UiT The Arctic University of Norway

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A growth comparison of allopatric and sympatric whitefish

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1 Introduction

Life history is important to fish biology. This theory describes the sequential pattern of events related to reproduction and survival that an organism will undergo from its first glimpse at life until its ultimate death. In other words, this theory will tell us what state a fish resource is in. It can be everything from when they reproduce, mature or how fluctuating their mortality is. Natural selection and resource differentiation push species to develop different traits to tackle external changes to habitats, which in turn creates different morphs with phenotypic variations that will help the organisms to adapt (Häkli, Katja, et al., 2018). This is often linked with resource use and competition. Adaptive divergence forces through by intra-specific competition creates and opportunity for resource polymorphism. Subarctic lakes formed by the last glacial melting are particularly known for these phenomena in their freshwater fish populations (Skúlason, et al., 1999). The different morph will through adaptive divergence inhabit different areas of a lake as they separate themselves from each other as ecological opportunities, adaptive radiations and phenotypic traits play a role (Häkli, 2019) (Kahilainen, et al., 2007). Further, life history plays an important part in survival through dynamics of energy allocated for growth and reproduction. A trade-off between growth and reproduction is central to evolutionary life history theory and is its best supported phenotypic prediction (Siems & Sikes, 1998). The amount of energy allocated for growth and reproduction is dependent on intrinsic and environmentally driven factors (Saborido-Rey & Kjesbu, 2005). For example, reaching maturity halts most of somatic growth, where energy is mostly focused on gamete production and reproductive behaviour. This creates an opportunity for fish to find the right strategy for survival through habitat choice and prey size. In lakes the fish that forages the littoral zone will have the best conditions as the littoral zone provides the most profitable niche as it sustains a high concentrate of large invertebrate prey (Præbel, et al., 2013). The second most advantageous zone is the pelagic zone where fish is provided with small-sized zooplankton (Præbel, et al., 2013). Adapting to these conditions is essential to maintain growth and reproduction which in turn will further survival efforts. Another factor that might affect the total growth and maturation patterns is the presence of other morphs or fish species, this might constrain trophic niches. According to Amundsen, et al. (2004) the LSR-whitefish morph living in allopatry will utilise both the littoral and pelagic niches to feed while when living in sympatry with the DR-whitefish morph it will be outcompeted in the pelagic as the DR-whitefish is better adapted to this habitat. This pushes the LSR-whitefish living in sympatry to only rely on feed for the littoral zone. In this study the focus will be on how growth and maturation is affected according to the composition of sympatric whitefish morphs.

The European whitefish (*Coregonus lavaretus*) is a highly polymorphic species that can have different distinctive morphs occurring in a single lake (Thomas, et al., 2019), inhabiting different areas of the lake. These morphs are differentiated by their morphological characteristics, especially through observing their gill rakers which are both heritable and ecologically important traits. The number of gill rakers a morph has is correlated with feed niche and the utilised size of prey (Kahilainen, et al., 2010). These gill rakers can be found to be either short, thick and sparse for effectively feed on larger benthic prey or longer and densely packed to feed on smaller zooplankton (Amundsen, et al., 2004). Other traits include head and pectoral fin traits, which are related to food selection, swimming ability or foraging efficiency. Sympatric morphs will mainly specialise to either benthic or pelagic niches where largest growth will be obtained by morphs habiting littoral or profundal zones (Amundsen, et al., 2004). The large sparsely rakered whitefish (LSR) forages the littoral zone which provides the most profitable niche, as it sustains a high concentration of large invertebrate prey (Præbel, et al., 2013). Outer characteristics include silvery sides with dark back and fins. The gill rakers have intermediate length and spacing. The densely-rakered whitefish (DR) is darker and smaller in size than the LSR-whitefish. It has pointed head shape, with the largest amount of dense, thin and long gill rakers (Præbel, et al., 2013). These characteristics makes it a great specialist at preying on pelagic zooplankton. The DR-whitefish utilises the pelagic which is the second most profitable niche in the lake with its small-sized zooplankton (Præbel, et al., 2013). A third morph is also present in some subarctic lakes. This morph is believed to have diverged repeatedly from the LSR-whitefish living in sympatry. It is presented as small sparsely rakered whitefish (SSR). This morph has a large head with large eyes and a pronounced subterminal mouth, its gill rakers are very short and widely spaced which makes it capable to prey on larger benthic prey from profundal sediments. Based on their characteristics these morphs have diverged into one resource specialised morph for each of the principal lakes habitats where they can exist in mono-, di, and trimorphic populations within a lake (Siwertsson, et al., 2010). Even though, the LSR-whitefish that lives in sympatry have the advantage of a profitable habitat with benthic prey, it seems that it cannot draw full effect of it. When it comes to competing with the specialised pelagic DR-whitefish for the pelagic niche the LSR-whitefish will have to renunciate. Living in sympatry rather than in allopatry could propose a difficult situation as food availability, increase in survivability, change in fishing exploitation and predator avoidance these factors contribute to overcrowding (Ylikarjula, et al., 1999). Under conditions of low resource availability fish would be subject to allocating resources mainly to maintain their biomass and only small amounts of resources will be invested into individual growth (Ylikarjula, et al., 1999). This is expected to alter age-at-maturation as juvenile fish will have trouble to compete with older fish for the same resources. Reduced juvenile survival selects for later maturation, and increased adult survival increases the age at maturity (Ylikarjula, et al., 1999). Therefore, it is expected to be a distinctive difference in maturation patterns between allopatric and sympatric LSR-whitefish.

European whitefish are present in northern Fennoscandia after colonising lakes after the last deglaciation (Häkli, 2019). The landscape is relatively flat with big coherent waterways that drains into two watercourses (Kautokeino-Alta & Tana watercourse), the lakes are not much deeper than 10-30m (Klemetsen & Amundsen, 2000). Traditionally the whitefish used to be harvested by nearby households, but this diminished quickly in the 50s. Consequentially, with lower fishing effort the whitefish population have become overpopulated and possibly creating situations of low availability and high interspecific competition which is resulting in whitefish becoming short growing and infested by parasites. The whitefish is mainly affected by the pike tapeworm (*Triaenophorus crassus*). Pike is the final host for the tapeworm. Inside the pike the worm releases its eggs in the intestines. When the eggs travel into water it hatches and are eaten by copepods. Then when the whitefish feeds on these copepods they become infected where the parasite infect the flesh of the fish. If a pike then predates an infected whitefish the cycle starts over as the parasite is back in the intestine of the pike (Klemetsen & Amundsen, 2000). As mentioned earlier, conditions of low resource availability will push individuals to allocate resources mainly to maintain their biomass. This creates a problem where age at maturation is affected and fish mature earlier at the cost of potential size to ensure survivability of its species. However, the presence of a predator such as the pike can have a positive effect on potential body size if the intra-specific competition is lowered as a consequence (Ylikarjula, et al., 1999). Even though there are few commercial exploitations of the whitefish locally in Norway, the neighbouring regions such as Finland utilise the whitefish resource intensively with high-quality whitefish in demand (Rahkonen, 2018). This indicates that there is a market for this resource for both recreational and commercial purposes. Whitefish can prove to be useful in Norway as well if the fish can reach its potential and if its quality is bettered. This have also been proven possible as there are cases where stunted fish populations have been reduced by intensive fishing to try and bring growth back but in most cases the whitefish population burst back to its preliminary condition (Amundsen, et al., 2002). However, these programs have trouble with the gear lacking in selectiveness which creates a problem where other fish species and younger fish are also caught. This could affect other species than the target species. Other problems with these programs are that they are time-consuming and expensive. However, the cost of doing nothing may be high as fish as a resource in the future will become valuable for both commercial and recreational purposes. We are also committed to sustainably manage species that exist within our borders. Therefore, implementing useful management theory with reliable ecological knowledge and learning over time could prove useful to find the best strategy for management. Adaptive monitoring and management are useful as they can evolve iteratively as new information emerges and research questions change (Lindenmayer, et al., 2011). This can help avoid repeating mistakes, adopt the most effective strategies and get the best possible results.

In this study I will investigate the growth and maturation patterns of the LSR-whitefish living in both allopatry and sympatry and see how life history traits are shaped by the presence of sympatric morphs by comparing stock from different lakes situated in the Alta- and Tana watercourse. Due to earlier findings that polymorphic LSR-whitefish have to restrict their diet (Kahilainen, et al., 2005), I hypothesize that somatic growth in monomorphic LSR-whitefish populations will be greater (1). Further, I expect that age at maturation will be lower for LSR-whitefish in monomorphic populations than in polymorphic populations, because of difference in growth between the populations (2). I also expect that DR-whitefish have a faster initial growth rate, smaller body size and early maturation than the sympatric LSR whitefish (3). I will also discuss if the use of an ecosystem-based management theory could help gain more knowledge to further understand the dynamics of the lake ecosystem.

2 Materials and Methods

2.1 Study site & data collection

16 lakes are analysed (see figure 1), these are situated in the Alta- and Tana watercourse in eastern Finnmark. Lakes that belong to the Alta drainage will drain into the Alta river further north. There are barely, if any, human activities at these locations. There are some recreational fishing in season but extensive fishing for household purposes are low for whitefish. Further, the area that these lakes are in are managed by a single landowner (FeFo) to ensure inhabitants of Finnmark access and rights to resources. The lakes contain different species of freshwater fish, apart from the whitefish there are perch, pike, brown trout, arctic charr, burbot, grayling

and minnow. Table X shows an overview of which species are present at each lake. Seven of the lakes have allopatric LSR-whitefish, five lakes have the sympatric LSR-whitefish and DR-whitefish and the last four have an intermediate morph.

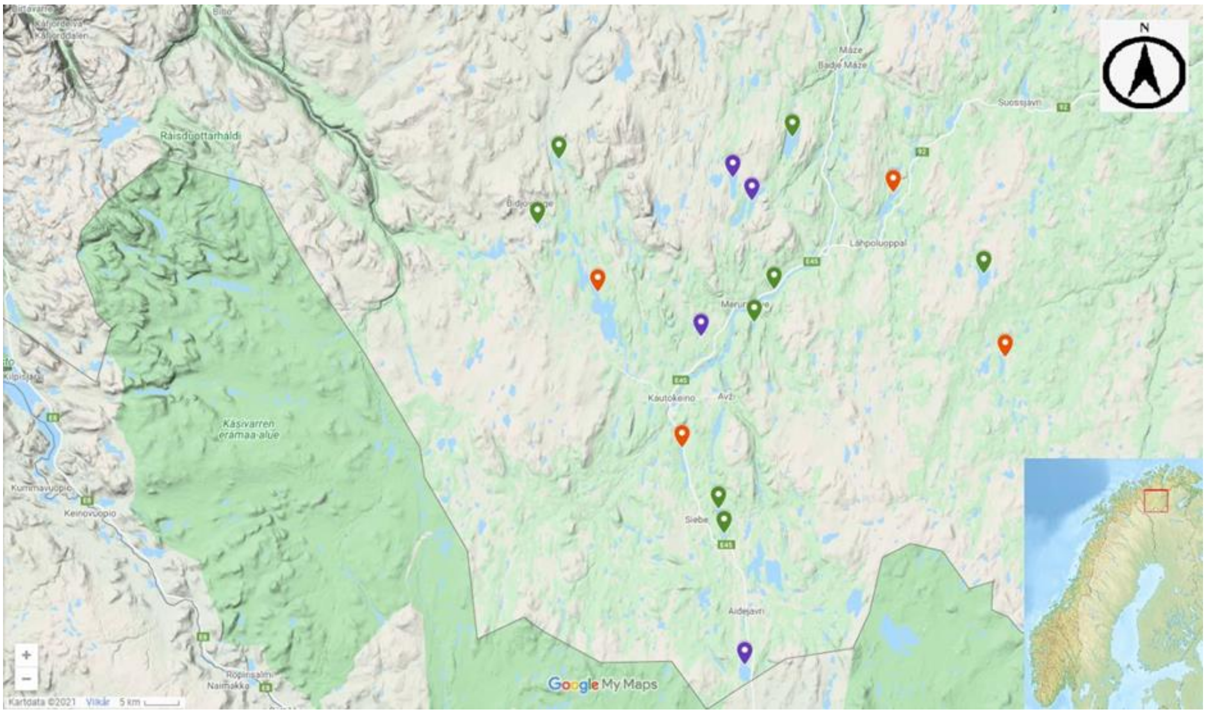

Figure 1, map showing lakes where material was collected. Monomorph lakes in green, dimorph lakes in orange and intermediate morph in purple. All sites are situated in Finnmark county.

2.1.1 Data material

The study will be made through analyses of existing data gathered on different field trips (trips made in 2001, 2005, 2007, 2008, and 2009) where whitefish is caught using multi-mesh gillnets. Benthic gillnet overview (BGO) was used for the littoral zone and profundal zone, and Floating gillnet overview (FGO) was used for the pelagic zone (0-6m). Even though, this collection has been performed a while age the situation in these lakes are somewhat unaltered. These field trips have collected information regarding habitat, weigh, length, age, sex, maturation, morphology, presence of other fish, parasites and otoliths. Length and weight were measured on site for each individual fish and age recording using otoliths were read in lab sessions. This information will be used to estimate length at age and length at maturity. Calculations are done using the R-software with scripts that are either made or using existing scrips (Ogle, 2013). The raw datafile will be cleaned where fish that are missing either maturation or age will not be a part of their respective analysis.

Table 1, Lakes that were included with their respective morph habitants. The count shown is after cleansing the data material for missing values.

