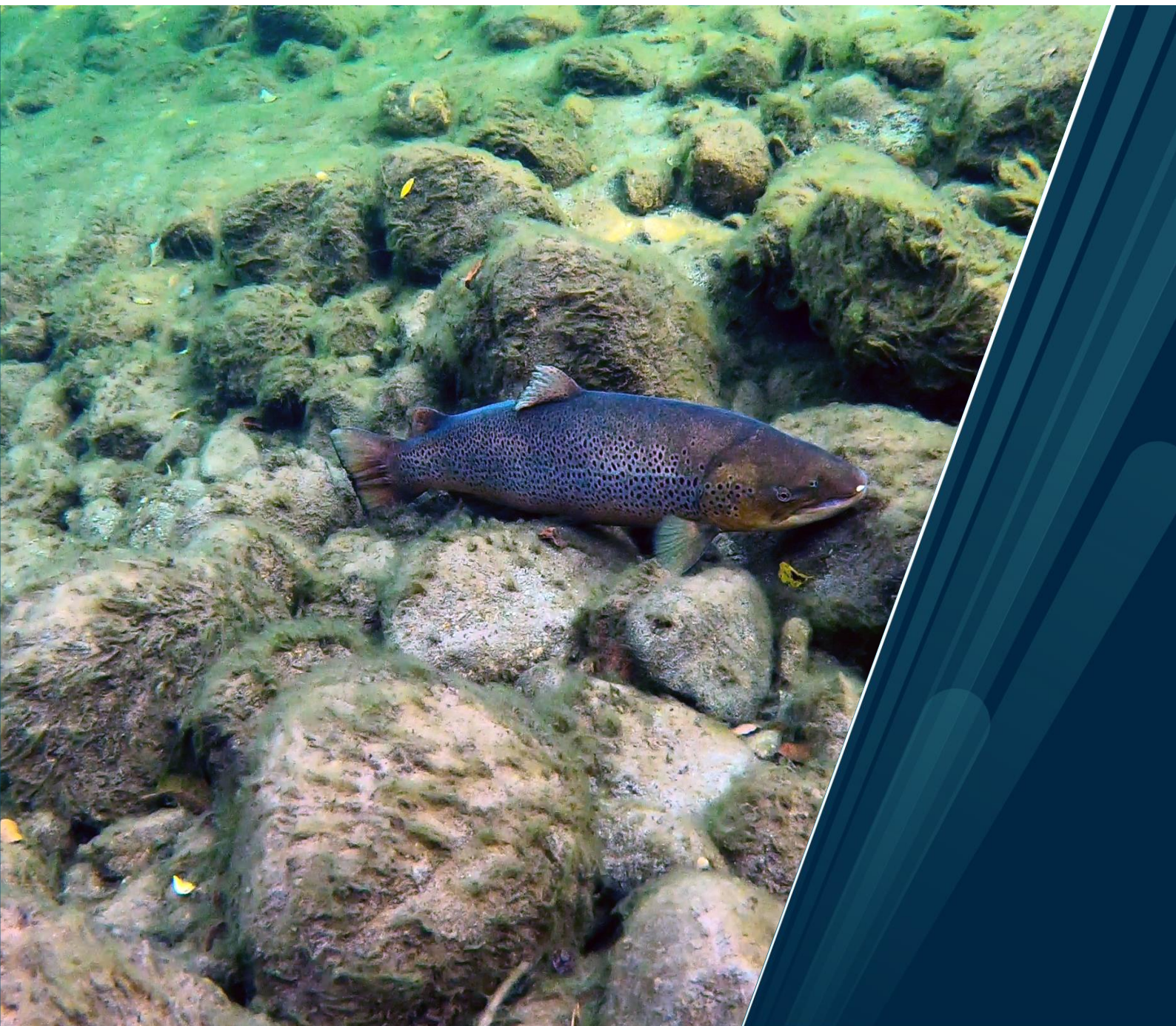Department of Arctic and Marine Biology

Fecundity and egg size in anadromous brown trout *Salmo trutta*

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Master's thesis in Freshwater Ecology BIO-3950 June 2020

ACKNOWLEDGEMENTS

Summary

1. Historically, anadromous salmonids provided a necessary provisioning service for Norwegian coastal settlements that has transitioned into the socio-cultural service that they provide today. Over the past decades, human impact has caused anadromous salmonid populations to decline. A recent assessment found many Norwegian sea trout populations to be in poor condition. Reference point management has been used to conserve and manage Atlantic salmon populations, and a similar approach is achievable for the sea trout. This requires data on reproductive traits such as fecundity and egg size due to their importance in establishing population forecasting models. The primary driver of fecundity and egg size is body size. Hitherto, knowledge on fecundity and egg size and their relationship to body size in sea trout is limited due to the body size ranges investigated.

2. The aim of this thesis was to quantify reproductive traits and their relationships to body mass and reproductive allocation in sea trout over a wide range of body sizes and a large geographical area. Two groups of wild sea trout ($n = 14 + 18 = 32$), and one hatchery-reared population of sea trout ($n = 25$) was investigated using basic quantitative methods (*e.g.,* weighing, measuring and counting) in combination with imaging techniques.

3. Gonad mass increased linearly with body mass for wild sea trout, and sublinearly with body mass for hatchery-reared sea trout. Absolute fecundity and egg size increased sublinearly with body mass. Relative fecundity decreased with body mass in sea trout. Egg size was smaller in hatchery-reared sea trout than in wild sea trout. Gonadosomatic index was independent of body size for the wild and hatchery-reared sea trout. The results indicated a trade-off between relative fecundity and egg size. Egg size decreased with gonadosomatic index in hatchery-reared sea trout. Within-clutch variation in egg size increased with body mass.

4. In conclusion, this thesis supports and adds to, previous studies on reproductive traits and their relationship to body size in sea trout. Resource limitations force sea trout to balance their energy between offspring quantity (*i.e.,* fecundity) and quality (*i.e.,* egg size), in a trade-off that appears environmentally and ontogenetically dependent. The decrease in egg size with body size in hatchery-reared sea trout supports previous findings for captive Pacific salmon. It attributes to population forecasting models and, as such, reference point management by the inclusion of large sea trout that previously has been missing.

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1 | INTRODUCTION

Historically, anadromous salmonids were important for Norwegian coastal settlements. Atlantic salmon *Salmo salar*, brown trout *Salmo trutta*, and Arctic charr *Salvelinus alpinus* once provided a necessary provisioning service (*e.g.,* food), that has since transitioned into a socio-cultural service (*e.g.,* recreation) (Liu, Bailey, and Davidsen 2019).

Over the past decades, human impact has caused declines in anadromous salmonid stocks in Norway (Anon 2017; Anon 2018; Anon 2019) and elsewhere (ICES 2013; ICES 2019). The vast majority of research on human impact on salmonids pertains to the negative effects on Atlantic salmon; nevertheless, several threats are shown to commonly affect anadromous brown trout (*e.g.,* salmon louse *Lepeophtheirus salmonis*) (Thorstad et al. 2015). Recent studies show that the situation for the anadromous brown trout (hereafter termed sea trout) is worsening and that populations may be negatively impacted by over-exploitation (Anon 2018; Anon 2019). A recent assessment of 430 Norwegian sea trout populations found that almost half were in poor condition due to human impacts (Anon 2019). Therefore, conservation and management measures are needed to mitigate the human impact and to reverse the negative trend found for many Norwegian sea trout populations.

The overarching objective for the management of anadromous salmonids in Norway is to conserve biodiversity and productivity for all naturally occurring populations (Klima- og miljødepartementet 2015). The importance of this objective is evident when considering the adaptations (*e.g.,* genetic and life-history) found among populations of Atlantic salmon (Wennevik et al. 2004), sea trout (Glover, Skilbrei, and Skaala 2003; Glover et al. 2003) and Arctic charr (Santaquiteria, Svenning, and Præbel 2016). However, adaptations to the local environment by populations requires knowledge on a fine spatial scale (*i.e.,* river level) to achieve finely tuned management actions (Hindar et al. 2010).

Management of Atlantic salmon is based on maintaining stock size above a population-specific reference point (Potter et al. 2003). Development of a population-specific reference point requires detailed knowledge on population dynamics (*e.g.,* recruitment and population structure) and the environment (*e.g.,* productivity and habitat quality) (Hindar et al. 2010). A reference point management strategy is achievable for sea trout, but important quantitative information on reproduction of sea trout is lacking (Anon 2019). Important, then, is the quantification of reproductive traits of sea trout due to their direct ties to population dynamics.

