



Investigating temporal variability and influence of condition on fecundity and spawning of spotted wolffish (*Anarhichas minor*) in Icelandic waters

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Abstract

Spotted wolffish (*Anarhichas minor*) is a poorly understood species which is often captured as part of mixed demersal fisheries across its range. Abundance has declined in many regions and there is a need for greater knowledge on its biology. To improve our understanding of reproduction of *A. minor*, we investigated inter- and intra- annual differences in fecundity, the influence of condition on fecundity and time scale of ovary development. From 2006 to 2021, 150 females *A. minor* were sampled in Icelandic waters. Of these females, 73 were also used to estimate spawning time together with an additional 334 females from commercial catch and surveys from 2006 to 2023. Backwards extrapolation of oocyte size indicates that vitellogenesis begins in December and is likely completed after 8–10 months. There was no evidence of either intra- or inter-annual differences in fecundity, indicating that downregulation is minimal and that fecundity of *A. minor* is stable between years. A positive relationship between oocytes size and fish length was detected, while body condition and hepatosomatic index had only a small influence on fecundity in comparison with weight. There was a negative relationship between length and relative fecundity and the exponent of the fecundity–length relationship was lower than exponent of the weight–length relationship. Therefore, total egg production is likely not proportional to the spawning stock biomass of *A. minor*, and unusually, total egg production would decrease with increasing proportion of larger fish in the population. The spawning season was estimated to be from middle of August to middle of October with peak of spawning in September.

Keywords *Anarhichas minor* · Vitellogenesis · Ovary development · Fecundity relationships · Spawning season · Oocyte size

Introduction

Teleost fish display a wide range of reproductive strategies, which encompass numerous traits such as, age/size at maturation, fecundity, egg size, spawning time, number of batches per season, level of parental care etc. Knowledge of these traits within a species, together with other aspects of their biology, can indicate the productivity and susceptibility of a particular species to changes in its environment, including effects of fishing pressure (Stobutzki et al. 2002; Hobday

et al. 2011). Such knowledge can also help identifying vulnerable life stages to direct disturbance, such as selective effect of fisheries on spawning populations (Scott et al. 2006; Zemeckis et al. 2014; Gunnarsson et al. 2016), or indirect disturbance through specific effects of fishing gears, other anthropogenic activities, and climate change (de Mitcheson and Colin 2012; van Overzee and Rijnsdorp 2014). Within a population, reproductive traits are known to vary both spatially and temporally due to variation in environment including prey availability, temperature, fishing pressure and genotypes (Bagenal 1966; Kjesbu et al. 1998; Yoneda and Wright 2004; Óskarsson and Taggart 2006; Rideout and Morgan 2007; Stares et al. 2007; Tobin and Wright 2011; McElroy et al. 2013; dos Santos Schmidt et al. 2020). Therefore, it is important to monitor reproductive traits to understand the spatial and temporal variability of the reproductive biology of a particular species' population within a particular environment and time frame.

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There is an increasing awareness that spawning stock biomass (SSB) does not adequately represent the reproductive potential of a stock (Trippel 1999). Many fish exhibit hyperallometric mass scaling of fecundity (Barneche et al. 2018) which can lead to a non-linear relationship between SSB and total egg production (TEP) (Marshall et al. 1998). Therefore, in order to evaluate how a stock's ability to produce viable eggs and larvae varies over time, an index encompassing a greater number of factors is needed (Trippel 1999). The TEP represents the maximum number of potential recruits to a population and is likely to better predict recruitment than SSB (Kraus et al. 2002; Marshall et al. 2003). To estimate TEP, knowledge of the concerned species fecundity is required. However, estimation of fecundity is often time consuming and time series are scarce. Fecundity can be estimated indirectly using relationships between fecundity and other variables such as length, weight, body condition and hepatosomatic index (Marshall et al. 2000; Lambert et al. 2003; Tomkiewicz et al. 2003), but of course, knowledge on how fecundity is affected by these variables is required.

Spotted wolffish (*Anarhichas minor*) is one of the four species of the genus *Anarhichas*. It is primarily found at depths of ~150–600 m and is distributed across the North Atlantic Ocean (Barsukov 1959). Females mature at length ranging from 55 to 85 cm and at 7–9 years old (Østvedt 1963; Beese and Kändler 1969; Templeman 1986; Gusev and Shevelev 1997; Gunnarsson et al. 2008). Female *A. minor* have an unusual ovary development strategy, in that, once oocytes reach the cortical alveolus (CA) stage, they will remain at this stage for several years prior to spawning for the first time (Gunnarsson et al. 2008). This oocyte development strategy has only been documented in two other species, Atlantic wolffish (*Anarhichas lupus*) and Greenland halibut (*Reinhardtius hippoglossoides*) (Gunnarsson et al. 2006; Kennedy et al. 2011).