Lake	Morphs	Classification	Count	Watercourse	Max depth
Biggijavri	Monomorph	LSR	132	Alta	52
Guorbajavri	Monomorph	LSR	98	Alta	7
Havgajavri	Monomorph	LSR	82	Alta	19
Jevdesjavri	Monomorph	LSR	89	Alta	13
Naggitjavri	Monomorph	LSR	136	Alta	17
Stuora Galbajavri	Monomorph	LSR	58	Alta	12
Vuolit Njivlujavri	Monomorph	LSR	75	Alta	16
Soapatjavri	Dimorph	LSR/DR	132/85	Alta	25
Stuorajavri	Dimorph	LSR/DR	109/125	Alta	30
Vuolgamasjavri	Dimorph	LSR/DR	112/32	Alta	30
Lahpojavri	Dimorph	LSR/DR	96/112	Alta	36
Vuoddasjavri	Dimorph	LSR/DR	104/93	Tana	32
Gædgejavri	Intermediate	LSR-DR	163	Alta	20
Datkujavri	Intermediate	LSR-DR	119	Alta	17
Vuolit Spielgajavri	Intermediate	LSR-DR	115	Alta	12
Måkkejavri	Intermediate	LSR-DR	154	Tana	30

2.1.2 Habitat

The sympatric morphs will often have differences in habitat and food selection (Amundsen, et al., 2004) as they differ in resource utilisation. The DR- whitefish is better adapted to its habitat in the pelagic where it will prey on zooplankton while the sympatric LSR-whitefish will prey on zoobenthos and roam the benthic habitat. The pelagic zone is the second most profitable niche (Præbel, et al., 2013). These morphs are strongly segregated by their habitat as there are limitations to competition. The sympatric LSR-whitefish is out-competed in the pelagic and therefore will have a restricted food availability. However, the LSR-whitefish that lives in allopatry will have a better availability to different feed and therefore utilises the most profitable niche (Præbel, et al., 2013). It feeds mostly on zoobenthos but may roam the pelagic to find other sources of food.

2.1.3 Age determination & maturation

Sagittal otoliths were analysed to determine age of the whitefish. These are located in the inner ear and will grow even though the fish has ceased growing. Otoliths consists of growth zones where one zone is transparent (hyaline) and the other is opaque. Each year two zones will appear on the outside of the stone in fish that habits either high or low latitude (Pedersen & Mikkelsen, 2017). Sagittal otoliths were analysed to determine age of whitefish. These are located in the inner ear. Otoliths are made up of calcium carbonate and contain a lot of information about fish life (Pracheil, et al., 2019). They can indicate migration, diet, growth and sound disturbances. Fish that resides in high (or low) latitudes will have two zones appear each year where the opaque zones often appear in the summer and the hyaline zones solidify autumm/winter (Pedersen & Mikkelsen, 2017), in this case the hyaline winter zones were counted to determine age. The otoliths were preserved in ethanol upon collection and when analysed with a microscope they were immersed in glycerol to view the growth zones more clearly, giving us the observed ages. Age composition is then calculated by finding the frequency of fish for each age. This is used for only as an indicator for mortality but cannot be used to state the mortality of the fish samples as there are other factors that will play a role of mortality.

To determine how far each fish had come in the maturation process, they were visually studied. The gonads were characterised as either mature or immature. Being caught in August/September the development of the gonads had come quite far, making it easy to distinguish between mature/immature individuals. Mature gonads will stretch beyond half the abdominal cavity, with eggs relatively larger than of immature fish.

2.2 Growth

Fish has indeterminate growth, will continue to grow after reaching maturity, however, it will rather allocate most of its food intake towards reproduction efforts slowing down growth considerably (Pedersen & Mikkelsen, 2017). To calculate individual growth von Bertalanffy's growth model (hereafter VBF) will be used. This model mathematical model is often applied to estimate individual growth in fish populations. The output of this model will be a visual plot that will have a fitted curve with that visualises the length at age relationship. It will also produce Linf which is the average theoretical maximum length that each fish can potentially achieve, while the K-value produced tells us about how fast a fish grows towards its acquirable size. It must be mentioned that as Linf is an average estimate there will be some individual fish in each lake that can achieve lengths than are larger than the average (Ogle, 2013). The growth equation can be expressed mathematically as:

$$L_t = L_\infty(1 - e^{-K(t-t_0)})$$

Where:

- L is the length of the fish, thus L_t is length at a given time or age
- L_∞ is where growth is zero, or asymptotic average length
- K is the growth coefficient
- t is the time (or age) of the fish
- t_0 is the age where the fish length would be zero

For my analysis on growth the values from Linf and K will be the most important. To find out how stable the estimate for these values are a confidence interval (95%) will be computed and added to each model.

2.2.1 Using R-software to create VBF-plot

To be able to use the R-software to produce the VBF-plots the whole dataset had to be cleansed of fish that did not contain information regarding length, age or morph. By removing these fish from the dataset, the lakes had less information to use which became apparent when producing the confidence intervals. To be able to produce these VBF-plots scrips that already are coded were used (Ogle, 2019). Some tweaks had to be made for the scripts to run my dataset. These included filtering the lakes and computing the plots by morph and lake by lake. The value "t_0" was fixed to be 0, this achieves a better fit for the model, and it is hard to assume what size individual fish will have before hatching. After producing each model, the values for Linf and K where extracted with their respective confidence intervals. These were put in a table and in an interval plot to visualise them further. The interval plot was made using "ggplot" in RStudio using a geom_pointrange script.

2.3 Size at maturity

To calculate size at maturation a logistic regression using binominal variables (maturity) and explanatory variable (age/length) was used. The dataset gives us the stage of maturation each individual had. Using this information with age and length maturity can be analysed. Maturation is classified as either immature “0” or mature “1”, areas where maturity is classified as “2” is set to mature “1” which makes it easier to analyse. Length is categorised into bins, were each length category is as narrow as possible but includes enough individuals so that the proportion mature in each bin is reliably estimated (Ogle, 2019). The analysis will be performed with RStudio, using an already created script (Ogle, 2019). Here the probability of fish being mature is calculated using the relationship between the success of being mature and the explanatory variable (age/length). The probability of being mature using the observed value of the explanatory variable is expressed as:

$$p = \frac{e^{\alpha+\beta_1 x}}{1 + e^{\alpha+\beta_1}}$$

Where x is the explanatory variable (either age or length). By using this equation in the R-script

(Ogle, 2019) we end up with a sigmoid curve. Further to find length or age at maturity at a certain percentage of mature fish within the population this equation is used:

$$x = \frac{\log\left(\frac{p}{1-p}\right) - \alpha}{\beta_1}$$

The output for A_x and L_x were plotted as a dotted line onto the produced sigmoid curve, giving a visual representation. The values that are attained from these plots are put in table. This makes it easier to compare the different lakes and morphs. These values include: the percentage of mature individuals at 150 mm, at what length 50 % of the population is mature, at what stage maturity is at 2 years and at what age 50 % of the population is mature. These values will help to find an indication of different maturation patterns between the lakes and the morphs.

3 Results

3.1 Age and length

Age composition in the different lakes showed that sympatric LSR-whitefish in dimorph lakes had many young fish, these lakes include Soupatjavri, Stuorajavri and Vuolgamasjavri. In the monomorph lakes the population had a high percentage of young fish in three lakes. 60 % of the population in Havgajavri were under age 3, Guorbajavri have 25 % of its population below age 2, and Stuora Galbajavri have 40 % who were under age 2. For the other monomorph lakes age composition show that they had more older fish (>5+).

50 % of the population in Havgajavri were 2 yearlings, while Guorbajavri had above 25% 1 yearlings and Stuora Galbajavri were represented with 40 % of its population with 1-yearlings. Naggitjavri (figure 2) had an older population where 25 % are 5 yearlings. The bar-plot showing age composition are to visualise age distribution in the lakes. Figure 2 shows a monomorph lakes with allopatric LSR-whitefish, while figure 3 shows sympatric LSR-whitefish. For other lakes age composition is included in appendix.

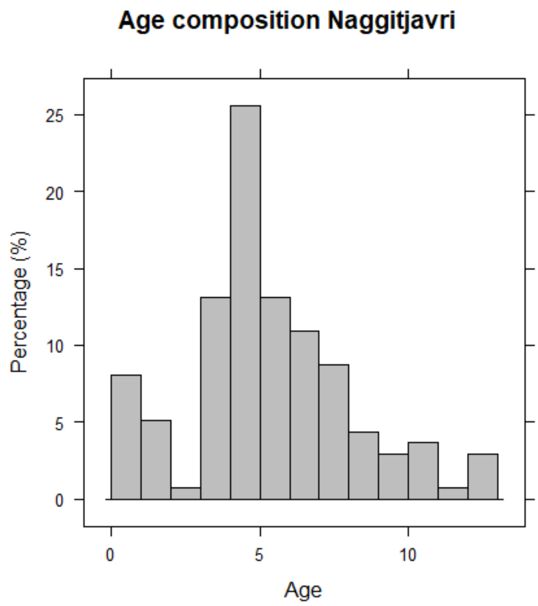

Figure 2, age distribution for allopatric LSR-whitefish in lake Naggitjavri. The frequency shows percentage of fish for each age

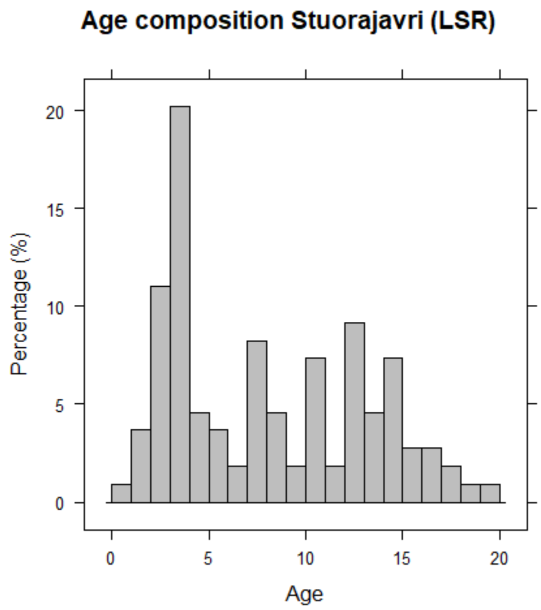

Figure 3, distribution of ages for sympatric LSR-Whitefish in lake Stuorajavri. This lake also contains the DR-whitefish morph.

Allopatric LSR-whitefish had higher mean length (228.7 mm) and maximum recorded length (362,4 mm) than both the sympatric LSR- and DR-whitefish. The average age however was lower, with age being <5 where both sympatric morphs average age is >6. For the two morphs living in sympatry mean length and age were quite similar. But, the sympatric LSR-whitefish had a higher average maximum recorded size (357,8 mm vs. 259 mm), showing that it can grow quite larger than the DR-morph.

Table 2, averages measured for the allopatric LSR-whitefish for each lake. The average size for all allopatric LSR-whitefish is shown at the bottom of the table. This only indicates the average size and age of LSR-whitefish in the included monomorph lakes.

Lake	Mean length	Median length	Max	Average age	Max
Biggijavri	230	240,5	347	8	16
Guorbajavri	234,41	255	428	6	18
Havgajavri	234,33	215,5	342	2,5	7
Jevdesjavri	218,13	209	383	6,5	18

Naggitjavri	201,43	205	361	5,75	13
Stuora Galbajavri	212,91	227	312	4,5	10
Vuolit Njivlujavri	270	268	364	5,25	12
Average size LSR-whitefish (allopatry)	**228,7**	**231,4**	**362,4**	**5,5**	**13,4**

Table 3, average size for LSR-whitefish in sympatry for each lake. At the bottom a total average for all the sympatric lakes is included for both the LSR-morph and the DR-morph.

Lake	**Mean length**	**Median length**	**Max**	**Average age**	**Max**
Lahpojavri	169	135	315	5	13
Soupatjavri	215	231	430	4,5	14
Stuorajavri	231	242	326	10	20
Vuoddasjavri	168	165	333	5,5	17
Vuolgamasjavri	224,5	214,5	385	7	17
Average size LSR-whitefish (Sympatry)	**201,5**	**197,5**	**357,8**	**6,4**	**16**
Average size DR-whitefish (Sympatry	**199,8**	**200**	**259**	**6**	**13**

3.2 Growth

3.2.1 Von Bertalanffy's growth model

LSR-whitefish in monomorphic lakes grew faster towards Linf than the sympatric LSR-whitefish. Biggijavri stands out as it had noticeably slower growth (K=0.23) than the other monomorphic lakes. The theoretical maximum length however does not seem to vary much between mono- and dimorph lakes. Jevdesjavri had very high CI (figure 9) in both Linf and K which indicates some issues with data material. The same goes for K in Vuoddasjavri where the spread was quite large (figure 9).

Linf between the two sympatric morphs differs, as the DR-whitefish does not seem to reach the same lengths. However, DR-whitefish in Vuolgamasjavri reached the highest Linf and had the lowest K-value for all the DR-morphs. Other than that, the DR-whitefish had quite fast growth towards Linf (see figure 10). Other than the sympatric LSR-whitefish in Soapatjavri the other sympatric LSR-whitefish' had relative slow growth towards Linf.