Reproduction is energetically costly, and the energy expenditure must be balanced

with survival, growth and maintenance. Reproductive investment in gonads, *i.e.,* total amount of energy invested in reproductive tissue, has been shown to increase linearly with body size for several taxa (*e.g.,* mammals, reptiles, fishes and invertebrates) (Hayward and Gillooly 2011). As such, body size is likely one of the most important life-history traits when considering reproductive investment (Miles and Dunham 1992). In general, the largest individuals invest the most energy in reproduction (Sibly and Calow 1986). A meta-study by Barneche et al. (2018) found that the amount of energy invested in reproduction increased with body size in 342 marine fish species. This is also the case for Atlantic salmon (Thorpe, Miles, and Keay 1984), brown trout (Elliott 1994; Elliott 1995; Lobon-Cervia et al. 1997; Jonsson and Jonsson 1997; Jonsson and Jonsson 1999), Dolly Varden trout *Salvelinus malma* (Gallagher et al. 2019) and coho salmon *Oncorhynchus kitusch* (Van Den Berghe and Gross 1984).

In fish, the amount of energy invested in reproduction can be approximated by total egg mass (*i.e.,* gonad mass), which is the product of the total number of eggs (*i.e.,* absolute fecundity) and mass of these eggs. (Duarte and Alcaraz 1989; Smalås, Amundsen, and Knudsen 2017). In salmonids, fecundity serves as a measure of the maximum number of offspring that may hatch, while an increase in egg size is associated with higher early-life survival of offspring (Einum and Fleming 1999). Limited resources cause individuals to prioritise their investments between quantity (*i.e.,* fecundity) and quality (*i.e.,* egg size) (Roff 1992). In a predictable environment, natural selection causes the development of a single

egg size that maximises fitness (Einum and Fleming 2000). This optimum egg size results in that the number and survival of offspring are at their maximum (Sibly and Calow 1986). Based on the model of Smith and Fretwell (1974), every population has an optimum egg size that is determined by environmental conditions. In fish, it is therefore common to observe extreme differences in egg number and egg size between spawning modes (*e.g.,* oviparous, viviparous and ovoviviparous), between spawning strategies (*e.g.,* benthic or pelagic) and between environments (*e.g.,* marine and freshwater). For example, Atlantic cod *Gadus morhua* spawn millions of small eggs in open waters during one reproductive cycle (see Thorsen et al. 2010), while large multiple sea-winter Atlantic salmon spawns some ten- to twenty-thousand relatively large eggs in their natal river (see Klemetsen et al. 2003). As such, females appear to allocate only enough energy to quality (i.e., egg size) to meet the requirements of their environmental conditions, with strategies adapted according to the stability of the environment. Thus, females should prioritise the development of adequate egg size before investing in quantity, which would make fecundity the most variable trait.

Fecundity and egg size are observed to increase with body size in Atlantic salmon (Van Den Berghe and Gross 1984; Thorpe, Miles, and Keay 1984) and brown trout (L'Abée-Lund and Hindar 1990; Jonsson and Jonsson 1999). Salmonids are observed to shift from producing many small eggs to fewer large eggs as they increase in body size, which causes relative fecundity to decrease (Jonsson and Jonsson 1999). This is typically linked

to a shift in reproductive investment strategy (Wootton 1990). A decrease in relative fecundity with body size has been found for brown trout (Jonsson and Jonsson 1999) and Arctic charr (Smalås, Amundsen, and Knudsen 2017). When the environment determines optimum egg size, the trade-off between egg number and egg size may drive differences among populations as populations with smaller optimum egg sizes are required to invest less egg size.

Existing studies on Norwegian sea trout cover a limited range of the body sizes achievable by sea trout. L'Abée-Lund and Hindar (1990) found that fecundity and egg size increased with body size in sea trout ranging from 24 to 77 cm (approximately 300-5500 g), while Jonsson and Jonsson (1999) found the same for sea trout ranging from 60 to 2000 g (approximately 200-550 mm). Nevertheless, further investigation is necessary to determine if the estimated fecundity-body size relationship and egg size-body size relationship hold for larger sea trout. That body size is important for reproduction in trout is evident from Goodwin et al. (2016) who found that a few large anadromous brown trout was the reproductive driver behind an entire English population of brown trout consisting of stationary and anadromous individuals. Additionally, Jonsson and Jonsson (1999) found differences among populations in fecundity and egg size on a geographical scale, which is likely an effect of variation in life-history (Jonsson and L'Abée-Lund 1993) in response to environmental conditions (*e.g.,* water temperature and resource availability). Hitherto, quantitative information on reproductive traits in northern Norwegian populations of sea trout is

lacking, and these traits need further investigation. As such, this study includes a broader range of body size in sea trout and populations from northern-Norway and southern-Norway.

In this thesis, I examine interindividual and interpopulation variation in fecundity and egg size and their dependency upon body mass and reproductive investment in sea trout from three regions, of which two populations are wild, and one population is first-generation hatchery-reared. Additionally, I investigate the relationship between egg size and fecundity for both wild and hatchery-reared sea trout, and provide data and consideration of within-clutch variation (*i.e.,* variation in egg size within individuals) in sea trout. I hypothesise that 1) gonad mass increases approximately linearly with body size in sea trout due to an energy investment that is proportional to body size. I further hypothesise that 2) absolute fecundity increases with body size and that 3) egg size increases with body size, which causes 4) relative fecundity to decrease with body size in sea trout in a trade-off between fecundity and egg size. I hypothesise that 5) gonad mass, fecundity and egg size vary among populations due to different environmental conditions that can be approximated by their geographical region. I also hypothesise that 6) individuals with a high gonadosomatic index (*i.e.,* gonad mass per body mass adjusted for gonad mass) have larger eggs than their low gonadosomatic index conspecifics of the same size. Finally, I hypothesise that 7) individuals produce homogeneous egg sizes (*i.e.,* low within-clutch variation) in line with the predictions of Einum and Fleming (2004) of a conservative bet-hedging strategy in salmonids.

2 | MATERIALS AND METHODS

2.1 | FISH CAPTURE AND SAMPLING

In total, 57 brown trout were sampled, of which 32 were wild, and 25 were first-generation hatchery-reared. The 32 wild sea trout comprise seven different populations, one from Nordland ($n = 14$) and six pooled populations from Hardanger ($n = 18$). The population of hatchery-reared brown trout was descendant of a sea trout population from Møre and Romsdal (Table 2.1).

For all fish, weight (W_t, g), fork length (F_L, mm), and gonad mass (W_g, g) were recorded (Ricker 1979), except for fork length for one fish from Nordland. Fish from Nordland was dissected for retrieval of gonads, while fish from Hardanger and Møre and Romsdal was artificially stripped for eggs.

Wild sea trout from Nordland were from River Skjoma located in Narvik municipality, Nordland county, northern Norway (Figure 2.1), and were collected from the 15th of August 2019 until the end of September 2019. The 14 fish result from two different methodological approaches of sampling; convenience and purposive sampling. The purposive sampling approach provided fish with a broad range of body sizes to reduce the necessity of extrapolation ($n = 9$), while the convenience sampling supplied additional fish ($n = 5$). Freediving equipment, flashlights, and landing nets were used to accomplish pur-

Figure 2.1: Map of Norway indicating the location of the rivers in the study

posive sampling. Convenience sampling was accomplished through recreational fishing by landowners and locals.

Sea trout from the Hardanger district comprises six pooled populations of wild anadromous brown trout (Figure 2.1). The 18 fish were gathered at the Eidfjord gene bank facility, Eidfjord municipality, Vestland county, western Norway. Fish were caught in the wild and brought back to the gene bank facility for artificial stripping of eggs.

Twenty-five sea trout were gathered from

the Herje gene bank facility, Rauma municipality, Møre and Romsdal county, western Norway. These were first-generation hatchery-reared fish in the repopulation program for river Istra (Figure 2.1) and were hatched and reared in captivity.

2.2 | LABORATORY ANALYSES

2.2.1 | FECUNDITY

Absolute fecundity (F_A, n), *i.e.,* the total number of eggs per individual, was estimated by weighing the entire gonad mass (W_g to the nearest 0.1 g (MyWeigh I1550), weighing and counting two subsamples, and then extrapolating for the entire gonad mass (Jonsson and Jonsson 1999). Thereafter, the relative fecundity (F_R, $^{eggs}/_g$), *i.e.,* the number of eggs per gram body mass, was calculated by dividing the absolute fecundity by the body mass (W_t, g) of the fish.