Spotted wolffish (*Anarhichas minor*) is a determinate spawner with large demersal eggs (4–7 mm) that are spawned in a single batch with an incubation period of 800–1000 °C degree-days, depending on incubation temperature (Falk-Petersen et al. 1999). Spawning takes place during summer and autumn, depending on geographical area (Templeman 1986; Gunnarsson et al. 2008). Based upon the large egg size and the low temperatures in which they inhabit, it is likely that vitellogenesis is initiated several months before spawning. Just before spawning, three groups of oocytes are usually present in the ovary of *A. minor*, the vitellogenic oocytes which will be spawned at the next spawning opportunity, oocytes at the CA stage that will be spawned the following year and a stock of previtellogenic oocytes from which oocytes for future spawning events are recruited (Beese and Kändler 1969).

Fecundity of *A. minor* has previously been examined in Iceland, Canada, Greenland, Norway and and Russia

(Maslov 1944; Beese and Kändler 1969; Templeman 1986; Gusev and Shevelev 1997; Gunnarsson et al. 2008). While spatial differences in fecundity were observed during these studies, *A. minor* of 60–120 cm have a fecundity of ~4 to 50 thousand eggs (Gunnarsson et al. 2008). However, none of the previous studies considered oocyte development stage which impacts the estimation of fecundity. As the ovary development proceeds, fish commonly decrease the number of vitellogenic oocytes through atresia (Vladykov 1956; Kurita et al. 2003; Skjæraasen et al. 2013). As a result, observed differences in fecundity between regions might be due to individual variation in oocytes development stage rather than spatial variation.

In the last decades, populations of *A. minor* have been declining. As a consequence, *A. minor* in the Northwest Atlantic has been listed as threatened by the Canadian Species at Risk Act (SARA) (Kulka et al. 2004). In European waters, *A. minor* has recently been classified as near threatened (Collette et al. 2015). In Icelandic waters, the species has been decreasing since 1996 and has now reached a historical low level. There is no targeted fishery for *A. minor* in Iceland, but they do have commercial value, and are mainly caught as bycatch in fisheries targeting other groundfish species. Spotted wolffish (*A. minor*) was added to the Icelandic Individual Transferable Quota (ITQ) system in 2018, however catches have largely exceeded advice since 2012 (MFRI 2023).

Spotted wolffish (*A. minor*) is a data poor species and there is an urgent need to gather information on its reproductive biology, population trends and harvest to implement proper conservation strategy to avoid its depletion. In the present study, we aim to improve the understanding of, *A. minor* reproductive biology and provide information which will be beneficial for conservation measures and management. Obtaining fecundity samples of *A. minor* can be difficult due to the low numbers for both the number of fish caught during surveys and the number of ungutted fish landed by the commercial fishery, sampling is therefore often opportunistic and difficult to plan. In addition, collecting fecundity samples too early in development can impact the results because of downregulation of fecundity. Therefore, it is necessary to have information on how the progress of vitellogenesis influences fecundity. The aim of the present study is to investigate (1) the temporal variation of fecundity over a period of 5 years (2006, 2008–2010 and 2019); (2) the effects of life-history traits such as condition, hepatosomatic index, length and weight on fecundity; (3) the temporal variation of fecundity within a year to assess how progress through vitellogenesis (upon measurement of oocyte size) impacts fecundity and (4) the distribution of spawning and timing of the spawning season of *A. minor*. This information will provide valuable biological inputs to the conservation

strategy and management plan of this near threatened and data poor species.

Materials and methods

Sampling

A total of 150 female *A. minor*, at the vitellogenic stage of oocyte development, were collected. Samples were taken from 2006 to 2010 during the annual Icelandic autumn groundfish survey (AGFS) which takes place in October ($n=27$) and from the commercial fishery ($n=89$). Additional samples were taken during 2014 in the same survey, AGFS ($n=1$) and the period of years, 2016 and 2018–2021, 2010 included from the Icelandic spring groundfish survey (IGFS) which takes place in February–March ($n=17$) and from the commercial fishery ($n=16$) (Table 1; Fig. 1). For each fish total length (L) (± 1 cm) was measured and for most of them, ungutted weight (W), gutted weight (W_g), liver and gonad weight were also measured to the nearest 1 g (Table 2). In 2006–2010, gonads were removed from each fish and placed in permeable plastic bags which were placed in 10% formalin, except for two gonads sampled during the IGFS which were analysed onboard. The ovaries were transported to the laboratory for estimation of fecundity and measurement of oocyte diameter. From 2014, no gonads were preserved in formalin, the ovaries sampled during the AGFS and IGFS were analysed onboard while the gonads sampled from the commercial catch in 2019 were analysed in the laboratory within 24 h after removal from the fish.