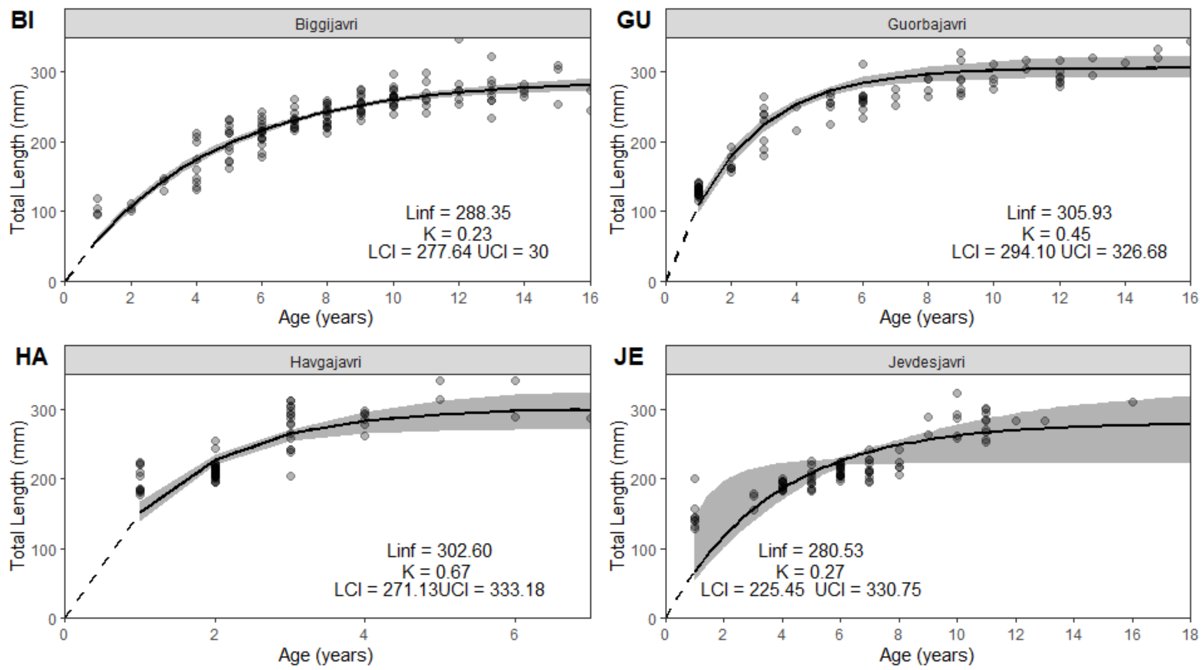

Figure 4, VBF-plot showing allopatric LSR-whitefish growth towards Linf. The shaded polygon shows 95 % confidence interval for the plot. Solid line are observed ages while dashed line is entire range of ages.

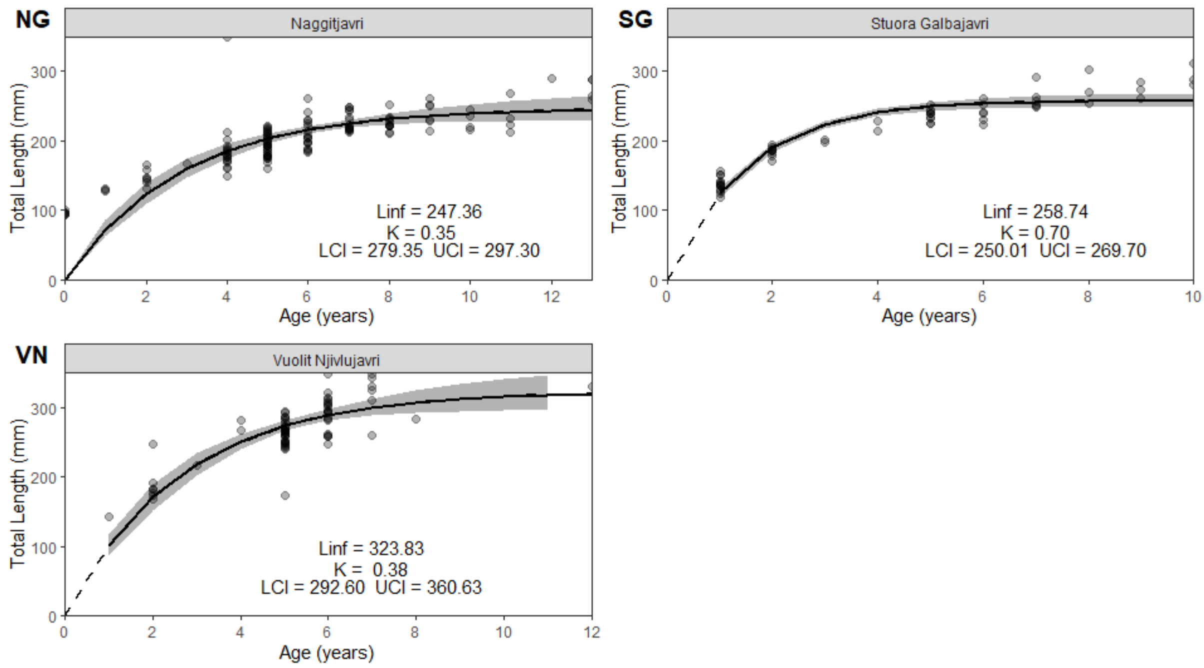

Figure 5, VBF-plot showing allopatric LSR-whitefish growth towards Linf. The shaded polygon shows 95 % confidence interval for the plot. Solid line is observed ages while dashed line is entire range of ages.

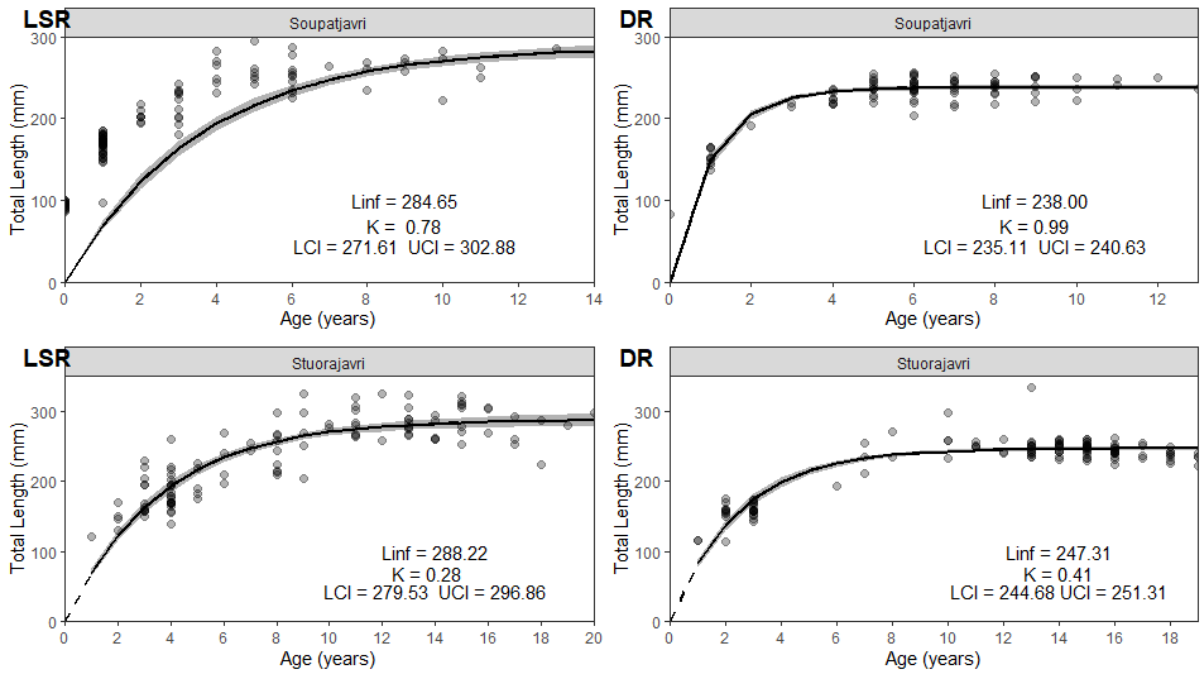

Figure 6, VBF-plot showing growth of sympatric morphs towards Linf. Shaded polygon shows 95 % confidence interval. Sympatric LSR-whitefish on the left and DR-whitefish on the right for each lake.

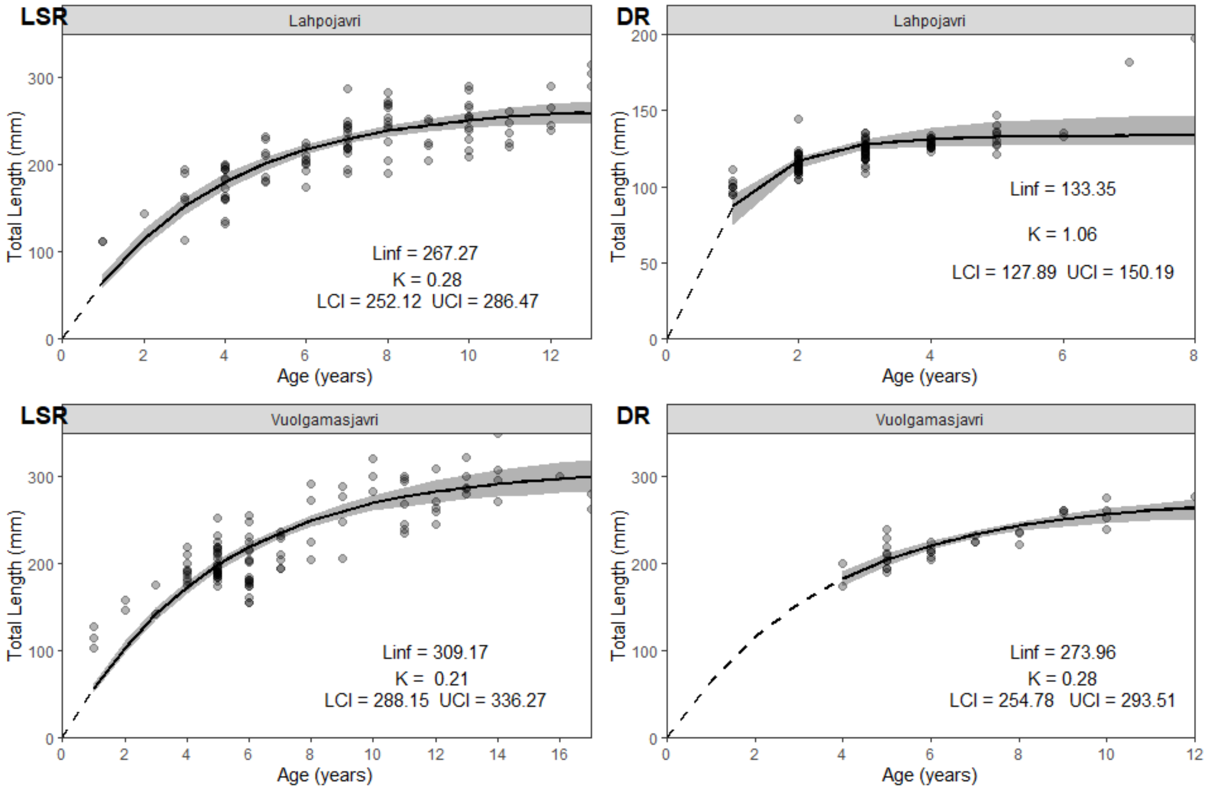

Figure 7, VBF-plot showing growth of sympatric morphs towards Linf. Shaded polygon shows 95 % confidence interval. Sympatric LSR-whitefish on the left and DR-whitefish on the right for each lake.

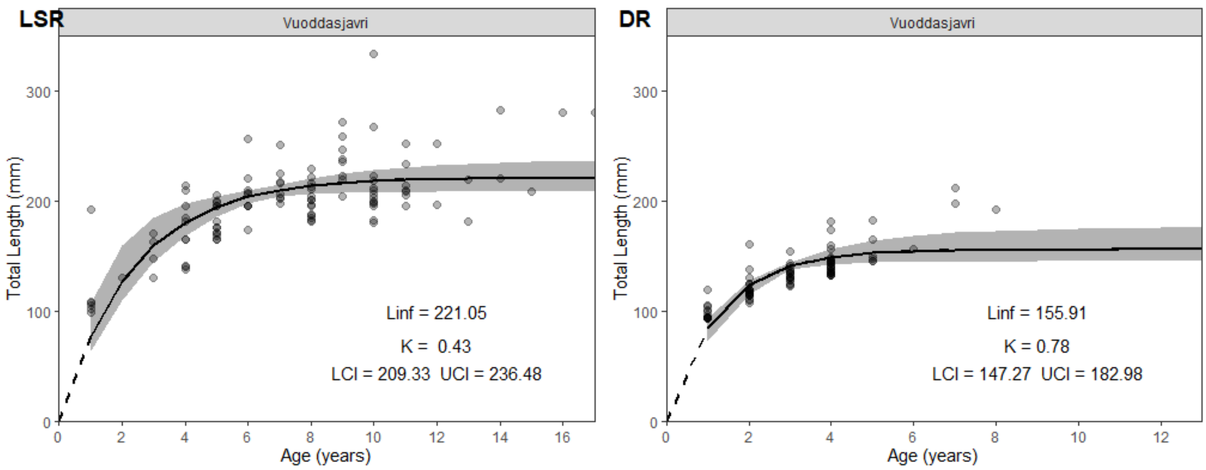

Figure 8, VBF-plot showing growth of sympatric morphs towards Linf. Shaded polygon shows 95 % confidence interval. Sympatric LSR-whitefish on the left and DR-whitefish on the right for each lake.