2.2.2 | EGG SIZE

In accordance with Fleming and Gross (1990) egg mass (W_E, g) was determined for 10 to 20 eggs per individual, and in addition diameter (D_E, mm) was estimated. This was accomplished by first weighting eggs to the nearest 0.0001 g (Precisa 100A-300M) and then by photographing the eggs under a stereomicroscope (Leica Wild MZ8) next to a millimetre measure (Leica, 0.1 mm precision) (picture resolution: 2560×1920 pixels [px]). The eggs were then analysed in ImageJ (Rueden et al. 2017) by creating a pixel standard ($^{px}/_{mm}$). By applying the Versatile Wand Tool, the area of the egg was calculated by ImageJ. By assuming eggs to be perfectly spherical, this allowed

for calculation of diameter (see equation 2.1).

$$D = 2r = 2(\sqrt{\frac{A}{\pi}}) \qquad (2.1)$$

where D is diameter (mm), r is radius (mm) and A is area (mm^2).

2.2.3 | GONADOSOMATIC INDEX

Gonadosomatic index (GSI, %) was calculated as the gonad mass (W_G, g) relative to the adjusted body mass ($W_t - W_g$, g) (see equation 2.2), and used as a measure of reproductive investment relative to body size in individual female fish (Bøhn et al. 2004; Mills and Eloranta 1985).

$$GSI(\%) = \frac{W_g}{W_t - W_g} \times 100 \qquad (2.2)$$

where W_t is the total body mass of the fish and W_g is the gonad mass of the fish in grams.

2.2.4 | PRESERVATION AND FIXATION

Egg diameter (D_E, mm) and egg mass (W_E) were recorded on samples stored on Gilson's fixative fluid (100 ml 60% alcohol, 800 ml distilled water, 30 ml 80% nitric acid, 18 ml glacial acetic acid, 20 g zinc chloride) for a total of 45 days. The effects of Gilson's fixative fluid on trout eggs was unknown, and therefore trial experiment was conducted to ensure comparability to fresh samples. Egg diameter (D_e) and egg mass (W_E) at day 45 were divided by a factor of 0.86 and 0.74 (Rinaldo, unpublished data), respectively, to adjust for changes in diameter and mass after conservation and fixation.

2.3 | STATISTICAL ANALYSES

Statistical analyses were carried out in the R 3.6.3 software (R Core Team 2020). For linear relationships, simple linear regression, two-way and one-way analysis of covariance (AN-COVA) was conducted to assess the correlation between the dependent variable and the continuous and factorial independent variables. For relationships without significant interactions between continuous and factorial variables, the one-way ANCOVA was followed up by a post hoc Tukey comparison of means. In cases with no linear relationship between the independent and dependent variable, a one-way ANOVA was conducted and followed up with a post hoc Tukey comparison of means. Within-clutch variation of egg size was measured as the coefficient of variation (*i.e.,* relative standard deviation) for a normal distribution with a modification for moderate sample sizes to avoid bias (see equation 2.3).

$$\widehat{C_V}^* = (1 + \frac{1}{4n}) \times \frac{\sigma_x}{\bar{x}} \qquad (2.3)$$

The presented models were tested as to assess whether, or not, they conformed to the underlying assumptions for the analysis of covariance. This was checked by first examining the models' diagnostic plots before conducting a series of statistical tests for the underlying assumptions. Homogeneity of the regression slopes was tested by checking for significant interaction terms. A Shapiro-Wilk test was performed to test for normality of residuals. Homogeneity of variance for residuals was tested with a Levene's test. Any potential outliers were identified by examining the standardised residuals of the models. However, outliers were not removed on a statistical basis, but their impact was discussed.

Most statistical analyses required logarithmic transformations of either the dependent or independent continuous variable, or both, to conform to model assumptions. The figures are, therefore, back-transformed before being presented.

The regression estimates and figures for the relationship between fecundity and body length is included for the benefit of others, but are not of primary interest. Therefore, the statistics of these relationships will not be discussed in this thesis.

Table 2.1: Sampling period, type of fish (wild or hatchery-reared), geographical region, river, fish body mass, fish age ($\bar{x} \pm \sigma_x$ and ranges) and number of fish in the analysis sorted by river.

Period	Type	Region	River	Body mass (g)		Age (yr)		No. of fish in the analysis	
				Mean	Range	Mean	Range	Fecundity	Egg size
2019	Wild	Hardanger	Osa	1031 ± 473	716-1575	NA	NA	3	3
2019	Wild	Hardanger	Sima	1967	NA	NA	NA	1	1
2019	Wild	Hardanger	Jondal	1196 ± 502	836-1911	NA	NA	4	4
2019	Wild	Hardanger	Ådland	733 ± 282	435-999	NA	NA	4	4
2019	Wild	Hardanger	Mundheimselva	645 ± 137	468-757	NA	NA	4	4
2019	Wild	Hardanger	Rosendalselva	763 ± 20	749-777	NA	NA	2	2
2019	Wild	Nordland	Skjoma	4053 ± 1635	1500-8050	10 ± 2.5	8-16	14	9
2019	Hatchery-reared	Møre and Romsdal	Istra	1849 ± 536	955-2995	5	NA	25	24

3 | RESULTS

3.1 | GONAD MASS

When analysed separately, gonad mass (W_g, g) did not significantly differ from a normal distribution for Nordland (Shapiro-Wilks: $W = 0.96$, $p = 0.075$), Hardanger (Shapiro-Wilks; $W = 0.97$, $p = 0.86$), and Møre and Romsdal (Shapiro-Wilks: $W = 0.96$, $p = 0.42$). The sample mean of gonad mass ($\bar{x} \pm \sigma_x$) was 677 ± 291 g for Nordland, 176 ± 87 g for Hardanger, and 407 ± 105 g for Møre and Romsdal.

There was a significant increase in gonad mass (W_g, g) with body mass (W_t, g) for the wild sea trout from Nordland and Hardanger, and the hatchery-reared sea trout from Møre and Romsdal. (Two-way ANCOVA, Table 3.1, Figure 3.1). The relationship between gonad mass and body mass differed between the wild and the hatchery-reared sea trout (Table 3.1). The increase in gonad mass per body mass in hatchery-reared sea trout from Møre and Romsdal was sublinear (0.77% increase in gonad mass per 1% increase in body mass). In contrast, the gonad mass in the wild sea trout from Nordland and Hardanger increased approximately linearly (1% increase in gonad mass per 1% increase in body mass). However, the wild sea trout from Hardanger had significantly larger gonad mass per body mass than the wild sea trout from Nordland (Table 3.1).

The ANCOVA model for the relationship between gonad mass and body mass conformed to the assumptions for an ANCOVA model. Residuals were normally distributed (Shapiro-Wilks: $W = 0.98$, $p = 0.6065$) and there was homogeneity of variance among the residuals (Levene's: $p = 0.50$).
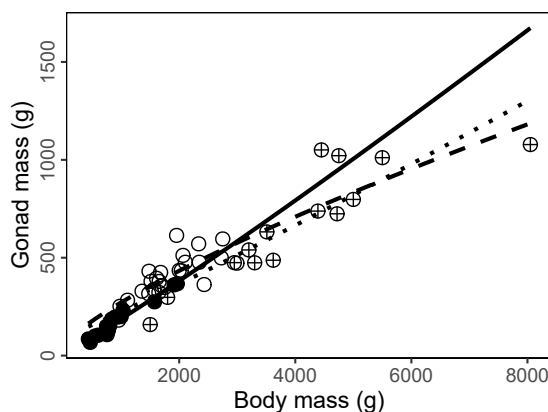
Figure 3.1: The predicted relationship between gonad mass (g) and body mass (g) for the wild sea trout from Nordland (······⊕), Hardanger (——●), and the hatchery-reared sea trout from Møre and Romsdal (- - -○) on normal scale.

3.2 | FECUNDITY

3.2.1 | ABSOLUTE FECUNDITY

Separate analyses of the sample distributions for absolute fecundity (F_A, n) found Hardanger to differ from a normal distribution (Shapiro-Wilks: $W = 0.87$, $p = 0.0152$), while Nordland (Shapiro-Wilks: $W = 0.94$, $p = 0.39$) and Møre and Romsdal (Shapiro-Wilks: $W = 0.95$, $p = 0.23$) did not differ from normal distributions. Absolute fecundity ranged from 3121 to 13871 eggs per fish for the wild sea trout from Nordland, and for wild sea trout from Hardanger absolute fecundity ranged from 933 to 3845 eggs per fish. In hatchery-reared sea trout from Møre and Romsdal, absolute fecundity ranged from 2361 to 7748 eggs per fish. For the wild sea trout from Nordland and Hardanger, mean absolute fecundity ($\bar{x} \pm \sigma_x$) was 6987 ± 2809 and 1850 ± 776, respectively. Hatchery-reared sea trout from Møre and Romsdal had a mean absolute fecundity of 4952 ± 1214.

