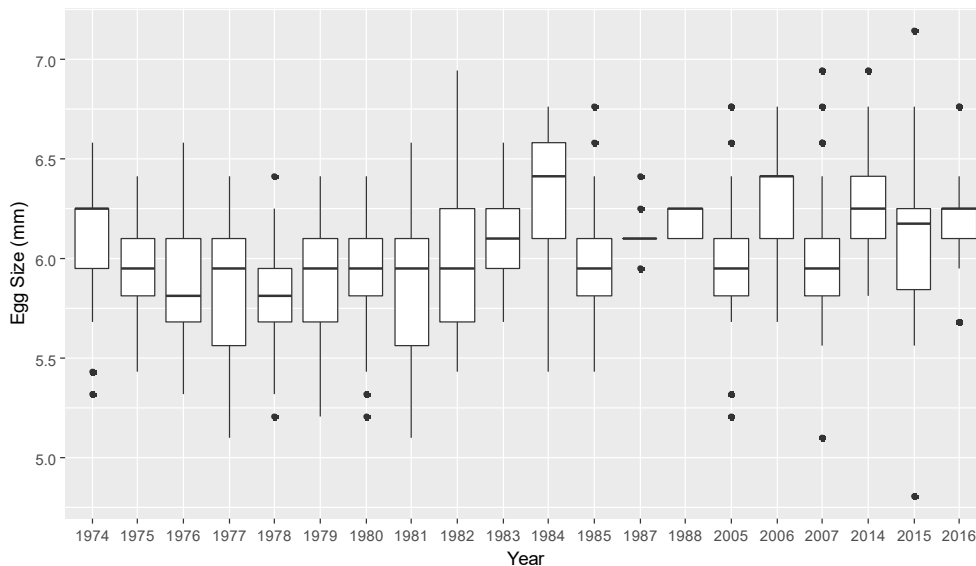


Figure 1: Changes of egg size over years showing maximum, minimum and median egg diameter in mm. Outliers refer to the abnormal distance of the data points from the mean value.

There was a strong positive relationship between egg-size and the length of female ($r^2=0.33$, $F_{1,1116} = 566$, $p<0.01$, Fig. 2) as well as between egg-number and length of female ($r^2=0.52$, $F_{4,1113} = 307.3$, $p<0.01$, Fig. 3). A quadratic polynomial model had lower AIC for both egg-size and egg-number compare to the non-polynomial model (egg-size: $\Delta AIC = 19$, egg-number: $\Delta AIC = 7$). Yes, AIC was lower for quadratic models. This fact seems intuitive, and suggests that there is a cap to how much larger (or more) eggs a female can produce as she gets larger (as mentioned in the discussion). The delta AIC represent the difference in AIC between the linear and quadratic model. So e.g the quadratic egg-size model was 19 “points” lower in AIC than then the linear model. Although the quadratic models had better fit to the data, I still choose to make my statistical conclusions based on the linear relationship because of the easier interpretation of these models.

Egg size showed strong correlation (linear regression) with the length of the females. With each centimeter of length increase, egg size increases by 0.0217342 millimeter (Figure 2).

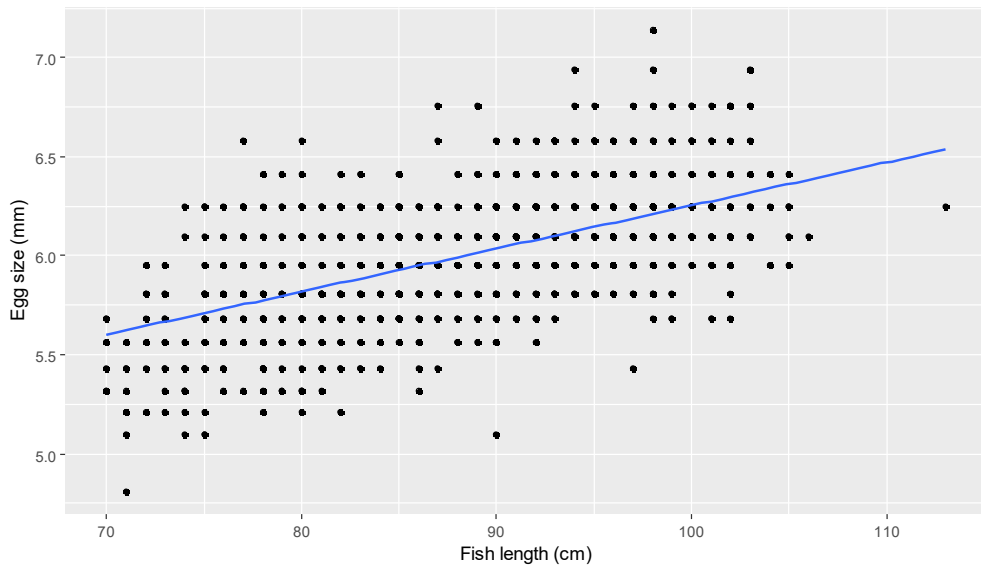


Fig 2: Relationship between egg sizes of the females with the length of the females ($y=4.08+0.021x$). Blue line is the fitted line from a linear regression model.