Estimation of fecundity

Fecundity was estimated gravimetrically (Bagenal and Braum 1970). All the oocytes were removed from the ovary, blended and washed in water. After the oocytes were drained, they were weighted (W_o), and two sub-samples weighted (W_{osubs}) counted manually with only oocytes > 2 mm being counted ($nosubs$). The aim was to have sub-samples with ~ 100 oocytes, which was estimated using the naked eye, thus usually contained more than 100 oocytes. Potential fecundity (F) was estimated by Eq. (1).

$$F = \frac{W_o}{W_{osubs}} \times nosubs \quad (1)$$

The mean of the two estimates of fecundity was used to determine F and used for further analysis. If the coefficient of variation between these two estimates was larger than 5%, a third subsample was taken. Relative fecundity (RF) was estimated using Eq. (2).

$$RF = \frac{F}{W_g} \quad (2)$$

Fish body condition

Relative fish body condition (K_p) was calculated for each fish with Eq. (3), with the assumption that individuals with a greater weight at length have greater energy reserves. Gutted weight was used to rule out any effect of the weight of the stomach contents. Predicted gutted weight (W_{pg}) was based on the estimated length–weight relationship using data from the 148 females collected (Eq. 4). Hepatosomatic index

Table 1 Number of female spotted wolffish (*Anarhichas minor*) sampled by years and months and length range

Year	Jan	Feb	March	May	June	July	Aug	Sept	Oct	Total (n)	L . range
2006				11		4	1	1	13	30	61–93
2007				3	2				1	6	72–99
2008	2			17			4	3	3	29	58–102
2009					18		3		10	31	52–96
2010			2		1	2	16		1	22	68–108
2014									1	1	–
2016		2								2	102–113
2018			6							6	89–108
2019			3				14	2		19	78–101
2020			2							2	90–98
2021			2							2	85–89
Total (n)	2	2	15	31	21	6	38	6	29	150	52–113
L . range	94–97	102–113	84–108	64–93	68–99	68–84	60–108	61–98	52–94		

L . range range of total length (cm)

Fig. 1 Location and number of females spotted wolffish (*Anarhichas minor*) sampled for reproductive biology measurements from the commercial fishery and research surveys

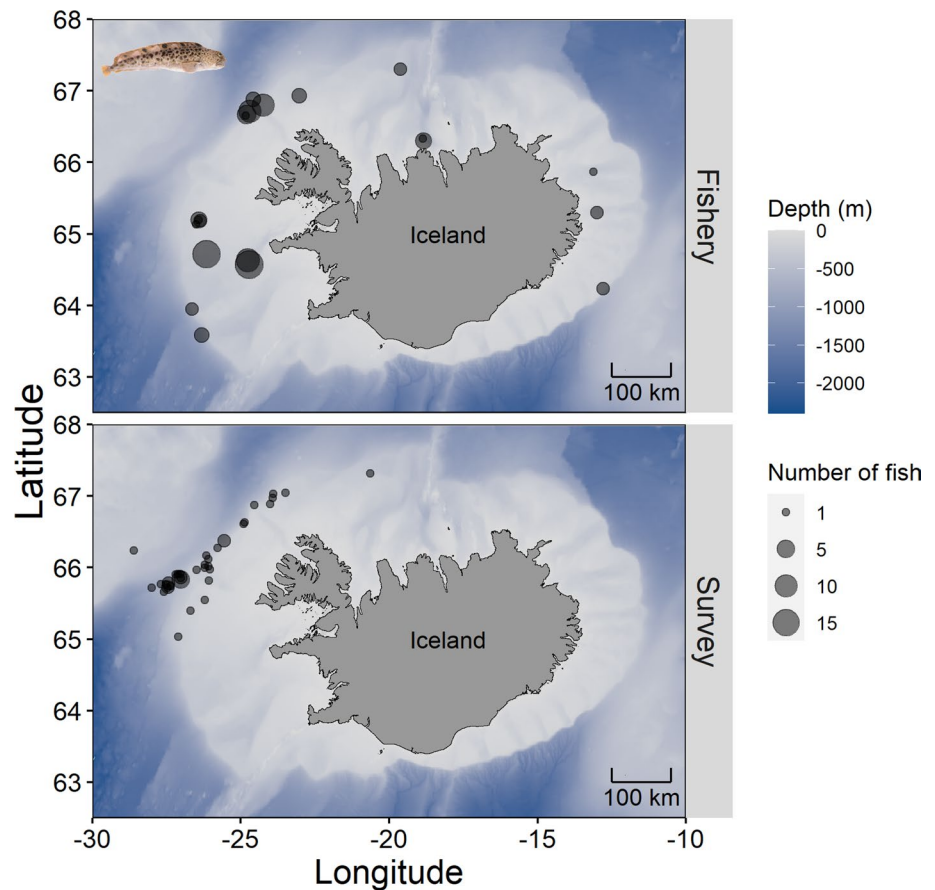


Table 2 Variables in this study, with its mean, standard deviation, range and number

Variable	Mean (SD)	Range	<i>n</i>
<i>L</i>	82.67 (10.58)	52–113	150
<i>W_g</i>	5803 (2020)	1049–12730	148
<i>HSI</i>	4.08 (0.95)	1.35–6.92	137
<i>K_r</i>	1.00 (0.12)	0.74–1.34	148
<i>GSI</i>	8.85 (7.81)	1.71–43.97	138
OD	3.76 (1.04)	2.13–6.57	120
<i>F</i>	11,101 (4351)	2383–33,472	150
<i>RF</i>	2.26 (0.48)	1.22–4.34	148
<i>RF P1</i>	2.14 (0.39)	1.23–3.51	71
<i>RF P2</i>	2.39 (0.54)	1.22–4.34	77