3.2.2 Interval plot for values from VBF

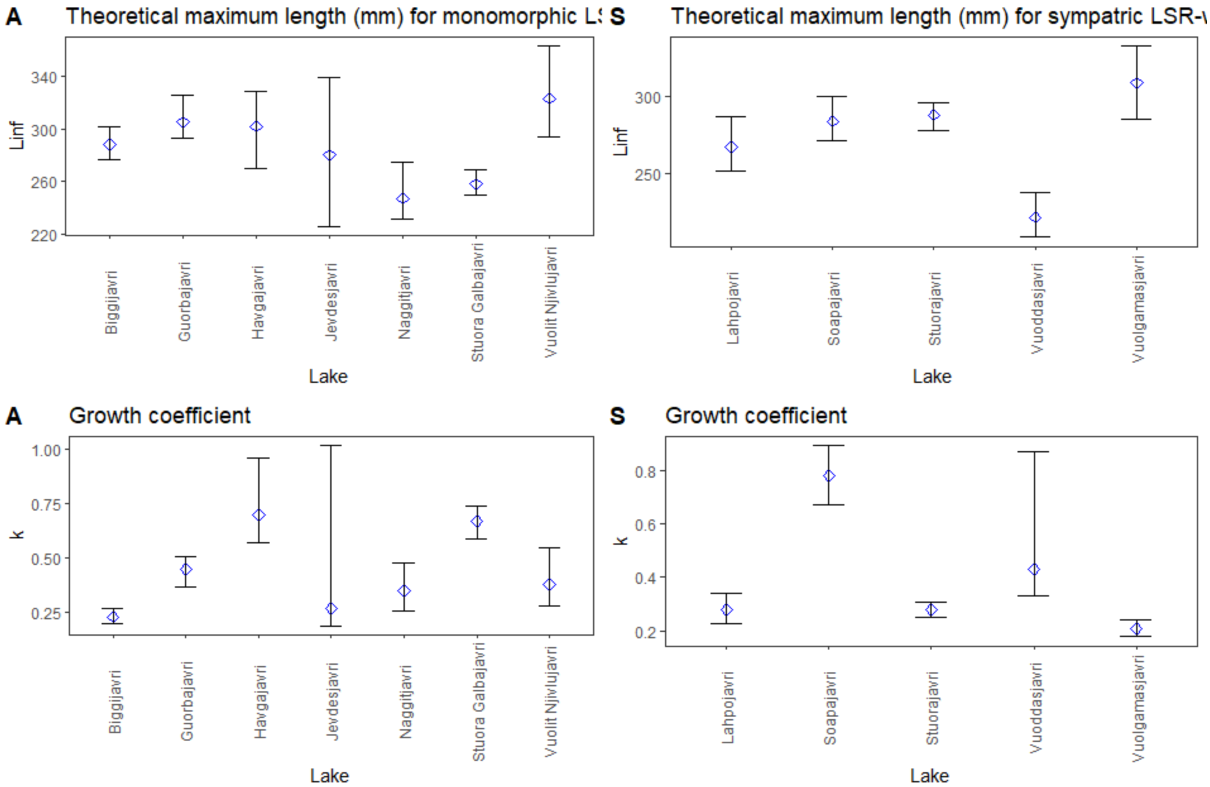

Figure 9, Linf with 95 % CI for allopatric LSR-whitefish top-left and for sympatric LSR-whitefish top-right. Respectively K-value is shown below with 95 % CI. Jevdesjavri stands out with a huge gap.

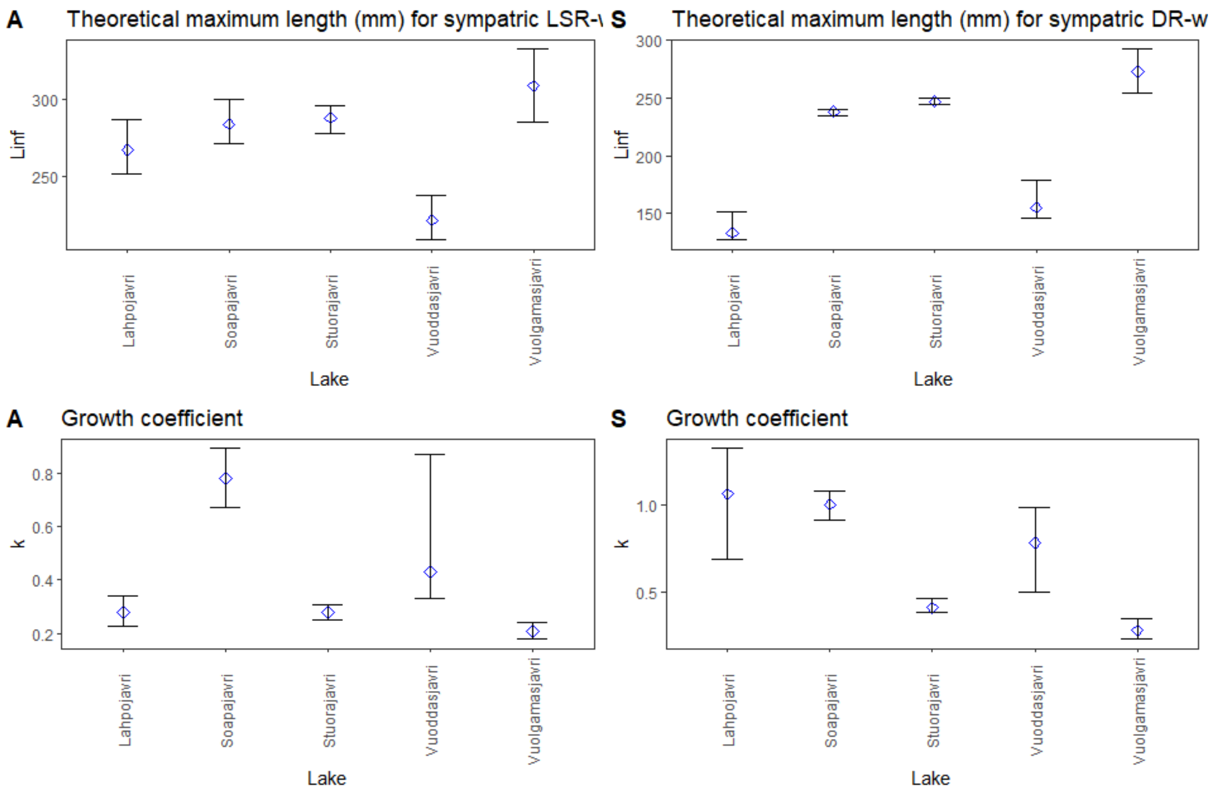

Figure 10, interval plot showing the difference of Linf- and K-values between the LSR-whitefish and DR-whitefish living in sympatry. Notably difference in K-value

3.3 Size at maturity

For the monomorph LSR-whitefish 50 % of the population were mature between the ages approx. 3-7. For the monomorph lakes with youngest A50 maturation seemed to begin before they reached age 2 (Guorbajavri, Havgajavri, Jevdesjavri) which implied early maturation. Biggijavri holds the LSR-whitefish that got oldest before the population had reached maturity. Maturity for the sympatric LSR-whitefish happened at an older age where A50 ranges from approx. 6-10 years which indicates that it matured somewhile later than the allopatric LSR-whitefish. In dimorph lakes it is only Vuoddasjavri that noticeably had begun maturation before reaching age 2 (table 6). For the DR-whitefish A50 seemed to happen a lot earlier than for both the LSR-morphs, however Stuorajavri holds a DR population that matured after reaching age 8. The other DR-whitefish reached maturity at ages approx. 2-3. This made Stuorajavri an exception from the others. The DR-whitefish had all started maturity processes at age 2.

Lengthwise the allopatric LSR-whitefish reached maturity within the lengths 112-316 mm (table 5). Where Jevdesjavri matured at the shortest length (112 mm) which seemed to be an exception from the other lakes which range from 209-316 mm. The sympatric LSR-whitefish matured between the lengths 178-274 mm (table 6), where two of the lakes had reached almost 30 % population maturity at 150 mm. This indicated that there is not much difference in length at maturity between the two LSR-whitefish. The DR-whitefish however showed that it is smaller when population is mature, with L50 ranging from 117-207 mm (table 7). Lahpojavri had almost 100% of its population mature at the 150 mm which was very noticeable.

Below are some examples of the graphs made for size at maturity. Graph for all lakes are included in appendix, while values from size at maturity analysis can be viewed in tables below.

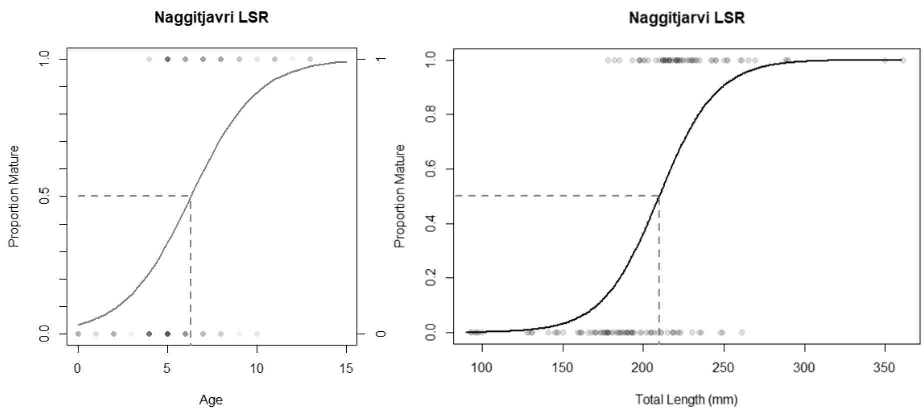

Figure 11, visualises size at maturity in lake Naggitjavri. 50 % of the allopatric LSR population mature at 209.76 mm and at age 6. It further shows that the population will reach full maturity if they can reach sizes above 250 mm. However, it must be taken into account that salmonoids can skips spawning.

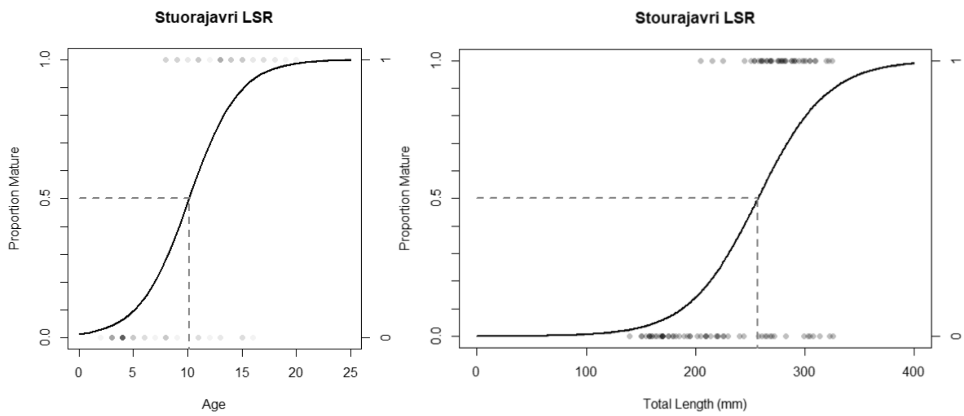

Figure 12. Here we have the size at maturity for a sympatric LSR population. Maturity for 50 % is reached at 257.13 mm and at around age 10.

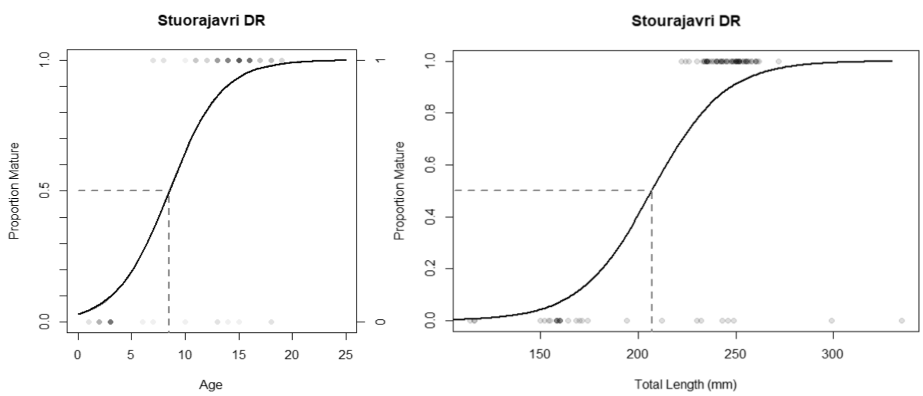

Figure 13, the DR-whitefish in Stuorajavri reaches 8 years and 206.89 mm in length when 50 % of its population is mature.

Table 4, Size at maturity values for the allopatric LSR-whitefish with parameters from VBF. The graphs are included in Appendix.

Lake	***Maturity at 150mm***	***L50***	***L∞***	***K***	***Maturity at 2 years***	***A50***
Biggijavri	0.08 %	225.4 mm	288.35	0.23	0.05 %	6.95
Guorbajavri	4.72%	247.67 mm	305.93	0.45	15.15 %	6.21
Havgajavri	0 .1 %	248.82 mm	302.60	0.70	14.22 %	2.79
Jevdesjavri	66.9 %	112.29 mm	280.53	0.27	16.38 %	3.24
Naggitjavri	47 %	209.76 mm	247.36	0.35	0.8 %	6.33
Stuora Galbajavri	0.048 %	240.99 mm	258.74	0.67	0.02 %	5.67
Vuolit Njivlujavri	0 % *(270 mm ->*	316.17 mm	323	0.38	0.00009 %	6.76

Table 5, Size at maturity values from the sympatric LSR-whitefish with parameters from VBF. The graphs are included in Appendix.

Lake	**Maturity at 150mm**	**L50**	**L∞**	**K**	**Maturity at 2 years**	**A50**
Soapatjavri	1.96%	273.95 mm	284.65 mm	0.78	3.92%	6.72
Stuorajavri	3.26%	257.13 mm	288.22 mm	0.28	2.73%	10.15
Vuolgamasjavri	0.2%	251.68 mm	309.17 mm	0.21	0.0005 %	8.26
Lahpojavri	29.57%	225.06 mm	267.27 mm	0.28	0.4%	7.41
Vuoddasjavri	25.02%	178.85 mm	221.05 mmm	0.43	11.56%	5.65

Table 6, Size at maturity parameters for the DR-morph living in sympatry. Graphs are included in Appendix.