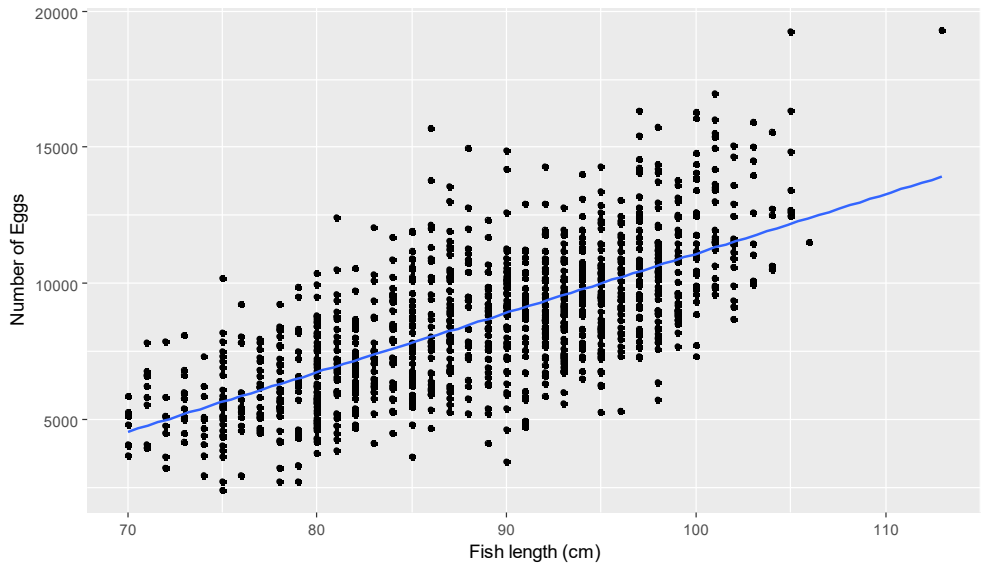


Fig 3: Relationship between number of eggs of the females with the length of the females ($y= -10753.399+218.4x$). Blue line is the fitted line from a linear regression model.

Significant positive relationships between year and egg-size was found in 6 of these size-classes ($p < 0.05$), and non-significant relationship was only established within the smallest size-class (70-75cm) (Figure 4). In contrast, only 3 out of 7 size-classes had significant relationship between egg-number and year ($p < 0.05$, size-class 80.1-85, 85.1-90 and 95.1-100, Fig. 5).

It is true that the three different periods do have unequal amount of observations. However, the regression was made between two continuous variables (i.e egg-size and year) and hence not “unbalanced” in the classical sense (i.e unequal amount of observations between levels in a categorical variables). It is unfortunate that my data lack observations for many of the years, and I have stated this in my revised thesis under the headline “limitations of the study”.

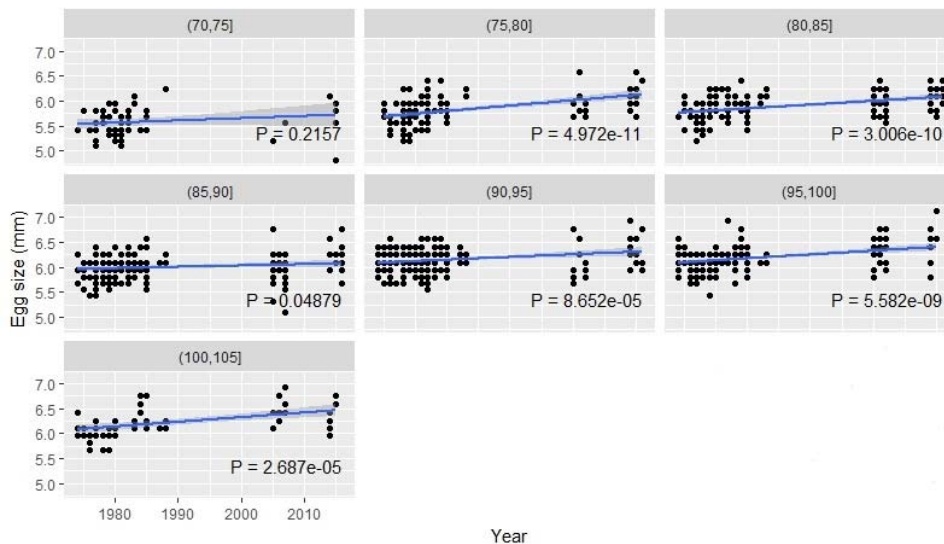


Figure 4: Egg size trend over years in 5 cm length classes mentioning p values in the grids.