L total length (cm), *W_g* gutted weight (g), *HSI* hepatosomatic index (%), *K_r* relative condition, *GSI* gonadosomatic index (%), OD oocytes diameter (mm), *F* potential fecundity, *RF* relative fecundity (oocytes g^{-1}), *RF P1* relative fecundity in January–June, *RF P2* relative fecundity in July–December

(*HSI*) was estimated with Eq. (5) and gonadosomatic index (*GSI*) with Eq. (6).

$$K_r = W_g / W_{pg} \quad (3)$$

$$W_{pg} = 0.008 \times L^{3.003} (R^2 = 0.91, n = 148, P < 0.001) \quad (4)$$

$$HSI = (\text{Liver weight} / W_g) \times 100 (\%) \quad (5)$$

$$GSI = (\text{Gonad weight} / W_g) \times 100 (\%) \quad (6)$$

Measurements of the oocytes

Oocyte diameters (OD) were measured for a total of 119 fish. Generally, *A. minor* oocytes are rather spherical in shape, however two measurements, major and minor axes of each oocyte were used to estimate the average oocyte diameter. Measurements were done using Leica image Q500 MC and Sigmascan except for those measured on-board during the IGFS where callipers were used. To estimate OD, the first ten vitellogenic oocytes from the first subsample from the fecundity estimation was used. In 2006, of the four

gonads sampled, 30 oocytes (instead of ten) were measured for two fish and a total of 20 oocytes were measured for the other two. Since all ovaries collected during the AGFS and the commercial fishery from 2006 to 2010 were preserved in formalin, the oocyte size was corrected to obtain fresh oocyte diameter using the formula from Gunnarsson et al. (2022).

Spawning time

To estimate spawning time of the Icelandic population of *A. minor*, trends in *GSI* and *OD* was used. Additional, fish sampled in commercial catch of pre-spawning and spent females in August–November (268) and AGFS (139; Table 5) between 2006 and 2023, were examined. Of these fish, 73 had also been used in the current fecundity study. To examine distribution of spawning, data from AGSF in the years 2006–2023 were location of females on aforementioned maturity stage was used as a proxy for spawning location and the bottom depth on station where they were caught was used to estimate the bottom depth of spawning.

Statistical analysis

To find the best model to describe fecundity $\log(F)$, stepwise linear regressions were performed using the following variables: $\log(L)$, $\log(W_g)$, *HSI*, K_r , year, month, period (see below) as an interaction with either $\log(W_g)$ or $\log(L)$, and day of the year, in the first model where year, month and period were treated as factors. It seemed that day of the year and length were not independent, therefore the data were split in two periods based on observed difference in relative fecundity between the months January–June (P1) and July–October (P2, Fig. 3). Oocyte diameter was excluded from the analysis as predictor variable for fecundity, as it was only measured for 119 fish, years with a sample size < 10 were also excluded in the first model (Table 1). As the variable years did not show a significant effect on fecundity, years with a sample < 10 were therefore included subsequent analysis. The most parsimonious model was selected based on Bayesian Information Criteria (BIC, Schwarz 1978; Sakamoto et al. 1986). The variables selected by the stepwise regression were used to estimate $\log(F)$ with linear regression. The same method was applied for estimation of *RF*, except that W_g was excluded and *L* was not transformed, in the stepwise linear regressions.

The influence on oocyte diameter was examined using the same approach. To examine the proportion of variance explained by each variable in the final model, an ANOVA was used. A *t* test was used to examine differences between exponents.

Weighted mean was used to estimate mean spawning depth.

All analysis and statistical tests were performed using R version 4.1.2 (R Project 2020).

Results

Potential fecundity

The observed potential fecundity (*F*) ranged from 2383 to 33,472 oocytes for 52 (W_g , 1049 g)–108 (W_g , 12,730 g) cm fish, respectively.

In the stepwise linear regressions, neither year, month, period, or day of the year, improved the model fit. Thus, the data collected during the different years were combined and the stepwise linear regressions were repeated using the same variables as before.

The best model to predict $\log(F)$ included $\log(W_g)$ and *HSI*, (Linear regression; $F_{2,136} = 267.7$, $R^2 = 0.80$, $p = < 0.0001$; Table 3; Fig. 2a). $\log(W_g)$ explained 79% of the variance in the model and *HSI* about 1%. To examine the influence of $\log(L)$ on $\log(F)$, W_g was excluded from the first model which then included $\log(L)$, K_r , *HSI*, day of the year, year (factor), season (factor) and month (factor). In this case the best model to predict $\log(F)$ included $\log(L)$, K_r and *HSI*, (Linear regression; $F_{3,135} = 178.6$, $R^2 = 0.80$, $p = < 0.0001$; Table 3; Fig. 2b). $\log(L)$ explained 76% of the variance in the model, K_r 3% and *HSI* 1%.