Absolute fecundity (F_A, n) increased significantly with body mass (W_t, g) in the wild sea trout from Hardanger and Nordland, and the hatchery-reared sea trout from Møre and Romsdal (One-way ANCOVA, Table 3.1, Figure 3.2a). There were significant differences in absolute fecundity per body mass among the wild and the hatchery-reared sea trout (Figure 3.2a, Table 3.1). The post hoc Tukey multiple comparisons of means revealed that there were significant differences between Hardanger and Møre and Romsdal ($p < 0.001$), between Nordland and Møre and Romsdal ($p = 0.001$), but not between Hardanger and Nordland ($p = 0.18$).

The ANCOVA model for the relationship between absolute fecundity and body mass conformed to the assumptions for an ANCOVA model. Residuals were normally distributed (Shapiro-Wilks: $W = 0.97$, $p = 0.26$) and there was homogeneity of variance among the residuals (Levene's: $p = 0.29$)

3.2.2 | RELATIVE FECUNDITY

Separate analyses of groups found that sample distribution of relative fecundity (F_r, $^{eggs}/_g$) for Hardanger (Shapiro-Wilks: $W = 0.97$, $p = 0.7$), Nordland (Shapiro-Wilks: $W = 0.94$, $p = 0.4$) and Møre and Romsdal (Shapiro-Wilks: $W = 0.98$, $p = 0.8$) did not differ from a normal distribution. The sample mean of relative fecundity ($\bar{x} \pm \sigma_x$) per kg was 2038 ± 267 $^{eggs}/_{kg}$ and 1776 ± 376 $^{eggs}/_{kg}$ for the wild sea trout from Hardanger and Nordland, respectively. For the hatchery-reared sea trout from Møre and Romsdal, mean relative fecundity was 2764 ± 544 $^{eggs}/_{kg}$.

Relative fecundity (F_R, $^{eggs}/_g$) decreased significantly with an increase in body mass (W_t, g) in the wild sea trout from Hardanger and Nordland (One-way ANCOVA, Table 3.1). This was also evident for the hatchery-reared sea trout from Møre and Romsdal. There were significant differences in relative fecundity per body mass among populations (Figure 3.2b, Table 3.1). The Tukey multiple comparisons of means revealed that the significant differences were between Hardanger and Møre and Romsdal ($p < 0.0001$), Nordland and Møre and Romsdal ($p = 0.0017$), but not between Nordland and Hardanger ($p = 0.18$). The hatchery-reared fish from Møre and Romsdal had higher relative fecundity per body mass than the wild

sea trout from Nordland and Hardanger (Figure 3.2b, Table 3.1).

The estimated relationship between absolute fecundity (F_A, n) and body length (L_f, mm) differed from that for body mass (W_t, g) (Table 3.2). The relationship between absolute fecundity and body length was concave (Figure 3.2c), in contrast to the convex relationship found between absolute fecundity and body mass (Figure 3.2a). Additionally, the relationship between relative fecundity (F_R, $^{eggs}/_g$) and body length (Figure 3.2d, Table 3.2) differed from that of relative fecundity and body mass (Figure 3.2b).

The ANCOVA model for the relationship between relative fecundity and body mass conformed to the assumptions for an ANCOVA model. Residuals were normally distributed (Shapiro-Wilks: $W = 0.97$, $p = 0.34$) and there was homogeneity of variance among the residuals (Levene's: $p = 0.1$).
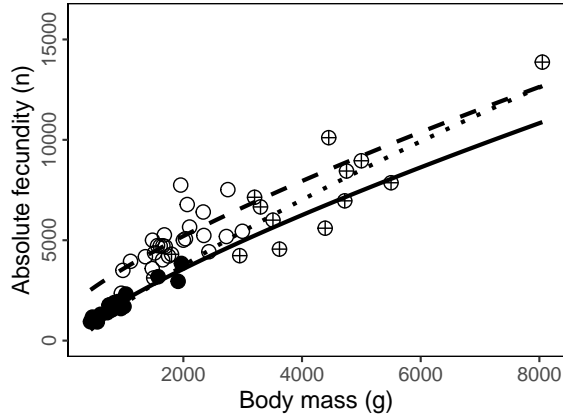
(a) The predicted relationship between absolute fecundity (F_A, n) and body mass (W_t, g) for the wild sea trout from Nordland ($\cdots\oplus$), Hardanger (——$\bullet$), and the hatchery-reared sea trout from Møre and Romsdal (- - -$\bigcirc$) on normal scale.
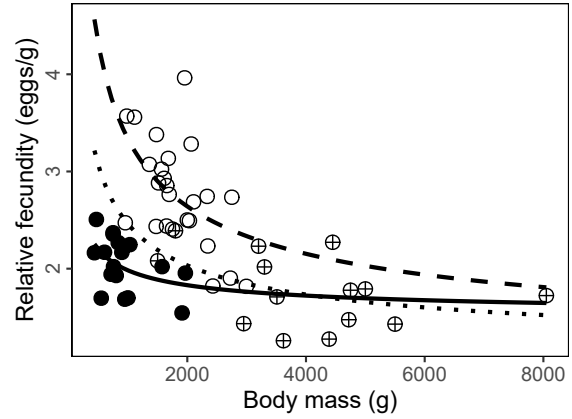
(b) The predicted relationship between relative fecundity (F_R, $^{eggs}/g$) and body mass (W_t, g) for the wild sea trout from Nordland ($\cdots\oplus$), Hardanger (——$\bullet$), and the hatchery-reared sea trout from Møre and Romsdal (- - -$\bigcirc$) on normal scale.
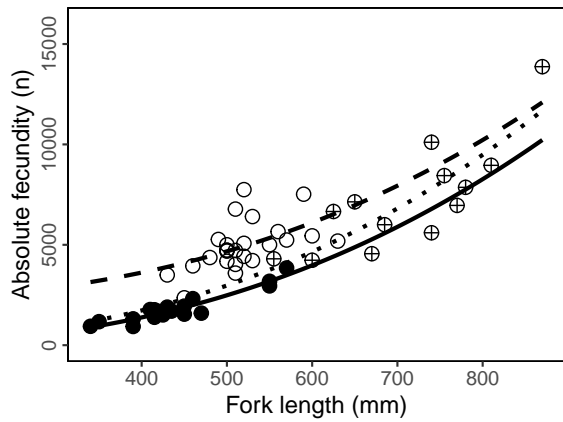
(c) The predicted relationship between absolute fecundity (F_A, n) and fork length (F_L, mm) for the wild sea trout from Nordland ($\cdots\oplus$), Hardanger (——$\bullet$), and the hatchery-reared sea trout from Møre and Romsdal (- - -$\bigcirc$) on normal scale.
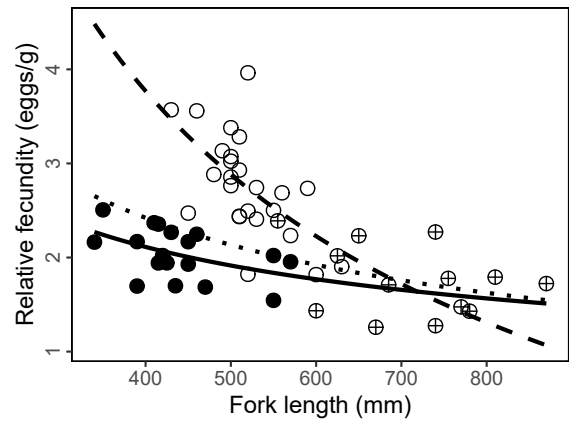
(d) The predicted relationship between relative fecundity (F_R, $^{eggs}/g$) and fork length (F_L, mm) for the wild sea trout from Nordland ($\cdots\oplus$), Hardanger (——$\bullet$), and the hatchery-reared sea trout from Møre and Romsdal (- - -$\bigcirc$) on normal scale.

Figure 3.2

Table 3.1: Analysis of covariance estimates for the relationship between the natural logarithm of gonad mass (W_g, g) and the centred natural logarithm of body mass (W_t, g), between the natural logarithm of absolute fecundity (F_A, n) and the centred natural logarithm of body mass (W_t, g) and between relative fecundity (F_R, $eggs/g$) and the centred natural logarithm of body mass (W_t, g) for the wild sea trout from Hardanger, Nordland, and the hatchery-reared sea out from Møre and Romsdal. Significant differences in slopes and intercepts are shown as superscripted asterisks (*), and Nordland and Møre and Romsdal estimates are relative to that of Hardanger. Standard error of the estimate is given in parenthesis and the model summary is given at the bottom.