Significant negative relationships between egg-size and egg-number could be detected in 4 out of 7 size classes ($p < 0.05$; 75-80, 80.1-85, 85.1-90, 90.1-95 cm). In the remaining 3 size-classes (70-75, 85.1-100 & 100.1-105 cm), no significant relationship could be established (Figure 5).

80.1-85, 85.1-90 and 95.1-100 cm size classes showed significant ($p < 0.05$) increase of egg numbers with year whereas for rest of the groups (70-75, 75.1-80, 90.1-95, 100.1-101 cm) didn't show significant ($p > 0.05$) positive correlation between year and egg number (Figure 6).

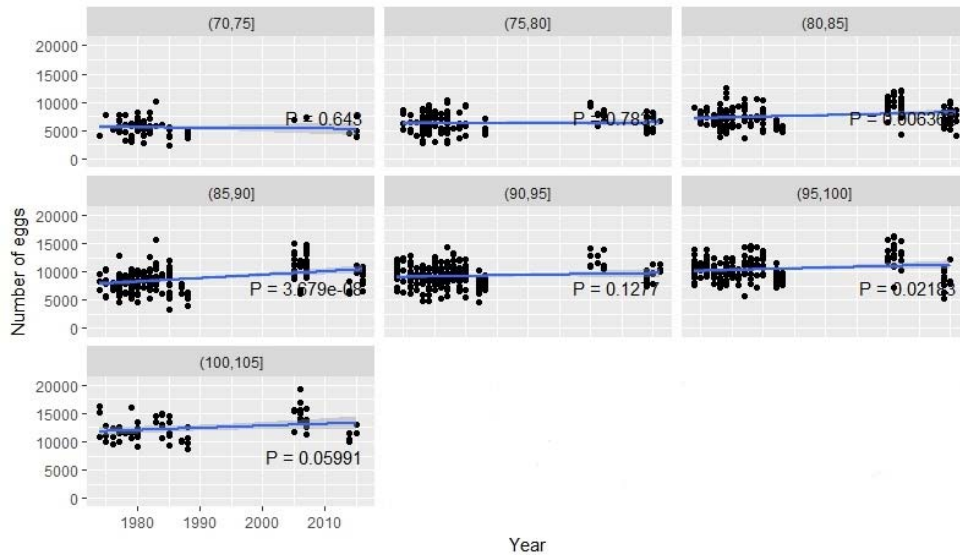


Figure 5: Total egg number trend for each female over years with p values in each segments.

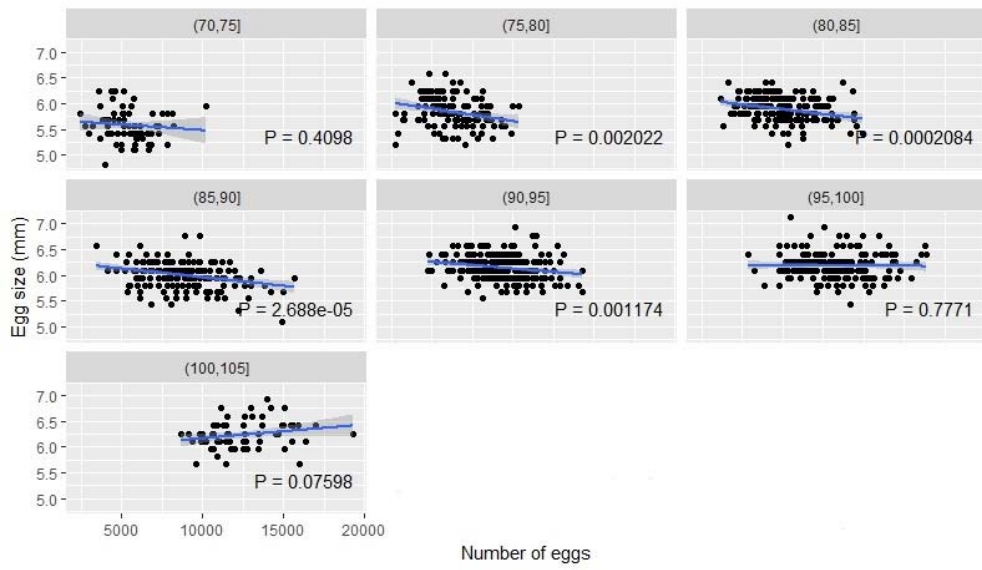


Figure 6. Relationship between number of eggs and egg-size (mm) in 7 grids where p value indicates significance level.