Lake	Maturity at 150mm	L50	L∞	K	Maturity at 2 years	A50
Soapatjavri	3%	199.68 mm	238 mm	0.99	34.70%	2.88
Stuorajavri	4.37%	206.89 mm	247.31 mm	0.41	6.46%	8.51
Vuolgamasjavri	64.11%	136.92 mm	273.96 mm	0.28	51.84 %	1.92
Lahpojavri	98.33%	117.33 mm	238 mm	1.06	27.26%	2.50
Vuoddasjavri	80%	126 mm	155.91 mm	0.78	37.91%	2.68

4 Discussion

4.1 Growth

The mean length from the dataset shows that the allopatric LSR-whitefish is marginally larger than both the sympatric LSR- and DR-whitefish, while the two sympatric morphs have more or less the same mean length. Regarding age composition, the allopatric LSR-whitefish is represented with younger fish than the sympatric morphs. The average maximum age is recorded in sympatric LSR-whitefish.

As expected, the allopatric LSR-whitefish shows that it has better growth than the sympatric LSR-whitefish. However, the difference in Linf is not as clear as expected. The allopatric LSR-reaches in most lakes an Linf higher than 300 mm while for the sympatric morph this only applies to Vuolgamasjavri (table 6). The biggest difference in growth is apparent in the growth coefficient (K) calculated with the VBF-function. Here the allopatric LSR-whitefish clearly with the exception of Biggijavri grows a lot faster towards Linf than the sympatric morph. This indicates that it gains more energy for somatic growth and that the advantage of grazing on zooplankton in the pelagic without competition from the specialised DR-morph is important. This intermediate growth rate towards Linf is also seen in another study, where Linf between the LSR-morphs in mono- and dimorph lakes gave no clear indication to be different, whereas the growth towards Linf and length at maturity was faster in allopatric LSR-whitefish (Smalås, 2011). The fast growth in the allopatric LSR-whitefish may be explained to reach such a size to avoid being predated and that its strategy is to gain enough energy as quick as possible to be able to start reproductive efforts when the desired size is reached. When the VBF curve starts to flatten out, this indicates that the fish is entering a reproductive phase where almost all energy attained will be given to gonad production rather than somatic growth.

The sympatric LSR-whitefish grows slower towards Linf. This might indicate that it has a more restricted diet, spending more time securing the growth needed for maturation and that finding enough feed is difficult. These results indicate that ecological factors related to the presence of another morph are affecting growth for the sympatric LSR-whitefish. Food availability plays a huge role in this as there might be less food available for sympatric LSR-whitefish as interspecific competition from the DR-whitefish will affect feeding success (Amundsen, et al., 2004). In monomorphic lakes the LSR-whitefish will be able to forage zooplankton in addition to benthic prey as it can freely wander into the pelagic looking for substitute feed. The sympatric LSR-whitefish however is not as lucky. The DR-whitefish will outcompete the LSR-whitefish as it is a much better competitor for pelagic prey (Smalås, 2011). This makes the sympatric LSR-whitefish highly dependent on benthic prey density for feeding success. This is a big limitation, which can explain why it grows slower to appropriate length. Further trade-off between desired growth and energy spent on predation might complicate growth if the relation between energy obtained and the energy used to catch prey is not optimised. Another important factor limiting growth for the sympatric LSR-whitefish are parasitic infections. Such infections may harm the sympatric LSR-whitefish through benthic feed as it coerced by its environment to rely solely on benthic feed which may hold harmful parasites (Amundsen, et al., 2004).

4.2 Maturation patterns

Findings in maturation patters indicate that the presence of another morph living in sympatry with the LSR-morph does affect age at maturation, as expected. While the allopatric LSR matures between the ages 3-7, the sympatric LSR-whitefish matures around the ages 6-10 which is significantly later (see tables 5-6). However, it seems that length at maturity is relatively the same for both morphs. This suggests that both the allopatric- and sympatric LSR-whitefish is triggered to puberty by gaining the same optimum body size that is needed for maturation. The biggest difference seems to be in how energy for reproduction is gained. Life history between allopatric and sympatric LSR-whitefish differ slightly as the allopatric morph can grow marginally larger than the largest sympatric morph. By considering that maturation seems to happen at similar lengths although, the sympatric LSR spend more time to achieve this length it would seem that the LSR-whitefish living in sympatry is affected more by its ecological surroundings than the LSR-whitefish in allopatry. Since acquiring energy is very important for reproduction and that growth rate differs between the morphs, there might be an issue with finding enough feed for the sympatric LSR-morph to convert to somatic and gonad growth. Changes in growth rate before maturation will often lead to changes in what age maturation occurs at, in other words if growth in young fish is reduced, maturation is expected to happen at an older age (Saborido-Rey & Kjesbu, 2005). This shows that there is direct link between growth and maturation in the whitefish morphs and that any disturbances in growth will affect maturation. Since the DR-whitefish outcompetes the sympatric LSR-whitefish a few problems arise. Poor food availability will make the young LSR-whitefish struggle to find food and struggle to compete with older fish for the same resources. Risk of predation occurs as having a smaller size gives them more predators, as certain predators will target whitefish that is smaller than 200 mm (Kahilainen, et al., 2005). All these factors will contribute to the differences in age at maturity between the sympatric and allopatric LSR whitefish.

Further, from comparing the sympatric LSR-whitefish and the DR-whitefish clear differences can be observed. Trends in the DR-whitefish results show that it is younger and shorter when the population matures than the sympatric LSR. Except for the lake Vuolgamasjavri, the DR-whitefish has much faster growth rate which indicates that it rushes to secure the right size for survival. The DR-whitefish can have multiple predators which will be able to consume DR-whitefish up til the size of 200 mm (Kahilainen, et al., 2005). Hence, because of the high probability of death, it must secure its species by growing fast as juveniles and reproduce early (Kahilainen, et al., 2005) to be able to avoid high juvenile mortality. Factors that can affect juvenile mortality could be predation, human activities, competition or poor food availability (Saborido-Rey & Kjesbu, 2005). Predation could be an important factor for high juvenile mortality as mortality is seen in both mono- and dimorph lakes. All these lakes have presence of pike which predates on whitefish. However, since not all lakes show the same pattern for mortality, we cannot state that predation alone is affecting mortality. Human activities can basically be excluded (except for fish removal programme in Stuorajavri in 81-83) as there are not any commercial exploitations and whitefish is not sought after regarding recreational fishing. The factor that is most likely to explain juvenile mortality is interspecific competition due to food niches becoming inaccessible in dimorph lakes for the sympatric LSR-whitefish which benefits older fish as they will push the younger fish to seek food elsewhere as they are competing for the same resources. Seeking feeding grounds away from the littoral zone will expose young sympatric LSR-whitefish for potential predators. In monomorphic lake competition could also explain mortality as younger fish will struggle to compete with older fish for the best resources. However, if there is enough smaller zooplankton, they have the possibility to prey on this.

4.3 Adaptive management

The whitefish stock in Finnmark as a resource has become limited. It has poor meat quality, grows short and is full of parasites. Management does not seem to create a sustainable solution to preserve and better this resource for the future, which is somewhat understandable as it holds no economical or recreational value. However, we have a commitment to sustain species that exist within our borders[1] and the cost of doing nothing might be far worse. The whitefish has a possibility to become a harvestable resource in the future. In neighbouring countries, the fish is in high demand, therefore there are possibilities. To be able to manage species such as the whitefish there is a need for using ecological knowledge and a proper management plan. Attempts have been made to better conditions for whitefish populations. Boosting growth by removing older whitefish and make place for younger fish to grow have been done. However, such efforts will take time to show its effects and must be maintained (Amundsen, et al., 2002). It is important to see lakes as exclusive ecosystems as there are many interactions between the different organisms living there. Feedback from these provide good information to how each resource is doing. Since the observed lakes have been subject to fishing earlier and the sudden stop in exploiting this resource may have created a problem where whitefish kept reproducing to fit the former mortality so that the population became overpopulated. This further creating a problem with feed availability and parasitic infections diminishes the potential of the whitefish as a resource. To alleviate this problem stock depletion programmes were carried out (Amundsen, et al., 2002) to gain more ecological knowledge on how to deal with overcrowded freshwater lakes. The project in Stuorajavri did not go as planned as the whitefish bounced back to its preliminary stage, however (Amundsen, et al., 2002) suggests that challenges occur as such programmes are time-consuming and expensive.

[1] Lov om forvaltning av naturens mangfold (naturmangfoldloven)

However, adaptive monitoring is a management type that might fit well for the whitefish problem. This type of monitoring is a process of gathering information about an ecosystem, where the result is that we can assess the ecosystems state. This is mostly done through observation and experiments. The biggest goal is to reduce uncertainties and is driven by human need. By creating an adaptive monitoring framework, we enable our monitoring programs to evolve iteratively as we gain new information and our research questions change (Lindenmayer & Likens, 2009). These monitoring programs are often used for listing endangered species and often use citizen science to gather data. This involves non-experts in the program which will lower costs, create higher manpower, public awareness and helps cover larger areas. A key factor to such programs is triple loop learning for both the management program and the involved non-experts (Humburg, et al., 2017), where the end result is creating involvement and awareness while we reflect on how we have learned. Enabling non-experts in decision-making gives them the opportunity to learn more about management objective and its status. This creates awareness, which in turn will help whatever we are studying. For instance, the study of whitefish, where contributors will learn more about the status of whitefish and possibly how critical their status is. In turn they might affect others into understanding the management of whitefish. Setting up clear objectives with adaptive monitoring might something that can help change the status for the whitefish over time.

4.4 Limitations

This study has exclusively focused on growth between a sympatric and allopatric whitefish, for future studies environmental factors such as temperature, effects from predators or parasites would be interesting to include to provide a clearer picture. Also, a larger dataset with more young fish will provide more accurate information in growth models. Comparing the growth to the intermediate growth proved difficult, therefore it was later excluded.

5 Conclusion

In conclusion, after analysing the growth of both allopatric and sympatric LSR-whitefish it is clear that the allopatric LSR have better growth despite having relatively same theoretical maximum length (Linf) and length at maturity. By having poorer growth, the sympatric LSR-whitefish will spend more time getting to appropriate size for maturity. In sympatry, the DR-whitefish matures earlier with a faster initial growth rate and at a smaller body size than the sympatric LSR-whitefish. However, the DR-morph limits the growth of the sympatric LSR-whitefish by outcompeting feeding niches that are available for the allopatric LSR-whitefish.

The whitefish in all have chosen a strategy for growth and maturation that ensures the survival of its species by starting reproduction at a given size (Saborido-Rey & Kjesbu, 2005).