	Dependent variable:		
	Gonad mass (g)	Absolute fecundity (n)	Relative fecundity ($eggs/g$)
Intercept	5.805***	7.980***	1.690***
	(0.074)	(0.057)	(0.134)
Møre and Romsdal	0.133	0.461***	1.099***
	(0.081)	(0.068)	(0.160)
Nordland	−0.326***	0.186*	0.490*
	(0.118)	(0.108)	(0.252)
Body mass (g)	1.082***	0.772***	−0.508***
	(0.093)	(0.061)	(0.142)
Body mass : Møre and Romsdal	−0.309**		
	(0.143)		
Body mass : Nordland	0.085		
	(0.138)		
Observations	57	57	57
R^2	0.947	0.935	0.603
Adjusted R^2	0.942	0.931	0.581
Residual Std. Error	0.161 (df = 51)	0.167 (df = 53)	0.393 (df = 53)
F Statistic	183.942*** (df = 5; 51)	252.890*** (df = 3; 53)	26.881*** (df = 3; 53)

Note: *p<0.1; **p<0.05; ***p<0.01

Table 3.2: Analysis of covariance estimates for the relationship between the natural logarithm of absolute fecundity (F_A, n) and the centred natural logarithm of fork length (L_F, mm) and between relative fecundity (F_R, $eggs/g$) and the centred natural logarithm of fork length (L_F, mm) for the wild sea trout from Hardanger, Nordland, and the hatchery-reared sea out from Møre and Romsdal. Significant differences in slopes and intercepts are shown as superscripted asterisks (*), and Nordland and Møre and Romsdal estimates are relative to that of Hardanger. Standard error of the estimate is given in parenthesis and the model summary is given at the bottom.

	Dependent variable:	
	Absolute fecundity (n)	Relative fecundity ($eggs/g$)
Intercept	7.922***	1.872***
	(0.077)	(0.151)
Møre and Romsdal	0.587***	0.827***
	(0.087)	(0.170)
Nordland	0.265*	0.177
	(0.158)	(0.309)
Fork length (mm)	2.504***	−0.883
	(0.332)	(0.650)
Fork length : Møre and Romsdal	−0.779	−2.817**
	(0.560)	(1.098)
Fork length : Nordland	−0.299	−0.123
	(0.544)	(1.066)
Observations	56	56
R^2	0.919	0.655
Adjusted R^2	0.910	0.620
Residual Std. Error (df = 50)	0.192	0.377
F Statistic (df = 5; 50)	112.843***	18.962***
Note:		*$p<0.1$; **$p<0.05$; ***$p<0.01$

3.3 | GONADOSOMATIC INDEX

The distribution of gonadosomatic index (GSI, %) did not differ from a normal distribution for the sample as a whole (Shapiro-Wilks: $W = 0.97$, $p = 0.19$), nor did it for Hardanger (Shapiro-Wilks: $W = 0.97$, $p = 0.71$), Nordland (Shapiro-Wilks: $W = 0.94$, $p = 0.45$) or Møre and Romsdal (Shapiro-Wilks: $W = 0.96$, $p = 0.45$) in separate analyses.

Gonadosomatic index (GSI, % was independent of body mass (W_t, g) in the sea trout from Nordland, Hardanger or Møre and Romsdal. Gonadosomatic index was more influenced by other factors (proxied by geographical region and type). There were significant differences in gonadosomatic index between the wild sea trout (Hardanger and Nordland) and the hatchery-reared sea trout (Møre and Romsdal) (One-way ANCOVA, Table 3.3). The Tukey multiple comparison of underpinned that hatchery-reared sea trout from Møre and Romsdal had higher gonadosomatic index ($\bar{x} \pm \sigma_x$, $29.3 \pm 6.3\%$) than Nordland ($p < 0.0001$) and Hardanger ($p = 0.001$), whilst wild sea trout from Nordland and Hardanger did not differ in terms of gonadosomatic index ($p = 0.2$). The sample mean ($\bar{x} \pm \sigma_x$) for Hardanger ($23.2 \pm 3.7\%$) was higher than the sample mean for Nordland ($19.9 \pm 4.86\%$) (Figure 3.3).

The ANOVA model for the differences in gonadosomatic index between geographic regions conformed to the assumptions for an ANCOVA model. Residuals were normally distributed (Shapiro-Wilks: $W = 0.96$, $p = 0.11$) and there was homogeneity of variance among the residuals (Levene's: $p = 0.14$).
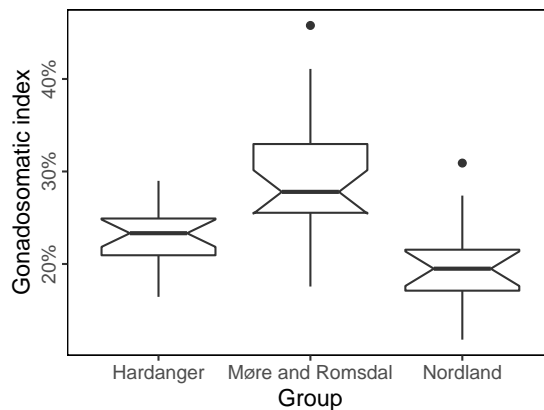
Figure 3.3: Gonadosomatic index (GSI, %) for the wild sea trout from Hardanger ($n = 18$) and Nordland ($n = 14$), and the hatchery-reared sea trout from Møre and Romsdal ($n = 25$). Notches show the 95% confidence interval of the median (—), while the notchbox shows the interquartile range (50% of the data). Outliers are shown as circles (●).

3.4 | EGG SIZE

The sample distribution of egg diameter (D_E, mm) did not significantly differ from a normal distribution for the entire sample (Shapiro-Wilks: $W = 0.97$, $p = 0.27$), nor for Hardanger (Shapiro-Wilks: $W = 0.98$, $p = 0.95$), Nordland (Shapiro-Wilks: $W = 0.93$, $p = 0.48$) or Møre and Romsdal (Shapiro-Wilks: $W = 0.96$, $p = 0.45$). The sample mean ($\bar{x} \pm \sigma_x$) of egg diameter was 6.1 ± 0.28 for Nordland, 5.6 ± 0.35 for Hardanger and 5.5 ± 0.17 for Møre and Romsdal.

Egg diameter (D_E, mm) increased with body size (W_t, g) for the wild sea trout from Hardanger and Nordland, and for the hatchery-reared sea trout from Møre and Romsdal. There were significant differences in egg size per body size among the three groups of sea trout (One-way ANCOVA, Figure 3.4a,

Table 3.4). The Tukey multiple comparisons of means found significant differences between the wild sea trout from Hardanger and the hatchery-reared sea trout from Møre and Romsdal ($p = 0.014$), but not between Nordland and Hardanger ($p = 0.90$), nor between Nordland and Møre and Romsdal ($p = 0.17$).

Gonadosomatic index (GSI, %) was significantly correlated to egg diameter (D_E, mm) (Two-way ANCOVA, Table 3.4). Additionally, there were significant interaction effects between region or type and gonadosomatic index on the slope of egg size (Table 3.4). The increase in egg size for the wild sea trout was positive, but differed between Nordland and Hardanger, while there was a decrease in egg size with gonadosomatic index for the hatchery-reared sea trout from Møre and Romsdal (Figure 3.4b). Body mass and gonadosomatic index as covariates improved the regression's predictability of egg size ($R^2 = 0.71$) in the analysis of covariance, but at the expense of body mass and gonadosomatic index as significant predictors and potential collinearity, and the model is as such, not included in the results.

The ANCOVA models for the relationship between egg diameter and body mass and egg diameter and gonadosomatic index did not conform to the assumptions for an ANCOVA model. In the model for the relationship between egg diameter and body mass residuals were not normally distributed (Shapiro-Wilks: $W = 0.94$, $p = 0.017$), but there was homogeneity of variance among the residuals (Levene's: $p = 0.08$). In the model for the relationship between egg diameter and gonadosomatic index the residuals were not normally distributed (Shapiro-Wilks: $W = 0.91$, $p =$

0.002), but there was homogeneity of variance among the residuals (Levene's: $p = 0.135$).

3.5 | TRADE-OFF

There was a negative relationship between egg diameter (D_E, mm) and relative fecundity (F_R, $^{eggs}/_g$) (One-way ANCOVA, Table 3.5, Figure 3.4c). There were significant differences in the trade-off between egg diameter and relative fecundity for the wild sea trout from Nordland and Hardanger, and the hatchery-reared sea trout from Møre and Romsdal. Egg size in the hatchery-reared sea trout decreased at a rate of -0.19 mm for every 1 egg increase in relative fecundity, which differed significantly from the wild sea trout from Nordland and Hardanger, where egg size decreased at a rate of -0.37 mm and -0.75 mm per 1 egg increase in relative fecundity, respectively (Figure 3.4c, Table 3.5).