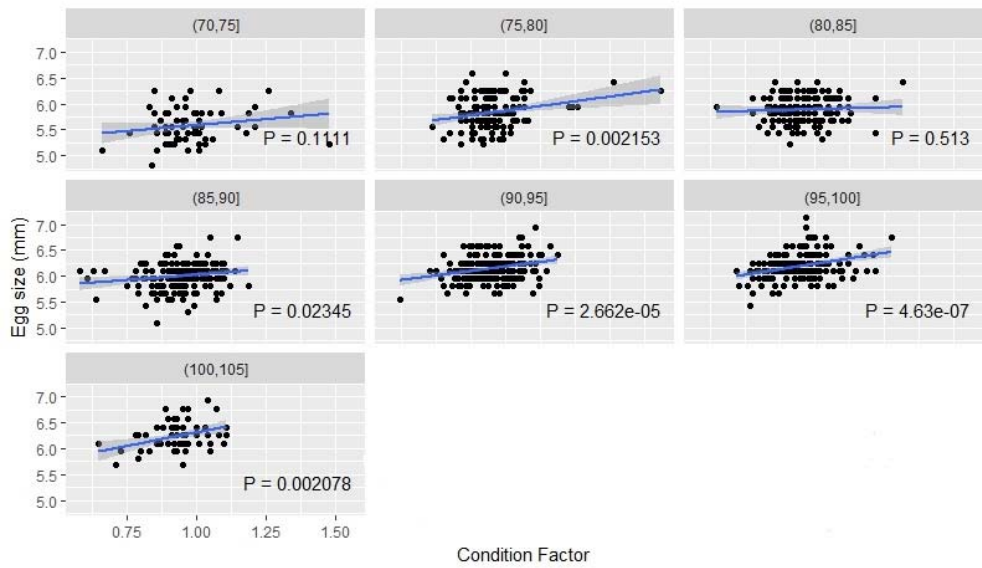


Fig 7. Relationship between egg-size and condition factor over 5cm interval size-classes of females.

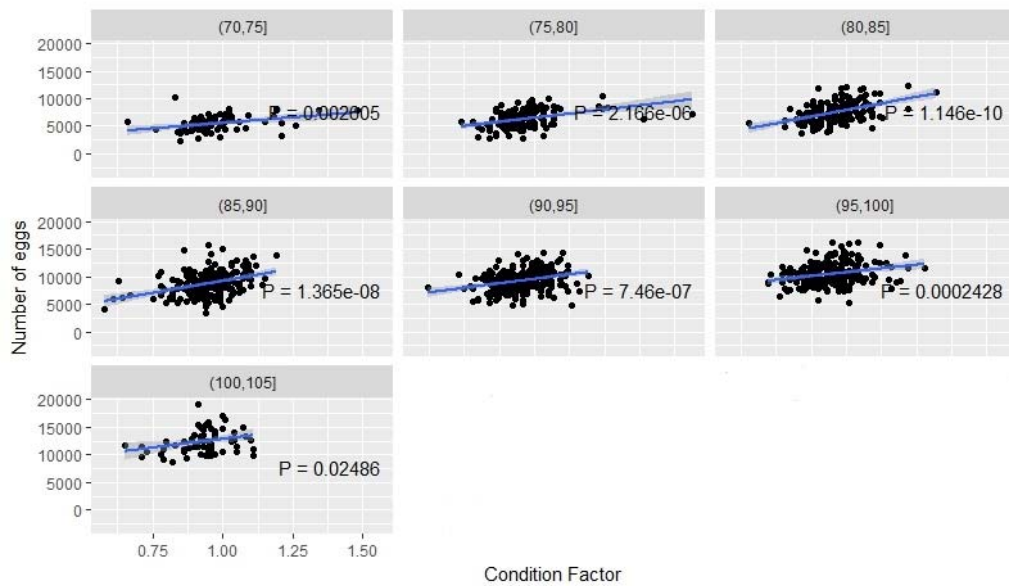


Fig. 8. Relationship between number of eggs and condition factor over 5cm interval size-classes of females.

There was significant positive relationship between condition factor and egg-size in 5 out of 7 size-classes ($p < 0.05$, Figure 7). No significant relationship could be found for size-class 70-75 and 80.1-85 cm fish. A significant positive relationship between egg-number and condition factor could be established within all size-classes ($p < 0.05$, Figure 8). There was no significant trend in condition factor over year for any size-class, except fish between 95.1-100 cm (Figure 9).