Relative fecundity

The relative fecundity (*RF*) ranged from 1.22 to 4.24 oocytes g^{-1} with a mean of 2.25 oocytes g^{-1} . The best model to predict *RF* included *L*, *HSI* and K_r (Linear regression; $F_{3,135} = 12.7$, $R^2 = 0.22$, $p = < 0.0001$; Table 3; Fig. 3). *L* explained 13% of the variance in the model, *HSI* 6% and K_r 4%. According to the model, if *HSI* and K_r were constant, the *RF* decrease 0.016 oocytes g^{-1} with increasing length cm^{-1} .

There was a negative relationship between *L* and *RF*, which is in accordance with that the exponent of length in power function used to describe the *F*–*L* relationship ($F = 0.1336 \times L^{2.562}$; $n = 150$, $R^2 = 0.74$) is significantly lower than the exponent in the W_g –*L* relationship which was 3.00 (Eq. 4; *t* test, $t_{150} = 2.56$; $p < 0.0057$; Fig. 4 and Table 4). Similarly, the exponent in power function used to describe the *F*– W_g relationship ($F = 7.4412 \times W_g^{0.8575}$, $n = 148$, $R^2 = 0.74$; Fig. 5 and Table 4) was lower than 1, or 0.853 with 95% confidence interval (0.768–0.948), which means that heavier fish have lower *RF* than lighter ones (Le Bris et al. 2015).

The interaction between season and length did not improve the final model to predict relative fecundity. However, according to Fig. 3. there is a difference in the *RF*–*L* relationship between periods or the data sampled in

Table 3 Estimates of linear regression for potential and relative fecundity and standard error

<i>F/RF</i>	Variables	Estimate	SE	<i>T</i> value	Sum of squares	<i>p</i>	Explained variance %
<i>log(F)</i> – <i>log(W_g)</i>	<i>log(W_g)</i>	0.804	0.037	21.75	3.559	<0.0001	78.7
	<i>HSI</i>	0.021	0.008	2.70	0.049	0.0078	1.1
	Intercept	0.982	0.132	7.44		<0.0001	
	Residuals				0.917		
	<i>log(L)</i>	2.497	0.128	19.52	3.430	<0.0001	75.8
<i>log(F)</i> – <i>log(L)</i>	<i>Kr</i>	0.276	0.062	4.48	0.136	<0.0001	3.0
	<i>HSI</i>	0.0202	0.008	2.66	0.049	0.0089	1.1
	Intercept	– 1.124	0.232	– 4.84		<0.0001	
	Residuals				0.911		
	<i>L</i>	– 0.016	0.004	– 4.53	3.874	<0.0001	12.5
<i>L-RF</i>	<i>HSI</i>	0.123	0.040	3.11	1.745	0.0023	5.7
	<i>Kr</i>	– 0.839	0.317	– 2.65	1.251	0.0090	4.0
	Intercept	3.943	0.386	10.22		<0.0001	
	Residuals				24.404		

Anova was used to determine explained variance of each of the predictor variables

F potential fecundity, *RF* relative fecundity (oocytes g⁻¹), *W_g* gutted weight (g), *L* total length (cm), *HSI* hepatosomatic index (%), *Kr* relative condition

January–June (P1) and July–October (P2). Therefore, the data was split by seasons and each dataset analysed as the original dataset. For P1 data the stepwise regression only chooses *HSI* ($p > 0.05$) as predictor variable. Which was showed in the final model to be insignificant influence on *RF*–*L* relationship, explaining less than 1% of the variance in it. For P2 the best model included *L* and *HSI* (Linear regression; $F_{2,71} = 10.99$, $R^2 = 0.24$, $p = < 0.0001$; $RF = 3.7933 + (L \times -0.023) + (HSI \times 0.101)$; Fig. 3). The *L* explained 21% of the variance in the *RF*–*L* relationship and *HSI* 3%. According to the model, if *HSI* was constant, the *RF* decrease 0.023 oocytes g⁻¹ with increasing length cm⁻¹. The mean *RF* for P1 was 2.14 oocytes g⁻¹ and for P2, 2.39 oocytes g⁻¹ (Table 2).

There was no relationship between *RF* and *L* for the P1 data, correspondently there was no difference between the exponent in the power function between *F*–*L* and *W_g*–*L* relationships (*t* test, $t_{71} = 0.80$; $p > 0.05$; Fig. 4; Table 4). However, when P2 data was used with same approach, *RF*–*L* relationship was negative and the exponent *F*–*L* and *W_g*–*L* relationships different (*t* test, $t_{77} = 3.22$; $p < 0.0009$; Fig. 4; Table 4).

Hepatosomatic and relative body condition indices

Hepatosomatic index was the highest in January (5.76%), from which it decreases steadily until May (3.68%). Afterwards, *HSI* values were relatively stable (Fig. 6a). Relative body condition generally increased from January (1.04) to June (1.10); It then decreased until October (0.89) when it reached its lower value (Fig. 6c).