The ANCOVA model for the relationship between egg diameter and relative fecundity did not conform to the assumptions for an ANCOVA model. Residuals were normally distributed (Shapiro-Wilks: $W = 0.98$, $p = 0.49$), but there was unequal variance among the residuals (Levene's: $p = 0.17$).

3.6 | WITHIN-CLUTCH VARIATION IN EGG SIZE

The within-clutch variation in egg size ($\widehat{C_V}^*$, %) increased with body mass (W_t, kg) for the wild sea trout from Nordland and Hardanger, and the hatchery-reared sea trout from Møre and Romsdal (One-way ANCOVA, Table 3.6). The variation in egg sizes within an individual

increased with 0.28 percentage points for every $1\ kg$ increase in body mass for hatchery-reared and wild sea trout (Figure 3.4d). The mean coefficient of variation was 4% for the wild sea trout from Nordland and 1.5% for the wild sea trout from Hardanger. For Møre and Romsdal mean coefficient of variation was 1.8%.
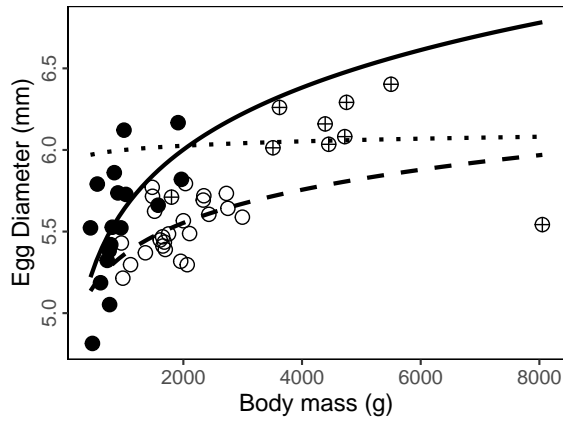
The ANCOVA model for the relationship between variation in egg diameter and body mass conformed to the assumptions for an ANCOVA model. Residuals were normally distributed (Shapiro-Wilks: $W = 0.96$, $p = 0.11$), and there was equal variance among the residuals (Levene's: $p = 0.052$).

(a) The predicted relationship between egg diameter (D_e, mm) and body mass (W_t, g) for the wild sea trout from Hardanger (——●) and Nordland (······⊕, outlier included), and the hatchery-reared fish from Møre and Romsdal (- - -○) on normal scale.
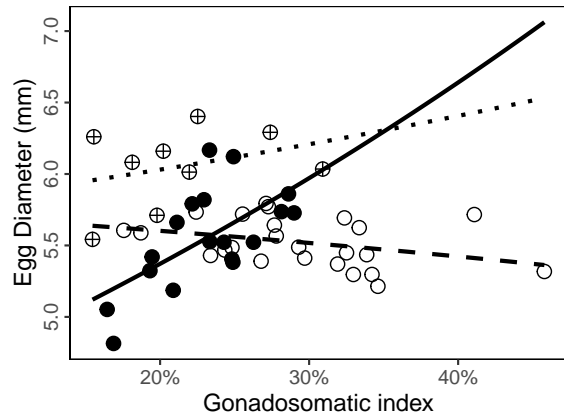
(b) The predicted relationship between the natural logarithm of egg diameter (D_E, mm) and gonadosomatic index (GSI, %) for the wild sea trout from Nordland (······⊕) and Hardanger (——●), and the hatchery-reared sea trout from Møre and Romsdal (- - -○) on normal scale.
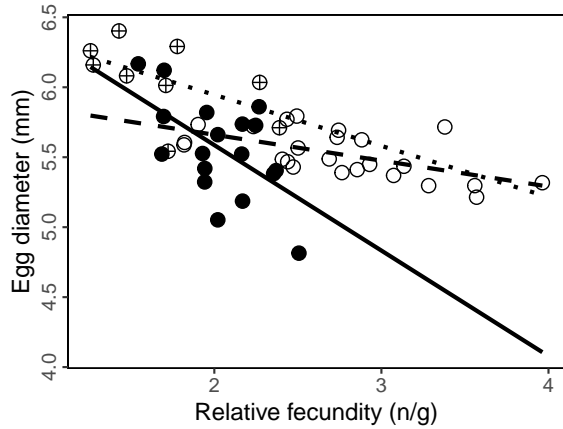
(c) The predicted relationship between egg diameter (D_e, mm) and relative fecundity (F_R, $eggs/g$) for the wild sea trout from Hardanger (——●) and Nordland (······⊕), and the hatchery-reared sea trout from Møre and Romsdal (- - -○) on normale scale.
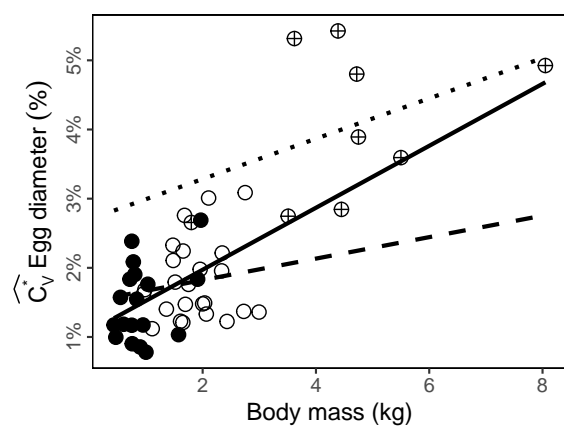
(d) The predicted relationship between the coefficient of variation for egg diameter ($\widehat{C_V}^*$, percentage points) and body mass (kg) in the wild sea trout from Hardanger (——●) and Nordland (······⊕), and the hatchery-reared sea trout from Møre and Romsdal (- - -○) on normal scale.

Figure 3.4

Table 3.3: Analysis of covariance estimates between gonadosomatic index (GSI, %) and the centred body mass (W_t, kg) for the wild sea trout from Hardanger, Nordland, and the hatchery-reared sea trout from Møre and Romsdal. Significant differences in intercepts are shown as asterisks (*), and Nordland and Møre and Romsdal estimates are relative to that of Hardanger. Standard error of the estimate is given in parenthesis and the model summary is given at the bottom.

	Dependent variable:
	Gonadosomatic index (%)
Constant	22.9***
	(1.6)
Møre and Romsdal	6.4***
	(1.8)
Nordland	−2.5
	(3.1)
Body mass (kg)	−0.2
	(0.8)
Observations	57
R^2	0.373
Adjusted R^2	0.338
Residual Std. Error	0.053 (df = 53)
F Statistic	10.513*** (df = 3; 53)
Note:	*p<0.1; **p<0.05; ***p<0.01

Table 3.4: Analysis of covariance estimates between the natural logarithm of egg diameter (D_E, mm) and the centred natural logarithm of body mass (W_t, g) and between the natural logarithm of egg diameter (D_E, mm) and gonadosomatic index (GSI, %) for the wild sea trout from Hardanger, Nordland, and the hatchery-reared sea trout from Møre and Romsdal. Significant differences in slopes and intercepts are shown as asterisks (*), and Nordland and Møre and Romsdal estimates are relative to that of Hardanger. Standard error of the estimate is given in parenthesis and the model summary is given at the bottom.

	Dependent variable:	
	Egg diameter (mm)	Egg diameter (mm)
Intercept	1.756***	1.742***
	(0.015)	(0.012)
Møre and Romsdal	−0.051***	−0.028*
	(0.018)	(0.015)
Nordland	−0.013	0.071***
	(0.031)	(0.022)
Body mass (g)	0.062***	
	(0.016)	
Gonadosomatic index (%)		1.100***
		(0.266)
Gonadosomatic index : Møre and Romsdal		−1.268***
		(0.296)
Gonadosomatic index : Nordland		−0.796**
		(0.384)
Observations	51	51
R^2	0.510	0.557
Adjusted R^2	0.478	0.508
Residual Std. Error	0.042 (df = 47)	0.040 (df = 45)
F Statistic	16.280*** (df = 3; 47)	11.319*** (df = 5; 45)

Note: *p<0.1; **p<0.05; ***p<0.01

Table 3.5: Analysis of covariance estimates for the trade-off between egg diameter (D_E, mm) and relative fecundity (F_R, $eggs/g$) for the wild sea trout from Hardanger, Nordland, and the hatchery-reared sea trout from Møre and Romsdal. Significant differences in slopes and intercepts are shown as asterisks (*), and Nordland and Møre and Romsdal estimates are relative to that of Hardanger. Standard error of the estimate is given in parenthesis and the model summary is given at the bottom.