No significant effect ($p > 0.05$) of origin on egg-size could be found within any size class, except for females between 95-100 cm where wild fish had smaller eggs than hatchery fish ($F_{208}=5.78$, $p=0.02$). Also, no significant effect of origin on number of eggs could be found within any size class, except for females between 80-85 cm, where wild fish had fewer eggs than hatchery fish ($F_{181}=8.49$, $p < 0.01$).

Table 2: Summary (estimate, standard error, t value and p value) of the multiple regression analysis for 80.1-85 cm length class where egg size

(mm) is response variable and year, condition factor and number of eggs are predictors.

	Estimate	Standard Error	t value	P value
Intercept	-12.67	2.016	-6.287	<0.001
Year	0.009212	0.001009	9.126	<0.001
Condition Factor	0.7807	0.1897	4.116	<0.001
Number of eggs	-0.00006917	0.000009196	-7.522	<0.001
Observations	183			
R ² /adj. R ²	0.3937/0.3836			

Table 2 shows that, egg size of 80.1 to 85 cm length females increases significantly with year, condition factor and number of eggs it produces. The result was same for 85.1-90 cm and 90.1-95 cm size classes.

Table 3: Pair test of variables (Sprat population of three years' average from 1975 to 2016, length, condition factor, egg size and number of eggs) with correlation and significance probability (p value). Bold numbers refer to the statistically significant relationships.

Variable	By Variable	Correlation	Significance Probability
Sprat	Year	0.444071526	0.002531
Length	Year	0.066749994	0.655749
Length	Sprat	0.201656031	0.189298
Condition factor	Year	0.247222027	0.093866
Condition factor	Sprat	0.317494961	0.035723
Condition factor	Length	-0.194941486	0.189148
Egg size	Year	0.363008153	0.012147
Egg size	Sprat	0.237445579	0.120666
Egg size	Length	0.836743683	2.38e-13
Egg size	Condition factor	0.073306395	0.624353

Number of eggs	Year	0.212211214	0.152132
Number of eggs	Sprat	0.400471329	0.007066
Number of eggs	Length	0.906886335	1.67e-18
Number of eggs	Condition factor	-0.047973915	0.748801
Number of eggs	Egg size	0.779359616	1.09e-10

Table 3 calculates that sprat population has been influenced by year and condition factor is influenced by sprat population inflation. Number of eggs also varied significantly with sprat population. Pair test between egg size and egg number also shows significant difference as figure 6 showed for several size classes.

Discussion

My results clearly show that larger females have both more and larger eggs than smaller females. Similar result has been recorded by Morita et al. (1999) for white spotted charr, *Salvelinus leucomaenis*. Johnston and Leggett (2002) found egg size to be correlated with maternal size for walleye (*Stizostedion vitreum*). Models developed by Hendry et al. (2001) also favored the correlation between egg size, egg number with maternal fitness. Body size has long been known to be an important characteristic in fish, and larger fish are often more competitive and less exposed to predators than smaller conspecifics (Schlosser, 1988). The drive to grow and become large is hence strong in many fish, and is likely the most important reason why most salmon display an anadromous life-history as they will access better feeding conditions in the sea compare to in their native river. My results further support the importance of growing large for salmon, as larger females also potentially gain fitness advantages in the form of larger and more eggs. my results also state that models with quadratic relationship between egg-size/egg-number and length are favored to non-polynomial models, which indicates that the effect of length on egg-size/egg-number decreases as fish gets larger. This suggests that, from the perspective of egg-size and egg-number, the fitness advantages from being

large decreases with size, and hence that the selection pressure on female size also decreases with size. Based on the F-value and the correlation coefficient (r^2), the model regressing egg-number showed a stronger significant relationship than the model regressing egg-size. This is in line with the findings of Hendry et al. (2001) as their model showed stronger relationship between maternal fitness and egg number, than between maternal fitness and egg size. They presented two scenarios here. Firstly, if the higher reproductive output of large females has negative density dependent effect on eggs survival and cannot provide better habitat, increasing females should produce higher amount of small eggs. Secondly, when offspring fitness is density dependent and large females can provide good habitat quality, large females should produce large eggs. But then the direction of this female size and egg size relationship will vary upon the collective strength of these two effects.