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Appendix

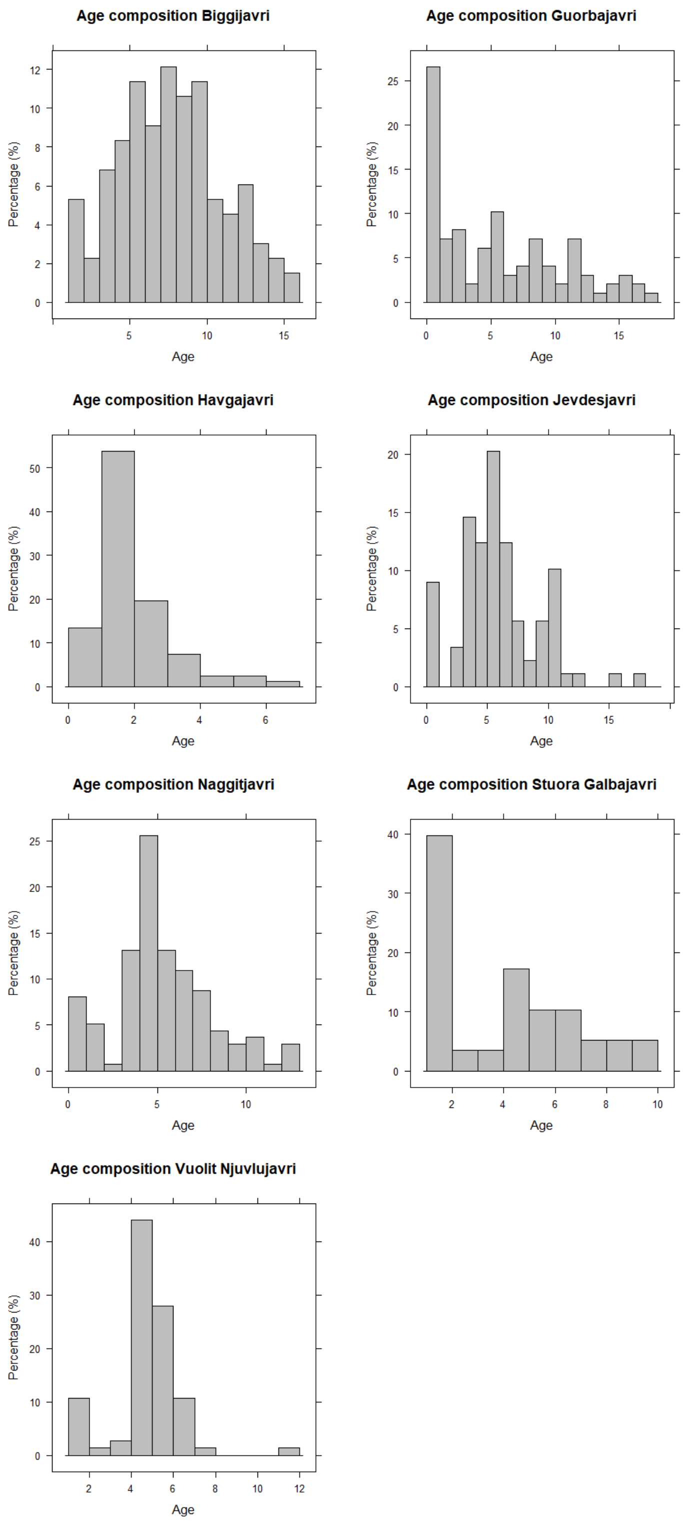

Figure 14, distribution of age for each of the monomorph lakes

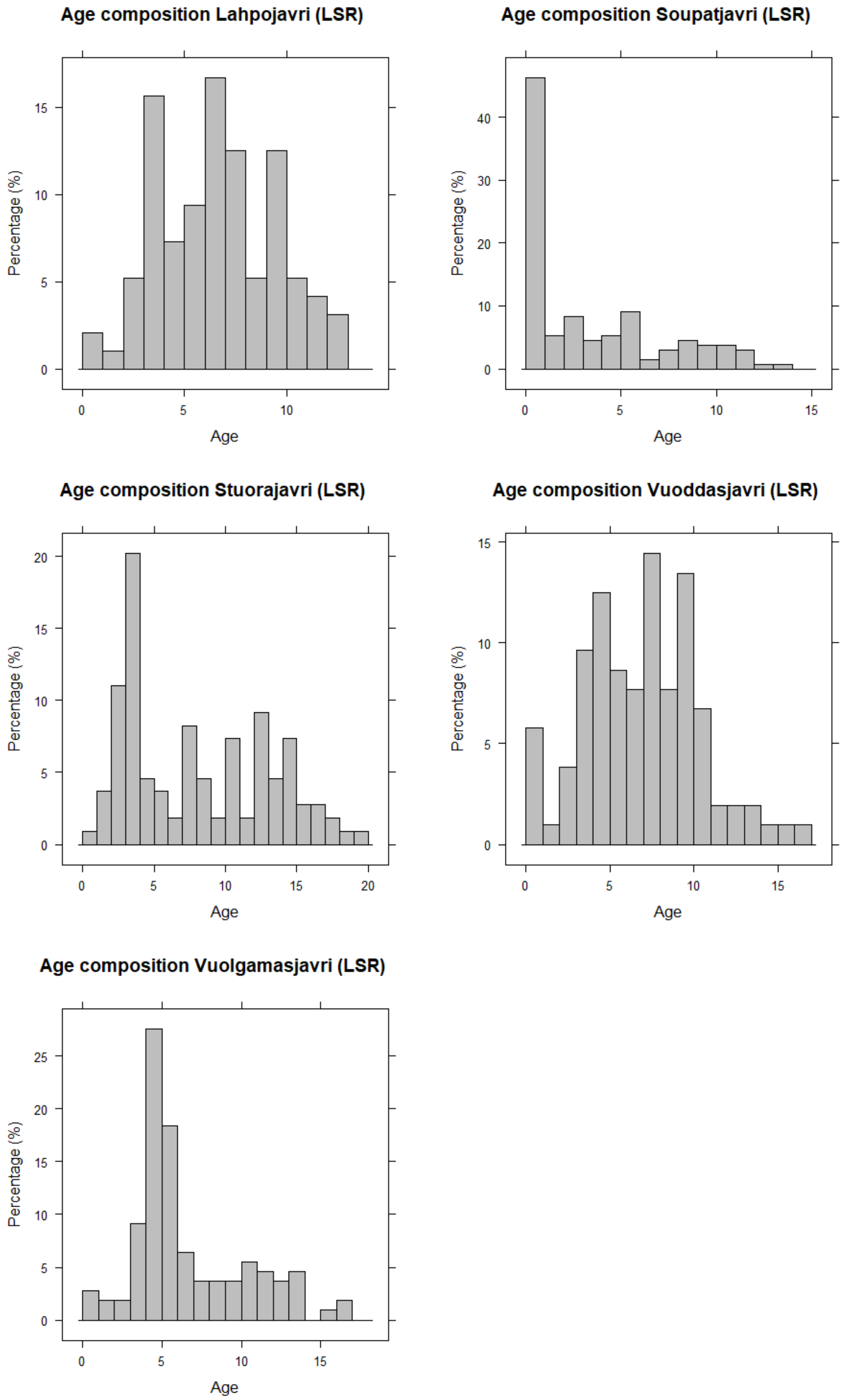

Figure 15, distribution of age for sympatric LSR-whitefish in dimorph lakes

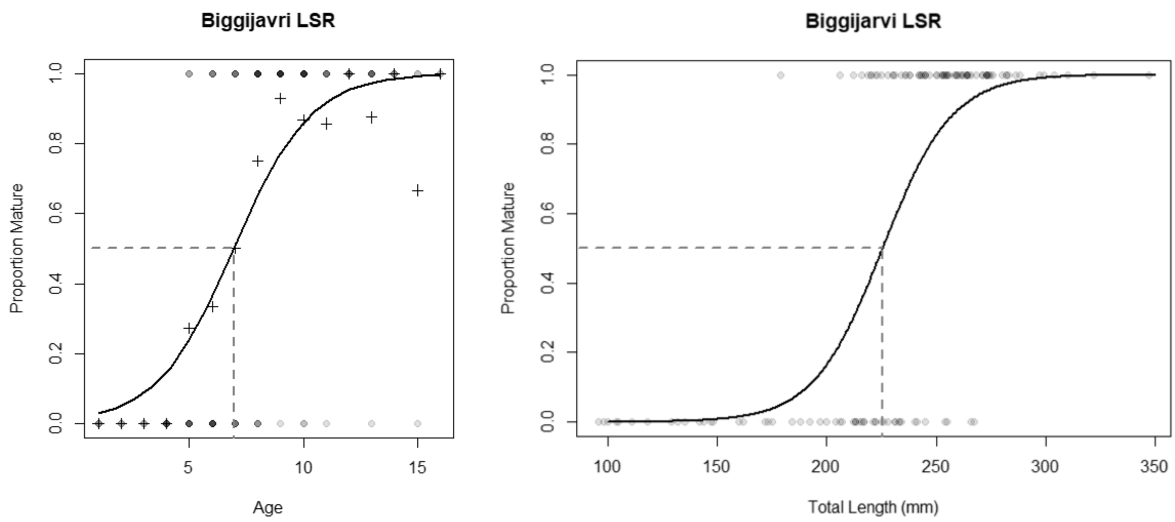

Figure 16, Fitted logistic regression of the proportion of sexual mature LSR-whitefish in Lake Biggijavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals are mature given by the logistic regression.

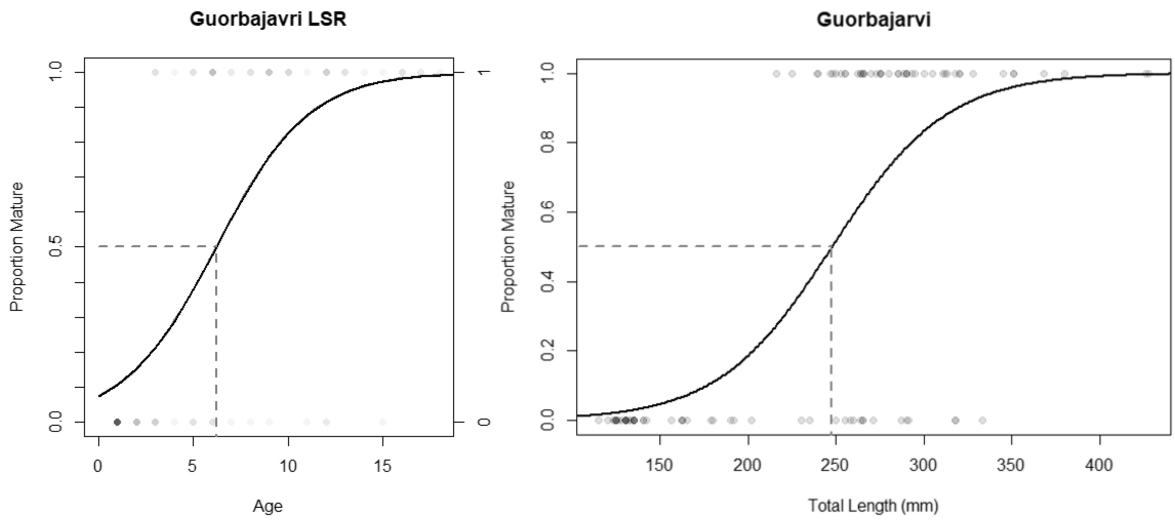

Figure 17,Fitted logistic regression of the proportion of sexual mature LSR-whitefish in Lake Guorbajavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals are mature given by the logistic regression.

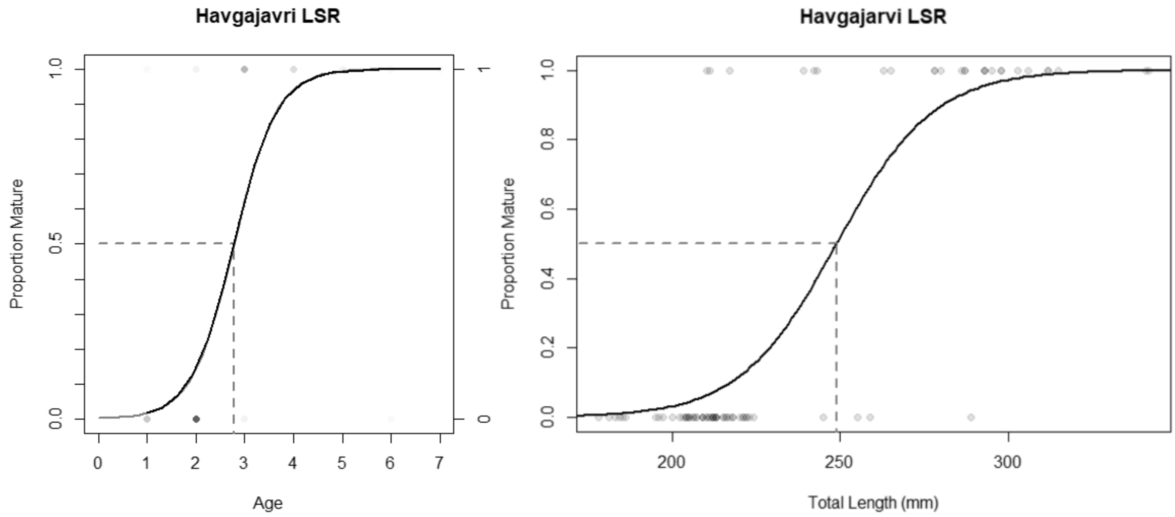

Figure 18, Fitted logistic regression of the proportion of sexual mature LSR-whitefish in Lake Havgajavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals in the population are mature given by the logistic regression.

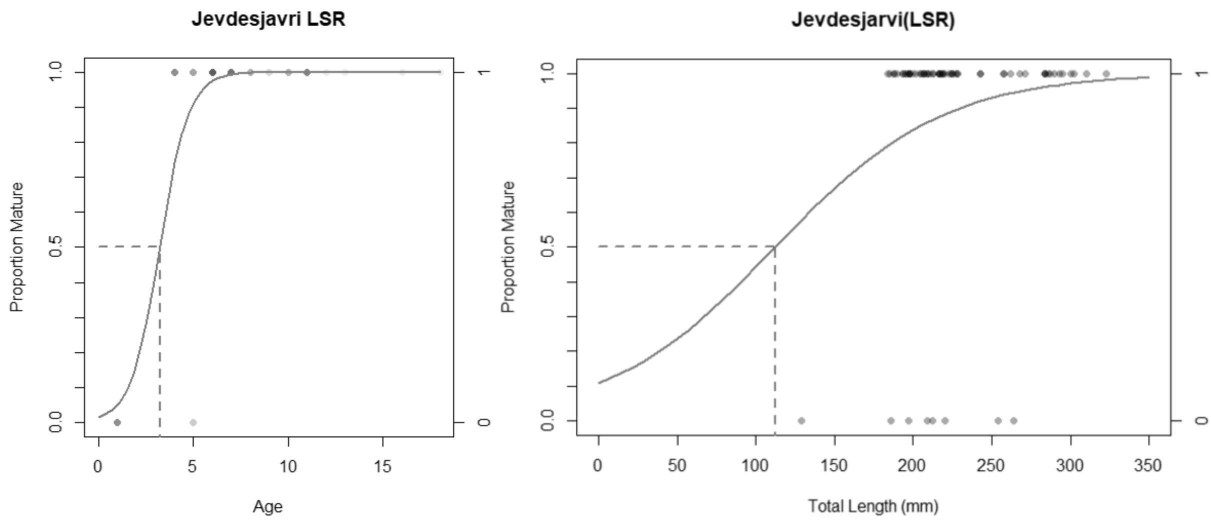

Figure 19,Fitted logistic regression of the proportion of sexual mature LSR-whitefish in Lake Jevdesjavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals in the population are mature given by the logistic regression.

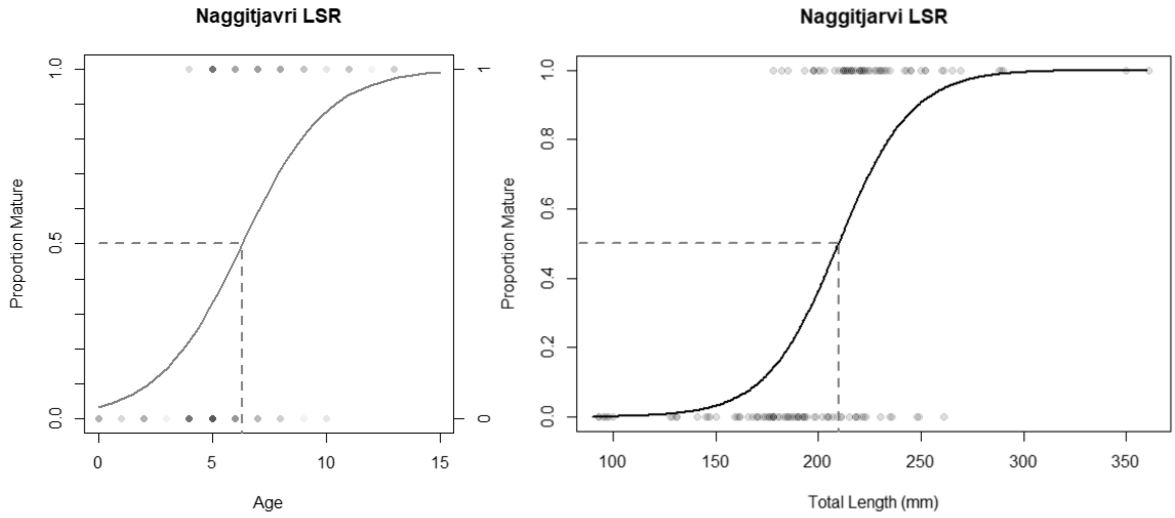

Figure 20,Fitted logistic regression of the proportion of sexual mature LSR-whitefish in Lake Naggitjavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals in the population are mature given by the logistic regression.