	Dependent variable:
	Egg diameter (mm)
Intercept	7.094***
	(0.413)
Møre and Romsdal	−1.064**
	(0.475)
Nordland	−0.417
	(0.533)
Relative fecundity ($eggs/g$)	−0.754***
	(0.201)
Relative fecundity : Møre and Romsdal	0.569**
	(0.218)
Relative fecundity : Nordland	0.388
	(0.279)
Observations	51
R^2	0.585
Adjusted R^2	0.539
Residual Std. Error	0.221 (df = 45)
F Statistic	12.693*** (df = 5; 45)
Note:	*p<0.1; **p<0.05; ***p<0.01

Table 3.6: Analysis of covariance for the relationship between variation in egg size (Coefficient of variation [$\widehat{C_V}^*$, percentage points]) and body mass (kg) for the wild sea trout from Hardanger, Nordland and the hatchery-reared sea trout from Møre and Romsdal. Significant differences in intercepts are shown as asterisks (*), and Nordland and Møre and Romsdal estimates are relative to that of Hardanger. Standard error of the estimate is given in parenthesis and the model summary is given at the bottom.

	Dependent variable:
	Coefficient of Variation (%)
Constant	1.2***
	(0.2)
Møre and Romsdal	0.05
	(0.002)
Nordland	1.5***
	(0.5)
Body mass (kg)	0.28**
	(0.1)
Observations	51
R^2	0.688
Adjusted R^2	0.669
Residual Std. Error	0.007 (df = 47)
F Statistic	34.616*** (df = 3; 47)

Note: *p<0.1; **p<0.05; ***p<0.01

4 | DISCUSSION

Reproduction is a fundamental feature of life on Earth. Salmonids provide a unique opportunity to investigate reproductive strategies due to their divergence between iteroparity and semelparity and between anadromous and stationary life-history strategies. That said, few members of the salmonid family display ecological variation on par with the brown trout (Elliott 1994; Klemetsen et al. 2003). Their adaptation to widely contrasting environments and individual and population-specific variation implies challenges for the management of the species. In this thesis, I investigated the broad trends in the reproductive traits of sea trout and tied in various theoretical frameworks as a cause of variation among and within populations and individuals. By adding to existing literature, the results in this study strengthen the quantitative foundation for the development of management tools, while highlighting the need for continued research on the topic.

Gonad mass was found to increase approximately linearly with body mass in the wild sea trout from Nordland and Hardanger. In short, this means that a two-kilogram sea trout has twice the gonad mass of a one-kilogram sea trout. What may cause this pattern to occur in wild populations? In essence, a linear increase in gonad mass with body mass should occur if the energy invested in egg production remains constantly proportional to the energy budget. This was observed by Karjalainen et al. (2016) for vendace *Coregonus albula*, and Jonsson and Jonsson (1997) for brown trout. In that case, interpopulation variation in gonad mass should manifest as a difference in gonad mass per body mass.

The wild sea trout from Hardanger were found to have significantly higher gonad mass per body mass than the wild sea trout from Nordland. That said, there is little overlap in body size between the two groups, as well as few data points, and more sea trout should be gathered before conclusions are drawn. Nevertheless, interpopulation variation in gonad mass is likely to exist.

Interpopulation variation in gonad mass may arise due to several factors. Firstly, a genotype-by-environment response to resource availability would likely cause populations that experience good environmental conditions to have a larger energy budget, which in turn could manifest as a higher gonad mass per body mass. Secondly, other environmental factors such as migration distance may cause populations that have long migratory routes to allocate fewer resources to gonad mass than other populations due to the energy cost of migration. However, in a study by L'Abée-Lund and Hindar (1990), migration distance (approximated by the river stretch available for anadromous salmonids) did not explain differences among seven Norwegian sea trout

populations. Nevertheless, migration distance was found to impact reproductive traits of Coho salmon in a study by Fleming and Gross (1989), and more studies are needed to conclude on the effect of migration distance on reproductive traits of sea trout.

Gonad mass in the first-generation hatchery-reared sea trout from Møre and Romsdal was found to increase sublinearly with body mass. This may be a consequence of the sample only including individuals belonging to one year-class, which in turn violates the assumption of independent samples for Møre and Romsdal. This regression of gonad mass in one year-class results in measuring individual reproductive investment strategies rather than the relationship between gonad mass and body mass in sea trout. The individuals that invest the most in growth should have less energy to invest in reproduction, and as such, the regression estimate is skewed in a negative direction compared to a sample consisting of multiple year-classes. Nevertheless, hatchery-reared sea trout had, on average, larger gonad mass per body mass than wild sea trout, indicating that a genotype-by-environment interaction is a plausible explanation for differences in gonad mass per body mass among populations.

The linear increase in gonad mass with body mass in wild sea trout has consequences for the relationship between the number and size of eggs and body size. If a constant energy investment in egg production is balanced (*i.e* there is a trade-off) between a continuous increase in the number and size of eggs, then neither may show linearity with body size as their product is equal to gonad mass, which by itself is linear with body mass.

Absolute fecundity was found to increase sublinearly with body mass in sea trout. In brief, this means that relative fecundity must decrease with body mass, which was also the case in this study. The results show that absolute fecundity increased with 77% with a doubling (*i.e.,* a 100% increase) in weight of sea trout, while relative fecundity was proportionally decreasing at 23%.

The estimate for the relationship between absolute fecundity and body weight is not directly comparable to that of Jonsson and Jonsson (1999) due to not distinguishing between first-time and repeat spawners. However, the estimated absolute fecundity and body length relationships for Hardanger ($slope = 2.5 \pm 0.3$) and Nordland ($slope = 2.27 \pm 0.5$) are similar to those found by L'Abée-Lund and Hindar (1990) for seven Norwegian rivers ($slopes = 2.0\text{-}2.8$) and by Elliott (1995) for River Leven, Dale Park Beck and River Duddon in north-western England ($slopes = 2.7 - 2.9$). Nevertheless, it appears that a wider range of body sizes causes the regression estimate for the fecundity-body size relationship to decrease. Thus, the sublinear increase in fecundity with body mass seems to be a generalisable trend for wild sea trout, and potentially hatchery-reared sea trout, when regressing for populations including both first-time and repeat spawners.

The results in this study show that egg size increased sublinearly with the body mass of sea trout. This relationship is similar to the findings of L'Abée-Lund and Hindar (1990) and Jonsson and Jonsson (1999) for sea trout, but a comparison of the estimates would not be valid due to study design. However, the general trend is a sublinear increase with body mass in sea trout. An increase in egg size with

body mass seems to be the rule, rather than the exception, in salmonids (Einum and Fleming 1999; Thorpe, Miles, and Keay 1984; Wootton 1998). Nevertheless, there are exceptions, as found by Smalås, Amundsen, and Knudsen (2017) for Arctic char morphs in Skogsfjordvatn, northern Norway, where egg size did not appear to depend on body size within a group of morphs but did differ among the morph types. Then, the question is; why should egg size increase with body size in sea trout?

Firstly, if sea trout undergo ontogenetic habitat shifts in spawning habitat, then egg size may increase according to abiotic conditions (Jonsson and Jonsson 1999). Van Den Berghe and Gross (1984) and Fleming and Gross (1990) observed that the spawning habitat preferences of Pacific salmonids transitioned from finer to coarser gravel with body size. Coarser gravel allows for higher through-flow of water, and thus, better oxygenation. Therefore, as a result of the interplay between water flow, oxygen availability and the surface-to-volume ratio of spherical objects, egg size may increase with body size in sea trout.

Secondly, Wootton (1990) suggested that the reproductive strategy could shift from one strategy for small individuals to another strategy for large individuals. The idea is that those small individuals have low fecundity compared to their large conspecifics and may try to gain higher fitness by hedging their bet on many small eggs and favourable environmental conditions. Jonsson and Jonsson (1999) disagree with this reasoning on the basis of 'what is good for the one should be good for the other'. Nevertheless, Jonsson and Jonsson (1999) showed that there was a shift from

small to larger eggs from first-time to repeat spawning sea trout of equal size. The suggestion of Wootton (1990) may explain this shift, or it may be an effect of the energy status of the spawner. For sea trout to become repeat spawners, they must undertake several feeding migrations to sea and may have a higher energy density than their first-time spawner conspecifics. As such, the change in egg size between the first-time and repeat spawners may result from the energy status of the fish.