There were positive trends in egg-size over time in all but the smallest size-class. Between 1974 and 2016, the egg size has increased in average by 3.7%, or 0.23 mm. The reason behind such increase is an intriguing question. Below I outline a few potential explanations:

Egg-size has increased because females have got better condition during the time-period

I recorded significant increase in egg size with increasing condition factor but we didn't find any strong trend in condition factor to increase in the females. But increased condition factor could explain the healthiness of the females and the survival chances of the eggs. My results show positive relationship between body condition and egg-size within all size-classes. This is in line with Healey (2001) and support that fish can invest more energy (yolk) into the egg (Rollinson and Hutchings, 2010) . However, my data also clearly show that there is no overall positive trend in body condition of females during the time-period. But we didn't take seasonal condition factor into account which has found to change seasonal weight of

gonad for perch, *Perca fluviatilis* (Le Cren, 1951). The food availability in the sea can change each year which may have a significant impact on the seasonal condition factor of the females. In addition, condition factor does not only reflect the feeding condition of the fish. It includes the gonadal development as a product of utilization of fat reserve during spawning period (Vazzoler and Vazzoler, 1965).

Egg-size has increased at the expense of the number of eggs

As neither larger nor better conditioned fish can explain the trend in egg-size, we must assume that the females have equal amount of energy to invest in reproduction today as they have had the last 50 years. My data show that there indeed seem to be a negative relationship between egg-size and egg-number, and hence that there may exist a trade-off between the number of eggs a female produce and the size of the eggs. This suggests that the number of eggs per female should have decreased during the study period. However, my results do not support this. In fact, the results suggest that it may actually be a weak positive trend in the number of eggs over time for 3 out of 7 size-classes.

Egg-size has increased because of influence of hatchery fish

However, recent study says that Baltic sea does not possess more than 10% wild smolts in its entire water system comparing to the hatchery reared smolts (Pedersen, 2009). According to Larsson (1984), 70% of Baltic salmon population is from hatchery reared origin. But in natural populations where supplemented hatchery fishes are in abundance, a trend towards smaller eggs have been found in North America (Heath et al., 2003). In Umeälven, it was found that wild salmons were more abundant than hatchery reared ones from 1974 to 1991. But my data has an average ratio of 1.7:1 of hatchery/wild. In those years, returning time of the migrated fishes are earlier for those who are larger than the others. The hatchery reared males and females returned on average 10 days later than the wild counterparts (McKinnell et al., 1994). Rearing type differs in the juvenile

experiences in the river and also affects their adult behavior in the river when they return (McKinnell et al., 1994). For both wild and naturally reared chum salmon, mean age at maturity increased with decreasing growth which Helle and Hoffman (1995) believed to be due to changes in oceanographic conditions or increased population density or both. In northern population, older age at maturity and limited amount of energy result in small number of larger eggs (Beacham and Murray, 1993).

Although Fleming et al. (2003) believed that the change of egg size could be related to underlying causes such as genetics, environment or both, according to Fox and Heath (2003b), change in egg size is corresponded with the shift from wild to hatchery rearing conditions and did not agree with the effect of environmental change. But Fleming et al. (2003) and Fox and Heath (2003a) both realized the importance of investigation to be precisely assured if hatchery supplementation is leading to any subsequent egg size decline over years by overtaking the evolutionary change which is the opposite scenario from my study.

Moreover, hatchery reared females have been found to pose less risk in breeding success than the males due to the failure of hatchery males to access in ovipositing (Fleming and Gross, 1993) which may influence egg survival and egg size.

Increase in sprat abundance may have indirect effect

The magnitude of sprat biomass escalation from late 1980s to mid-1990s was pronounced compared to herring population (Köster et al., 2003). Researchers suggest both abiotic (salinity, temperature) factor and biotic (copepods and cladocerans abundance) factor (Casini et al., 2006) to be responsible for this erection nature in Baltic sea. Greater amount of thiamine and fat due to young sprat as a prey to Baltic salmon resulted in inadequate supply of thiamine in proportion to the energy content and unsaturated fatty acids in female body which led them to M74 syndrome and higher condition factor (Keinänen et al., 2012, Mikkonen et al., 2011).

This sprat and M74 relationship may help the explanation to go to a scientific direction but we need data from other populations to be exact about this hypothesis.