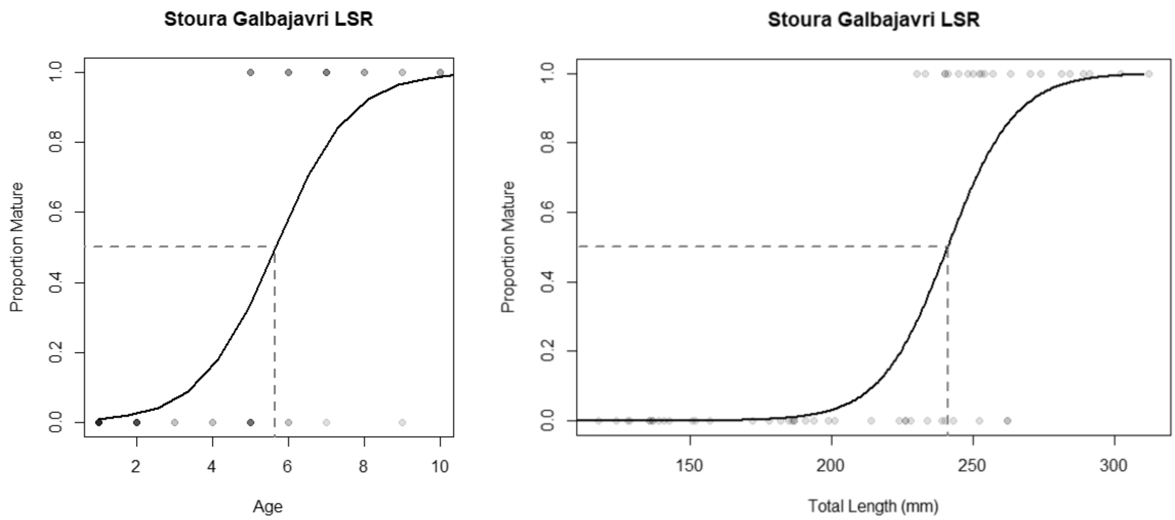

Figure 21, Fitted logistic regression of the proportion of sexual mature LSR-whitefish in Lake Stuora Galbajavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals in the population are mature given by the logistic regression.

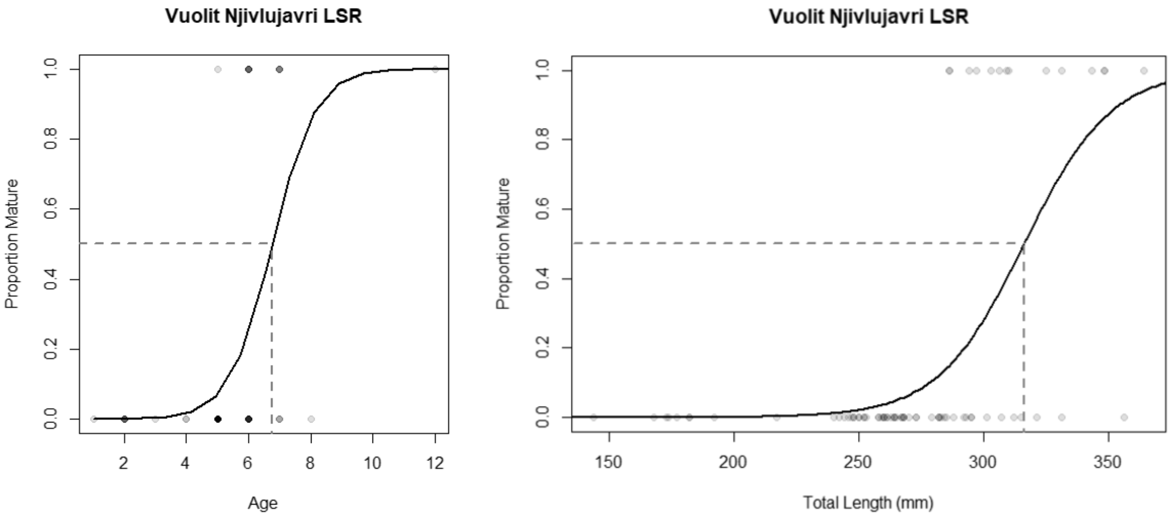

Figure 22,Fitted logistic regression of the proportion of sexual mature LSR-whitefish in Lake Vuolit Njivlujavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals in the population are mature given by the logistic regression.

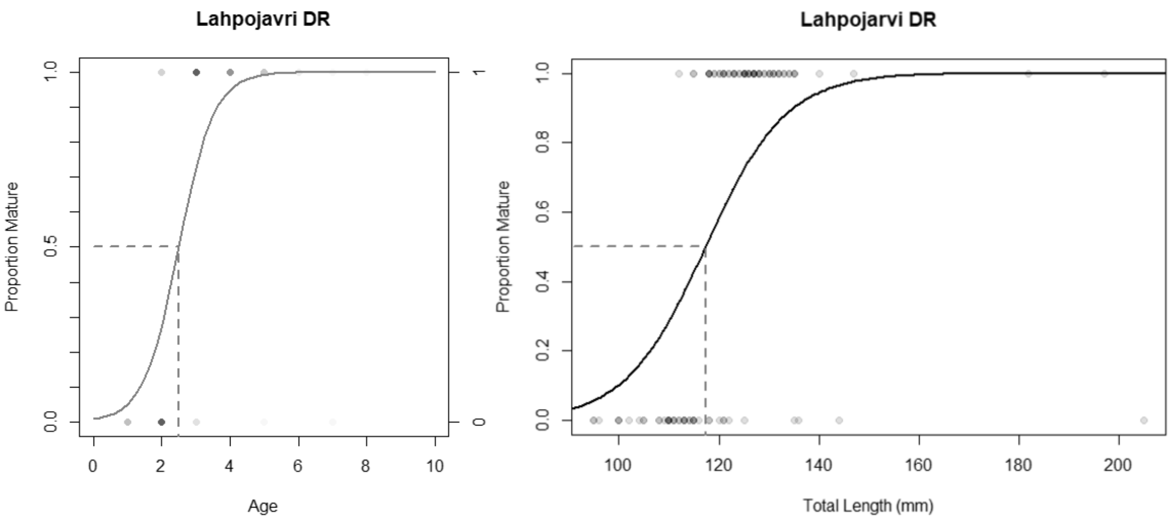

Figure 23, Fitted logistic regression of the proportion of sexual mature sympatric DR-whitefish in Lake Lahpojavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals in the population are mature given by the logistic regression

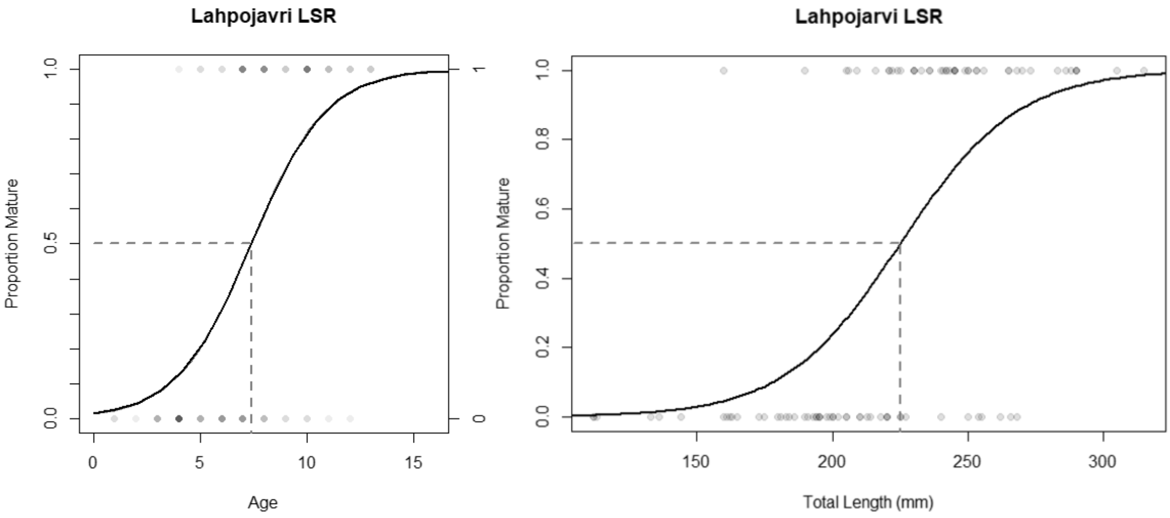

Figure 24, Fitted logistic regression of the proportion of sexual mature sympatric LSR-whitefish in Lake Lahpojavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals in the population are mature given by the logistic regression

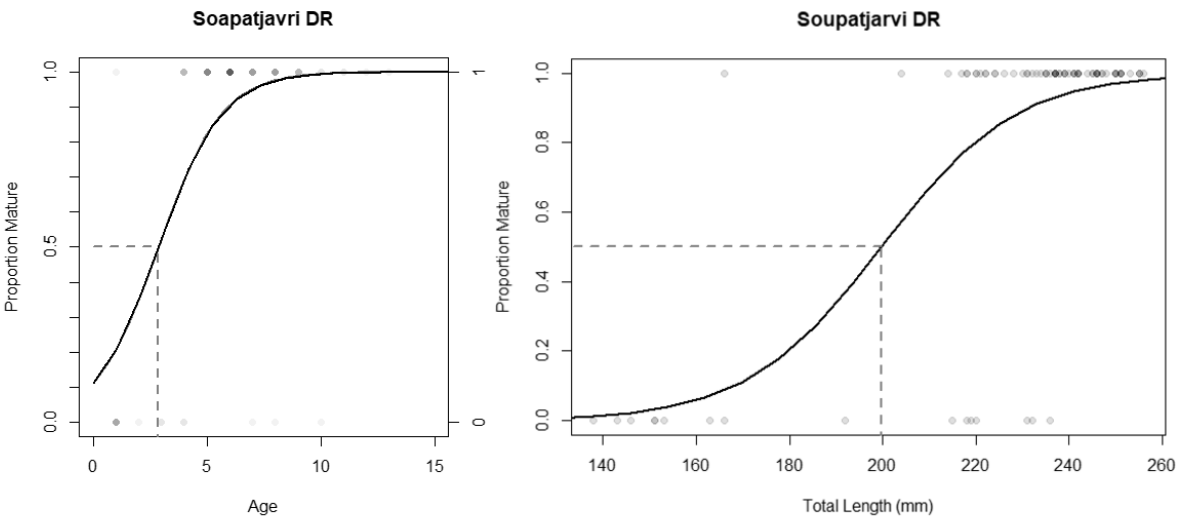

Figure 25, Fitted logistic regression of the proportion of sexual mature sympatric DR-whitefish in Lake Soupatjavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals in the population are mature given by the logistic regression

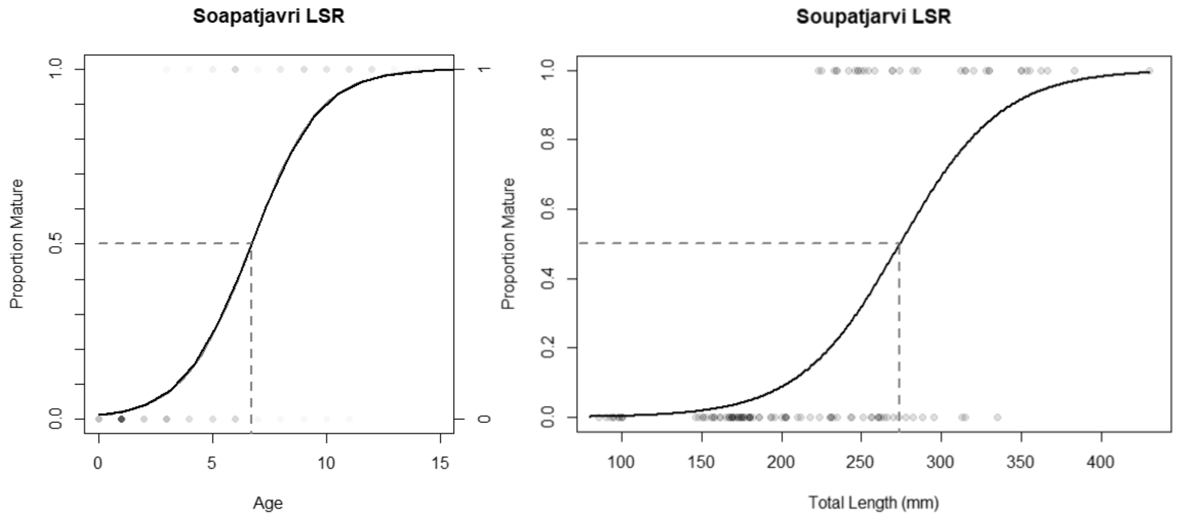

Figure 26, Fitted logistic regression of the proportion of sexual mature sympatric LSR-whitefish in Lake Soupatjavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals in the population are mature given by the logistic regression