One obvious factor is often disregarded, especially for iteroparous salmonids. Few studies include a range of ages that is representative for the entire life-span of the species. As observed in Arctic charr, total reproductive energy allocation increases until individuals reach senescence at which point egg production fails (Jonsson et al. 1988). This may cause a bell-shaped curve in which egg sizes goes from small to large and back to small, and is also a plausible explanation for the small eggs observed for the 8 kilogram, 16-year-old sea trout in this study. However, a study that includes more fish towards the end of their life-span is required before any conclusions can be drawn.

As previously stated, egg size is important in determining offspring survival (Einum and Fleming 1999). Based on the egg size optima model of Smith and Fretwell (1974), fecundity should be the most variable of the two (Smalås, Amundsen, and Knudsen 2017). Theoretically, this may be the reason for differences in fecundity and egg size among populations. Mathematically, populations with a small optimum egg size should be able to allocate more resources in the number of offspring than populations with large optimum

egg size. While it is not directly evident from the two populations of wild sea trout, it appears that the hatchery-reared sea trout may have a smaller optimum egg size and, therefore, allocate more resources to fecundity. This may be explained by the optima-model of Smith and Fretwell (1974). Given that a stable heterogeneous environment yields a smaller optimum egg size, then a genotype-by-environment interaction may cause a lower energy investment in egg size, thus, freeing resources for investment in fecundity.

The hatchery-reared sea trout invested heavily in fecundity compared to the wild sea trout. This may be a phenotype-response to the environment caused by resource availability and homogeneity. Heath et al. (2003) found rapid changes in egg size of captive salmonids compared to wild conspecifics. They argued that relaxation of natural selection might cause maladaptations in egg size of captive salmonids. That said, egg size in salmonids is partly plastic and may develop in response to maternal growth or spawning habitat (Fleming et al. 2003). Nevertheless, this investment in fecundity at the expense of egg size found in captive salmonids may have consequences for stocking programs (Heath et al. 2003; Fleming et al. 2003).

The trade-off regime differed among the two groups of wild sea trout and between the wild and hatchery-reared sea trout. The wild sea trout from Nordland invested more in egg size than the wild sea trout from Hardanger. There are several explanations for this; first, the sea trout from Hardanger may experience higher survival in offspring from small eggs than sea trout from Nordland. Second, the sample composition may include more repeat spawners

from Nordland than from Hardanger, which again is shown to affect the investment in egg size and egg number (Jonsson and Jonsson 1999).

Additional variation in egg size may be caused by order of which egg production occurs in teleosteans. In teleosts, the number of primary oocytes is determined prior to vitellogenesis ending (Andersen 1992). The vitellogenesis (*i.e.,* loading of nutrients to eggs) is a continuous process lasting until spawning (Andersen 1992; Wiegand 1996; Lubzens et al. 2010). As such, if the number of eggs that mature requires more resources to reach optimum size than what the individual can acquire during the feeding season, then eggs will reach a sub-optimum size. However, Tyler and Sumpter (1996) and Lubzens et al. (2010) argue that oocyte growth and development is an interactive process in teleosts, and as such, the number of mature eggs, rather than their size, should decrease (Karjalainen et al. 2016). Anyhow, if the maturation of eggs in onset before ending vitellogenesis, and maturation is an irreversible process the argument holds. That is unless individuals can delay spawning after maturation of eggs.

Gonadosomatic index was not correlated with body mass in wild sea trout. Gonadosomatic index in the two groups of wild sea trout was approximately 20%, which appear common in salmonids (Jonsson and Jonsson 1997). It, therefore, functions as a measurement of relative reproductive investment. The results in this study may indicate, although not conclusively, that egg size increase with gonadosomatic index in wild sea trout. Important to note is that gonadosomatic index by itself does not appear to provide a sufficient explanation for

egg size in sea trout. However, by the inclusion of body size as a covariate, the regression may explain 71% of the variation in egg size; however, this may be an effect of multicollinearity. Additionally, gonadosomatic index seems to be more determining for egg size in small individuals (*i.e.,* the contrasting regression of egg size on gonadosomatic index between Nordland and Hardanger) than for large individuals.

While this thesis cannot conclude on any of the above explanations for why egg size should vary with body size, it does support that nutritional status of the individual is an important determinant for egg size in sea trout. This is evident from the egg size-gonadosomatic index relationship found for sea trout in this study.

Within-clutch variation in egg size was found to increase with the body mass of sea trout. Simulations ran by Einum and Fleming (2004) found that selection in Atlantic salmon should be towards a homogeneous large egg size in line with a conservative bet-hedging strategy, however, they did not include increased variation in egg size with body mass. While this increase in within-clutch variation with body mass does not contradict the findings of Einum and Fleming (2004), the increase in egg size variation with body mass in salmonids should be included in modelling to improve the simulation outcome.

Why the variation in egg size should increase with body mass is not entirely clear. A plausible explanation for this would be a physiological limitation. When the volume of gonads increases, it may become more challenging to distribute resources to eggs evenly. The eggs that are proximal to the capillaries may receive more energy than those that are distal to the capillaries. The within-clutch egg size,

may, therefore, vary more in large individuals than in small individuals. However, this may be beneficial rather than disadvantageous. Depending on where the line between physiological restriction and reproductive strategy is drawn, the variability found in egg size may resemble a small-scale diversified bet-hedging strategy. Whether, or not, the increase in within-clutch variation found for sea trout in this study supports a diversified bet-hedging strategy is difficult to determine without establishing any measure of large variability attaining to sea trout. Nevertheless, if most eggs are centred around an approximately optimal size, the cost of investment in a few large eggs at the cost of a few small eggs balances to zero, in which the few large eggs have higher survival than the smaller eggs and, thus, should benefit from this phenomenon.

Some limitations of this study should be noted. First, the methodology chosen may have caused systematic errors. The dissection of mature female sea trout may cause inclusion of immature eggs and connective tissue that would slightly increase the fecundity estimate. The artificial stripping of eggs may cause some eggs to remain in the body cavity and not be accounted for, thus, decreasing the fecundity estimate. Second, random error may be present in the extrapolation of fecundity from subsamples. Third, back-estimation of egg size after conservation and fixation on Gilson's fixative fluid could lead to estimation of too small or too large eggs, and this also applies to the assumption of eggs to resemble perfect spheres. Fourth, this is a short-term study and fluctuations in environmental conditions may skew the estimates in the direction of years with either good or bad environmental conditions

without the ability to determine which direction. Fifth, the sea trout from Hardanger were pooled due to low sample size for each river, and as such may not be representative for any river. Sixth, the sample size is minimal due to 1) the reproductive value of mature female sea trout in wild populations combined with declines of many sea trout populations, and 2) time constraints. The low sample size causes higher uncertainty in estimates. Seventh, models regarding egg size did often not conform to the assumptions of the ANCOVA, and as such, adds uncertainty to the estimates and standard error of the estimates.

In conclusion, this study has added to the existing literature on the reproductive traits in sea trout by extending on the previously investigated body size ranges and geographical span. The study supports the hypothesis (1) of that gonad mass increases approximately linearly with body mass in sea trout. The findings further supports the hypotheses, and previous findings, of that (2) absolute fecundity and (3) egg size increases with body size in sea trout, but also other anadromous salmonids. It shows that (4) while the overall strategy of sea trout is to increase egg size at the cost of fecundity, individuals and populations may differ in their allocation between fecundity and egg size (*i.e.,* there is a strategy-dependent trade-off of fecundity and egg size). The trade-off between relative fecundity (*i.e.,* quantity) and egg size (*i.e.,* quality) indicate that populations may have different optimum egg size, and that the investment in egg size may change in accordance to spawning habitat. It indicated that the hypothesis of that (5) there were variations in reproductive traits among sea trout populations, but that caution should be exercised when interpreting these results due to that the variation may be caused by sample structure. The study further supports the hypothesis of that (6) gonadosomatic index, an approximation of energy status, of the individual, is important in determining egg size in sea trout. Lastly, it indicates that variation in egg size increases with body size; however, it is not opposing to having a low within-clutch variation in egg size. As such, it neither supports, nor refutes, the hypothesis of (7) low within-clutch variation in egg size in sea trout.

Future research on geographical variation, seasonal variation, and variation in river topography and their relationship with reproductive traits in sea trout may be important for conservation and management of Norwegian sea trout populations. Further, the inclusion of within-clutch variation and its relationship with body size should be included in the modelling of reproductive strategies in salmonids. Lastly, the effects of Gilson's fixative fluid on salmonid eggs should be further investigated to provide better grounds for comparisons among studies using Gilson's fixative fluid as a conservative prior to analyses.

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