Other factors that can explain the selection towards larger eggs

Changing attributes of Baltic sea

The change of experiences by the females during the migration can be a major predictor towards the selections made by the females to shape the tradeoff between more eggs or larger eggs. Wild sockeye salmon (*Oncorhynchus nerka*) in the Pacific Ocean, started to produce larger eggs when incubation temperature are getting higher with years (Braun et al., 2013). In addition, low sea surface temperature and severe ice conditions appear to change the distribution of small salmon (O'Connell et al., 1992). The declined salinity and change in biomass of zooplankton community in the Baltic Sea have reduced the herring and cod abundance (Flinkman et al., 1998). Climate change in Baltic basin is affecting the amount of freshwater flow into the sea (Graham, 2004) and as that freshwater source i.e, river is the nesting site of salmon, it may have potential impact on selection strategies of salmon egg size in the wild. Meier (2006) expected an increase of average temperature in Baltic Sea from 1.9°C to 3.2°C in the late 21st century. Climate change in northern Europe is causing to become the water warmer and fresher which is resulting in alteration in species community in the Baltic (MacKenzie et al., 2007).

Beyond body size

Larger eggs take more time to emerge than smaller eggs as found by Rombough (1985) for chinook salmon (*Oncorhynchus tshawytscha*). This study also says that the alevins from smaller eggs emerge from the gravel at smaller size than the larger eggs. But Cutts et al. (1999) revealed that early emergence of Atlantic salmon (*Salmo salar*) fry favors claiming better feeding territories earlier and this event is a better predictor of dominance

than body size. So, the bigger fries those emerged late, may found the best feeding territories already occupied. If larger eggs are not always good to lay, then why did the females choose this trait?

Oxygen intake

Einum et al. (2002) explained in the favor of larger egg size selection by the females that if bigger females deposit larger biomass of eggs per nest with an increase of egg size, it will reduce the egg numbers and potentially the oxygen consumption by the eggs. This selection can help larger eggs to develop resistance against anoxic conditions growing over years.

Selection will favor larger offspring (from larger eggs) if food abundance is limited (Hutchings, 1991) which could be explanatory for Baltic salmon if we could provide evidence showing the downward trend of feeding ground or prey fishes for salmonids. Hutchings (1991) also mentioned that if females produce smaller eggs, initially the chances of predation over them is probably higher. This selection can not only be explained through the events in sea as feeding condition (before migrating to the sea) of females in the freshwater can also be responsible for this.

Inter and intra population variation

Though we didn't take population effect in our study, Beacham and Murray (1993) suggested not to take latitude difference into account but regional variation into account for egg size because eggs get larger with increasing temperature but the change of egg size in higher or lower latitude is not because of the temperature, but the age at maturity. To conclude about the intra-population (sharing the same geographic location) egg size variability in fish, Einum and Fleming (2002) suggested in their review that, selection favoring the within population variation is more intense in larval stage (post-hatching) than in the egg stage (pre-hatching).

Survival and feeding success in later life stages

Duarte and Alcaraz (1989) assumed that increased egg size should increase the survival chances (low mortality). And that would lead to better feeding condition as a predator on smaller prey items, with increased swimming speed and most importantly larval survival against starvation in longer yolk period (McGurk, 1986).

Limitations of the study

I didn't have the access to the data on how long the females were in the freshwater system before they migrated to Baltic Sea. For chum salmon, larger native rivers (lengths > 8 km, drainage area > 100 km²) have been showed to give higher length in same age class and thus expected to have larger eggs than those were reared in smaller rivers. Thorpe et al. (1984) found Atlantic salmon females to produce more but smaller eggs when they grew rapidly in freshwater (rivers).

I couldn't cross check if the selection protocol of females for breeding program was same during the whole study period which could give us information about traits they (fishes) might select during their stay in the sea. To scrutinize the trend, I also analyzed the sprat population and M74 data to observe if there is any relationship of sprat population increase with fat reserve and egg size improvement of the salmons. But I couldn't build up such a positive relationship. As increased fat in fish body is mostly invested in reproductive activity (yolk reserve) than fish muscle, I expected it to have an impact on egg size.

If I had the data on distance of migration of the females, that could explain egg size trend more precisely because Beacham and Murray (1993) described that major freshwater migration distance has effect on salmonids egg size because they spend a larger budget of their energy in migration by reducing the allocation to gonadal development. According to Leggett and Carscadden (1978) northern population who spawn in thermally harsh environments, allocate greater energy reserve in migration to ensure post-

spawning survival. Salmon populations having the most difficult migration routes lay fewer and smaller eggs (Fleming and Gross, 1989).

The positive correlation between egg size and condition factor based on length classes were not strong enough to claim our hypothesis but more study is required on what is salmon eating in the Baltic sea to explain the reason behind acquiring higher condition index. Climatic effects (increasing sea temperature and declining salinity etc.) and the rise of sprat population are also not to be ignored and might have impacted the selection of the females to decide between more eggs or larger eggs. It is also unfortunate that I lack a data for a lot of years in my time series. This make all conclusions regarding trends less reliable and have to be considered when interpreting the results in my thesis.