To examine the influence of *HSI* on *log(F)*–*log(W_g)*, mean of *HSI* was reduced or increased by one SD (Fig. 2a; Tables 2, 3). For *F*, the change resulted in an increase/decrease of 140–1040 oocytes or a 4.3% change depending on the weight of the fish. For a fish of average weight (5803 g), this resulted in 560 oocytes change. In the step-by-step regression model, good predictors for *log(F)*–*log(L)* and *RF*–*L* relationships, were beside *log(L)* or *L*, *K_r* and *HSI* (Table 3). Therefore, mean of both *HSI* and *K_r* was either increased or decreased by one SD to examine the influence of both *HSI* and *K_r* on *log(F)*–*log(L)* and *RF*–*L* relationships (Fig. 2b, 3; Tables 2, 3). For the *log(F)*–*log(L)* relationship the change was increase/decrease of 375–2605 oocytes depending on the length of the fish or a 11.4% change. For the average fish length (82.7 cm), this resulted in increase/decrease of 1200 oocytes. For the *RF*–*L* relationship the change was ± 0.017 oocytes g⁻¹ or 0.6–0.9% depending on the *L* of the fish. For a fish of average *L*, the change was 0.7%.

Gonadosomatic index and Oocyte's diameter

The mean gonadosomatic index generally increased from January (2.16%) onwards, until September when it reached its maximum (31.99%). It then decreased in October (16.16%). The largest increase between months was between August (10.63%) and September (Fig. 6b).

The mean oocyte diameter (*OD*) increased linearly from 2.61 mm in January to 5.80 mm in September. Oocyte diameter then decreased between September and October to 4.35 mm (Fig. 6d). To examine influence of month (factor),

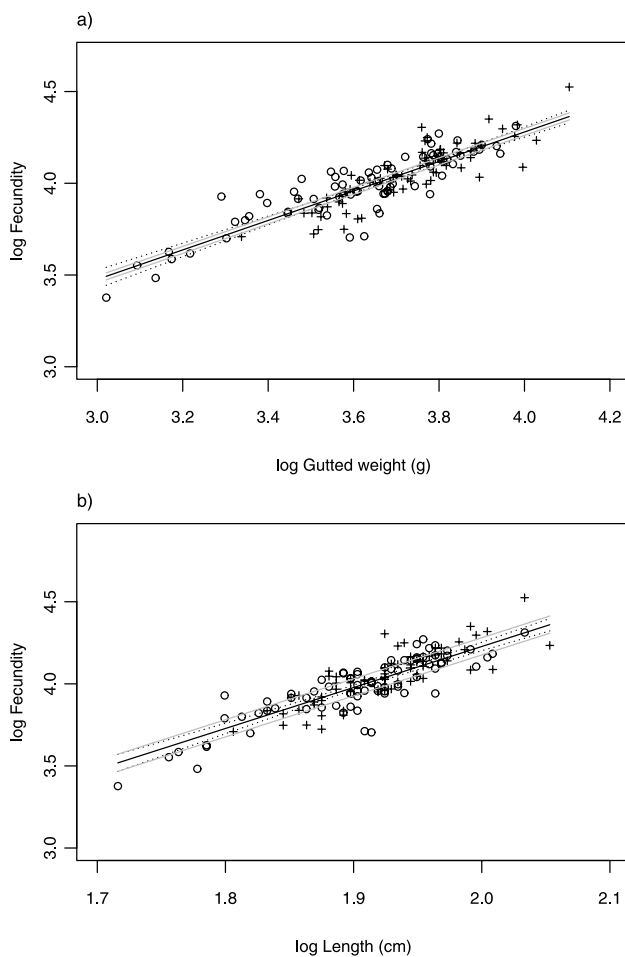


Fig. 2 Correlation between **a** log Potential fecundity and log fish gutted weight (W_g), **b** log Potential fecundity and log fish total length (L). The crosses represent observed fecundity in the period January–June and the open circles in the period July–October. The black lines represent predicted values from the best linear regression where in **b** both mean of hepatosomatic index (HSI) and relative condition (K_r) was used with $\log(L)$, and the grey lines represent predicted fecundity when both variable's mean (HSI and K_r) was decreased or increased of one SD (Tables 2, 3). The same approach applies for **a**, but the predicted variables were $\log(W_g)$ and HSI . The broken lines represent 95% confidence interval estimated when mean values of HSI and K_r were used

year (factor), day of year, HSI , K_r , and L on OD these variables were included in the first model. According to stepwise regression day of the year (ANOVA; $F_{1108} = 103.76$, $p < 0.0001$), L (ANOVA; $F_{1108} = 6.14$, $p = 0.0148$) and HSI (ANOVA; $F_{1108} = 5.94$, $p = 0.0164$) were the best predictors of OD in the final model. Day of the year explained 46% of the variance, L 3% and HSI 3%. The final linear regression equation to predict OD was $OD = 0.442 + (\text{day of the year} \times 0.012) + (0.023 \times L) + (-0.186 \times HSI)$, $R^2 = 0.51$, $F_{3108} = 38.1$, $p < 0.0001$). When assuming constant HSI and L , the model predicts that oocyte diameter increases about $0.012 \text{ mm day}^{-1}$ from the 25th of January to 9th of October.