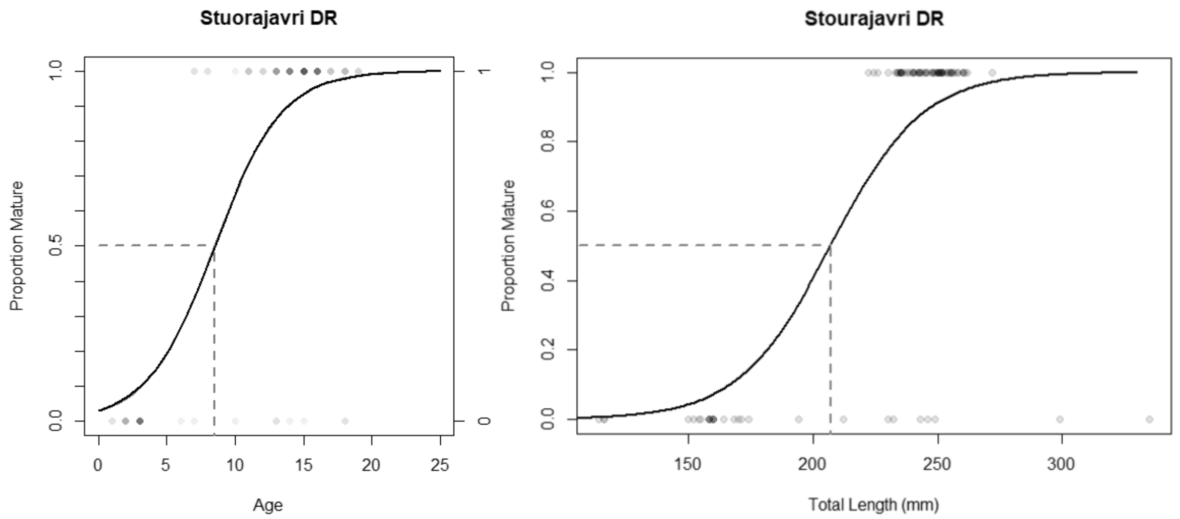

Figure 27, Fitted logistic regression of the proportion of sexual mature sympatric DR-whitefish in Lake Stuorajavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals in the population are mature given by the logistic regression

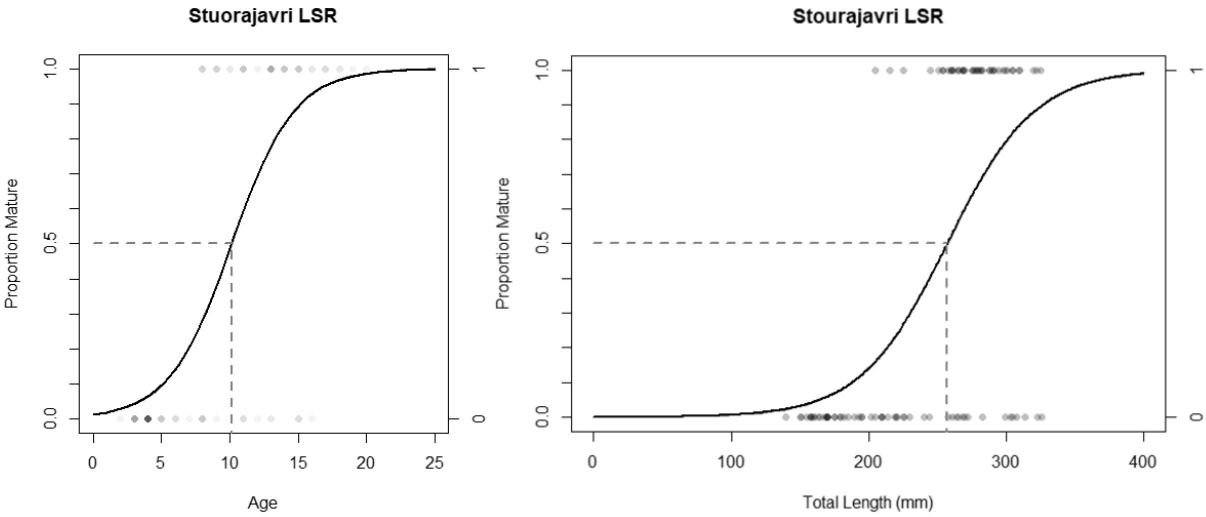

Figure 28, Fitted logistic regression of the proportion of sexual mature sympatric LSR-whitefish in Lake Stuorajavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals in the population are mature given by the logistic regression

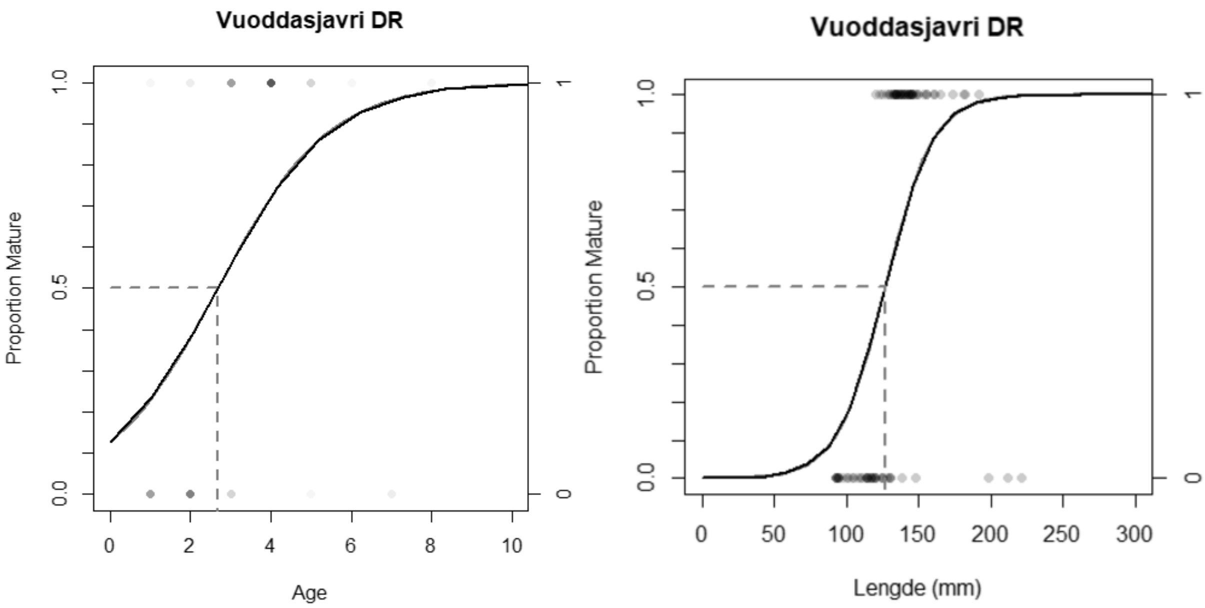

Figure 29, Fitted logistic regression of the proportion of sexual mature sympatric DR-whitefish in Lake Vuoddasjavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals in the population are mature given by the logistic regression

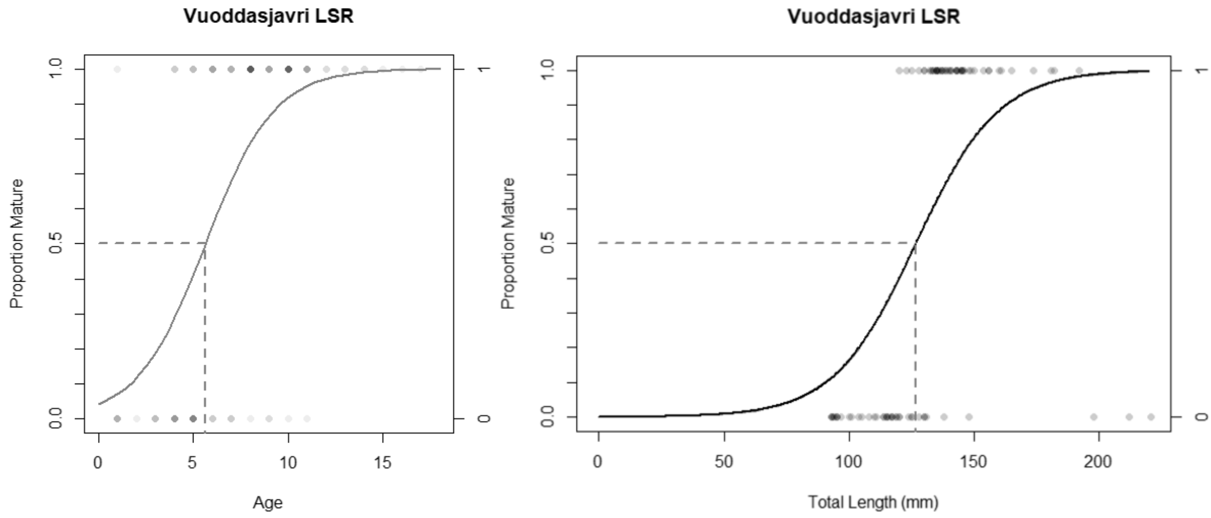

Figure 30, Fitted logistic regression of the proportion of sexual mature sympatric LSR-whitefish in Lake Vuoddasjavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals in the population are mature given by the logistic regression

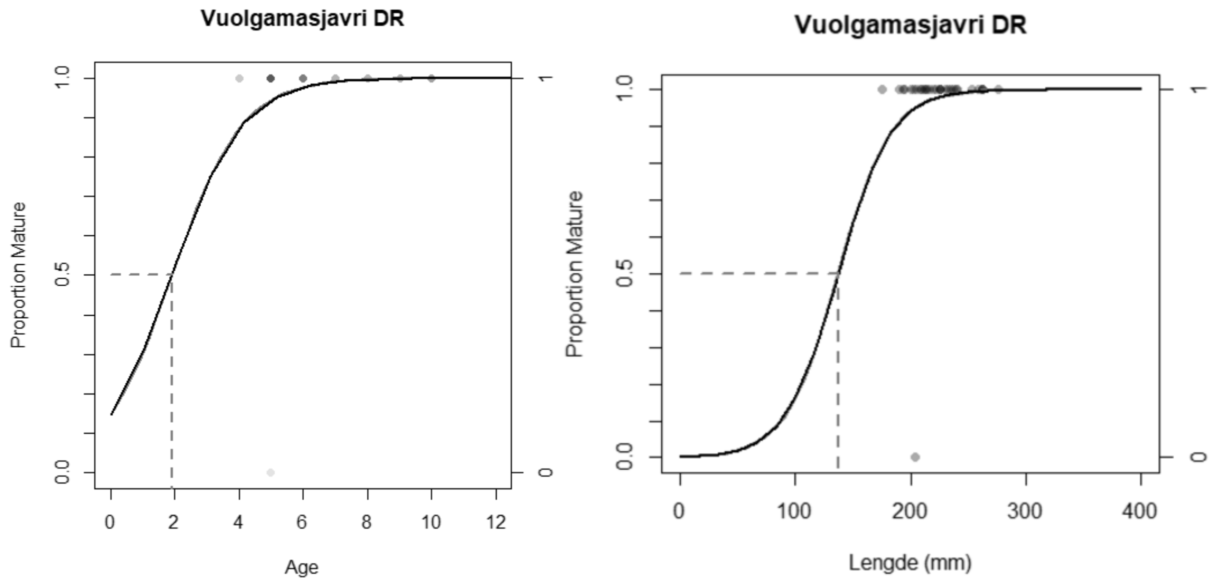

Figure 31, Fitted logistic regression of the proportion of sexual mature sympatric DR-whitefish in Lake Vuolgamasjavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals in the population are mature given by the logistic regression

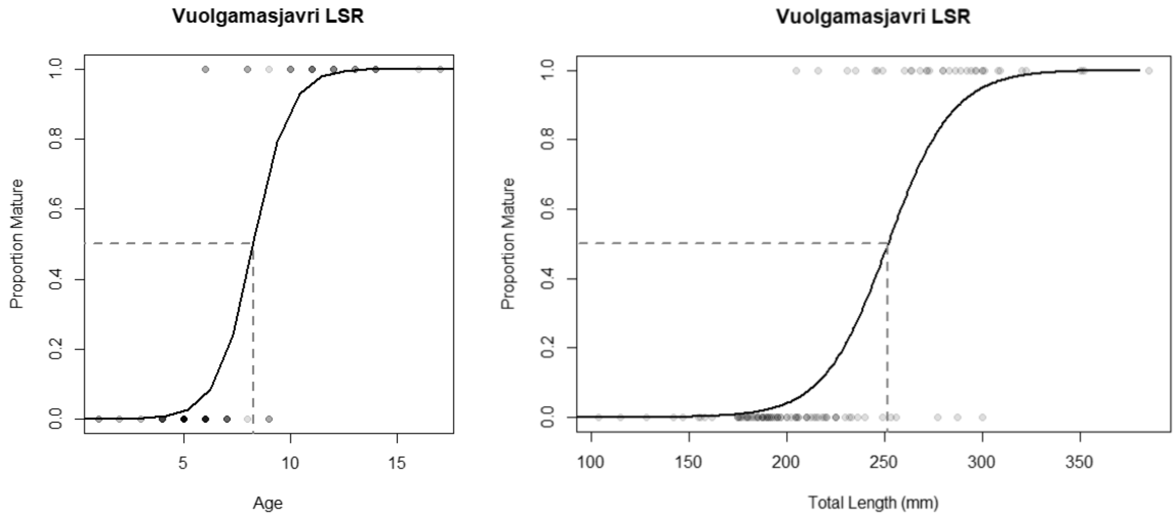

Figure 32, Fitted logistic regression of the proportion of sexual mature sympatric LSR-whitefish in Lake Vuolgamasjavri dependent on age (years) to the left and length (mm) to the right. Dots represent individual fish, and the stippled lines depicts where 50% of the individuals in the population are mature given by the logistic regression