Conclusion

Baltic salmon females don't violate the established concept of larger females (length and weight) produce larger eggs. I found a trend in increasing egg size over years which could be explained by combination of changes in life history traits through selection, the increasing restoration of salmonids spawning habitats in Scandinavia and the changes in the Baltic sea during the study period. My study claims the necessity of further study on the food of salmons in the Baltic to relate the body condition of the females. Further study on feeding status of salmons in Baltic Sea is required to analyze the energetic condition investment of that energy in reproduction.

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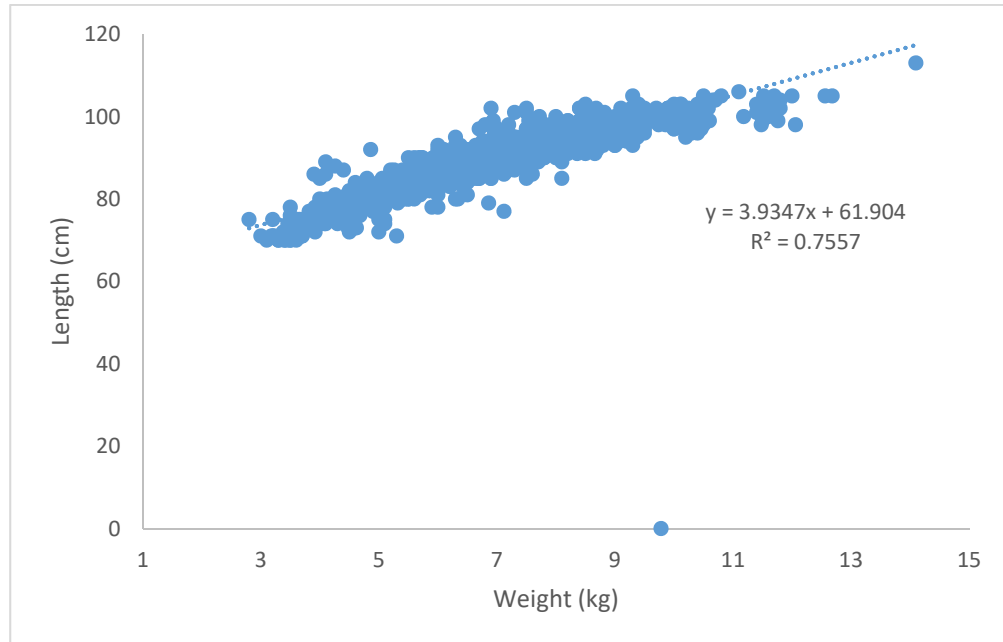
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Appendix 1

Relationship between fish weight and length



SENASTE UTGIVNA NUMMER

- 2017:15 Analysing the seal-fishery conflict in the Baltic Sea and exploring new ways of looking at marine mammal movement data
Författare: Ornella Jogi
- 2017:16 Importance of sampling design using an eDNA monitoring approach for pond-living amphibians
Författare: Sabrina Mittl
- 2017:17 Responsiveness in the Swedish moose management
Författare: Marie Löfgren
- 2017:18 Socio-ecological predators of moose body condition across a latitudinal gradient in Sweden
Författare: Regina Gentsch
- 2018:1 The effect of ecological forest restoration on bumblebees (*Bombus* spp.) in the boreal forest
Författare: Raisja Spijker
- 2018:2 Why did the moose cross the road? – Quantifying diel habitat selection and movement by moose, and its potential application for moose-vehicle-collision mitigation.
Författare: Jacob Coleman Nielsen
- 2018:3 Golden Eagle (*Aquila chrysaetos*) genomics across Scandinavia – Population structure and effects of marker selection
Författare: Måns Näsman
- 2018:4 Grazing impacts on savanna vegetation states and its role in albedo changes
Författare: Joana Fernandes
- 2018:5 Factors affecting damage to Scots Pine in a multiple ungulate species system
Författare: Matthew Knibb
- 2018:6 Supplementary feeding of game; an attitude survey of hunters, forest owners and farmers
Författare: Micaela Johansson
- 2018:7 The effect of nest box temperature on the breeding success of Pied Flycatchers (*Ficedula hypoleuca*) in northern Sweden
Författare: Jorina Boer
- 2018:8 Resource distribution in disturbed landscapes – the effect of clearcutting on berry abundance and their use by brown bears
Författare: Matej Domevšič
- 2018:9 Presence and habitat use of the endangered Bornean elephant (*Elephas maximus borneensis*) in the INIKEA Rehabilitation project site (Sabah, Malaysia) - A pilot study -
Författare: Laia Crespo Minguenza