When using the model to predict OD, changing L and HSI by one SD, resulted in an increase/decrease by $\sim 0.07 \text{ mm}$ or 1.4–3.6% for the largest to the smallest oocytes, respectively (Table 2, Fig. 7). To examine the influence of length on oocyte size the day of the year was given the value 257 or middle of September and HSI its mean value in September or 3.5 and the equation above used with different length. The oocytes diameter in mm was 4.20, 4.43, 4.66, 4.89 and 5.12 for 60, 70, 80, 90 and 100 cm long fish, respectively. Accordingly, in middle of September, a 100 cm fish had, on average, oocytes $\sim 22\%$ larger than that of a 60 cm fish.

Time, depth and distribution of spawning

According to GSI and OD spawning begins in August with a peak in September and is ongoing in October (Fig. 6b, d). According to data from commercial catch, 18% of female.

Anarhichas minor had spawned in the period 13th August to 22st August, in September 80% had spawn and all in October (Table 5). However, According to AGFS 72% was spent in October. However, in AGFS none pre-spawning female was catch after 17th October (Table 5). According to this the spawning period of *A. minor* in Iceland is from middle of August to middle October with peak of spawning in September. The bottom depth at spawning location in AGFS was at the range 133–610 m, mean depth was 345 m, $SD = 138.7$. *A. minor* spawn mainly in slope north-vest of Iceland, some spawning is also north of country and south-east of it, there seems to be none or little spawning south and south-west of Iceland (Fig. 8).

Discussion

Fecundity in fishes has been shown to be highly variable, both spatially and temporally (inter-annually) (Rideout and Morgan 2007) but there are also species which show limited variation between years (Kennedy and Ólafsson 2020). Despite the limited sampling, the current study indicates that fecundity of the *A. minor* did not vary between years. Various stages of oocyte development ranging from early to late vitellogenesis were observed, and no evidence for downregulation was found.

Comparison of results from the current study and previous studies indicates that fecundity of *A. minor* is similar across the North Atlantic (Fig. 9). The fecundity of *A. minor* in Barents Sea may be slightly higher than in Iceland. However, the fecundity data from Maslov (1944) consisted of 12 fish, of which, 3 were 120 cm long and therefore the results are not directly comparable to the present study. The data from Gusev and Shevelev (1997) are average fecundity of average length, therefore it is difficult to test statistically any differences between the Barents Sea and the present study.

Fig. 3 Relationship between relative fecundity (RF , number of oocytes g^{-1}) and total length (L). The crosses represent observed fecundity in the period January–June and the open circles in the period July–October. The black lines represent predicted values from the best linear regression where both mean of hepatosomatic index (HSI) and relative condition (K_r) was used with L , and the grey lines represent predicted fecundity when both variable's mean (HSI and K_r) was decreased or increased of one SD (Tables 2, 3). The dotted lines represent 95% confidence interval estimated when mean values of HSI and K_r were used. The dashed line represents predicted values based on data sampled in July–October (Linear Regression, $RF = 3.793 + (-0.023 \times L) + (4.08 \times 0.101)$)

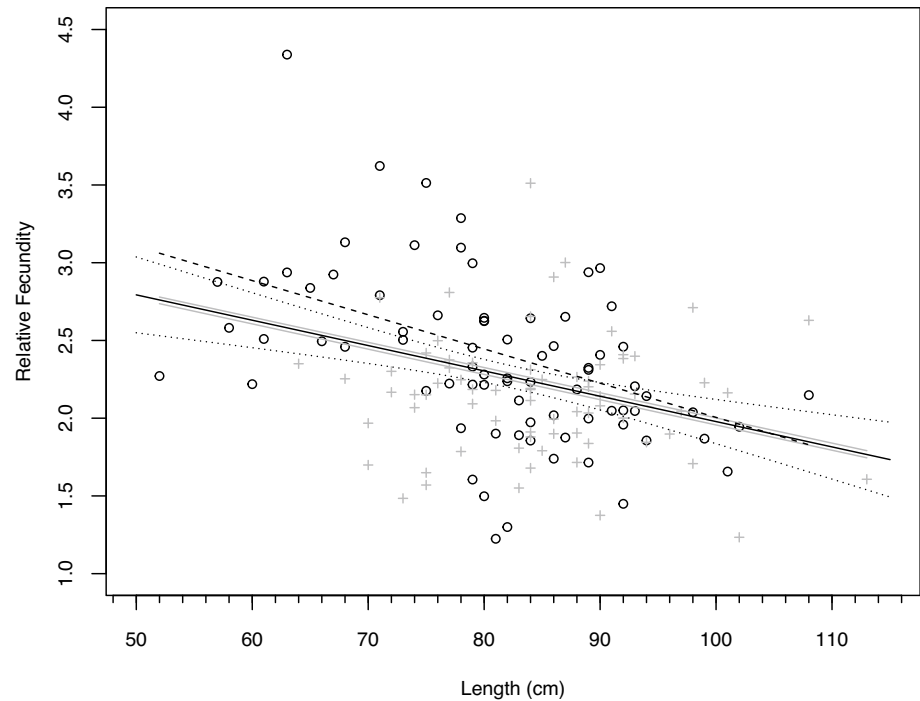
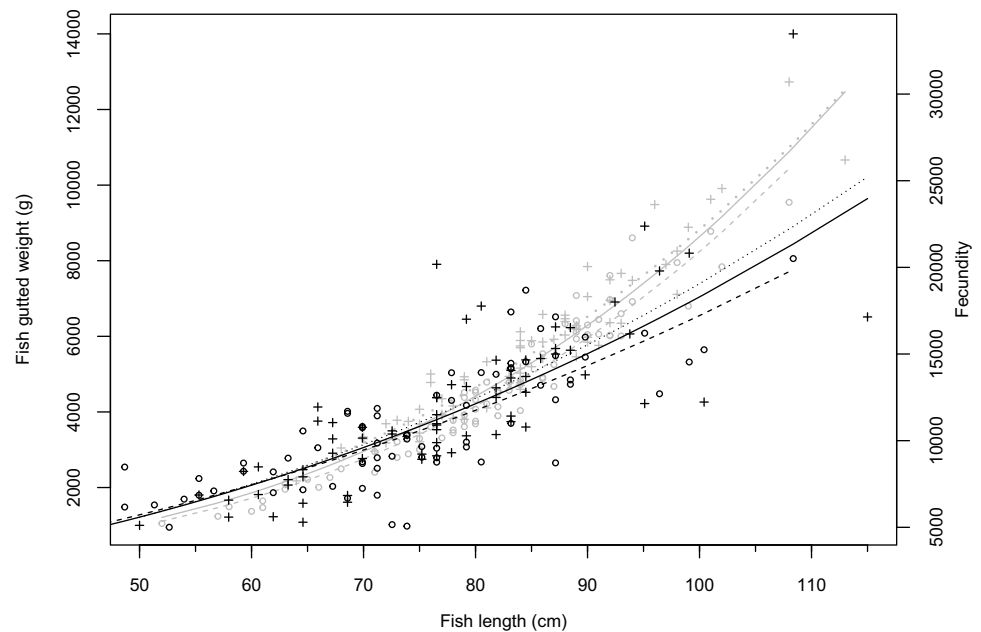


Fig. 4 Power regressions for potential fecundity (F) versus total length (L) and gutted weight (W_g) versus L . The crosses represent observed values in the period January–June and the open circles in the period July–October. The grey symbols are observed values for L – W_g relationship for spotted wolffish (*Anarhichas minor*) females, the line predicted values based on all data, the grey dotted line the period January–June and grey dashed line the period July–October. The same approach applies for the F – L relationship, but the symbols and the lines are black. See Table 4 for estimates for the lines



Similar, Beese and Kändler (1969) combined data from Barents Sea to west Greenland and in the study of Templeman (1986) only fecundity of three fishes was estimated (Fig. 9).

Although period was not included in the final model to predict RF , presumably as it was overridden by K_r and HSI in the step regression, it was decided to divide the data into two separate periods as visual inspection of the data indicated a difference in RF between these two periods (Fig. 3). The trend in these two indices is different between

periods, in P1 K_r is increasing while HSI is decreasing and in P2 K_r is decreasing while HSI seems to be stable. In P1 there was no relationship between RF and L , but in P2 this relationship was negative. Accordingly, there was no difference between the exponent in F – L and W – L relationship in P1, but it was in P2 (Fig. 4; Table 4). The reason for this difference is unclear but may be a result of the small sample size and further research is required.

Table 4 Estimate of intercept (a) and exponent (b) of power regressions of total length versus gutted weight, potential fecundity versus total length and potential fecundity versus gutted weight

Relationships	a (SE)	b (SE)	Data (n)
	0.008 (0.003)	3.006 (0.082)	P1 + P2 (148)
W_g-L	0.016 (0.008)	2.866 (0.110)	P1 (71)
	0.006 (0.003)	3.069 (0.104)	P2 (77)
	0.132 (0.091)	2.562 (0.153)	P1 + P2 (150)
$F-L$	0.089 (0.096)	2.656 (0.240)	P1 (71)
	0.288 (0.241)	2.380 (0.188)	P2 (79)
	7.441 (2.898)	0.858 (0.045)	P1 + P2 (148)
$F-W_g$	3.268 (2.021)	0.951 (0.070)	P1 (71)
	17.291 (8.315)	0.760 (0.056)	P1 (77)

W_g gutted weight (g), L total length (cm), F potential fecundity, P1 + P2 all data, P1 data from January–June, P2 data from July–December

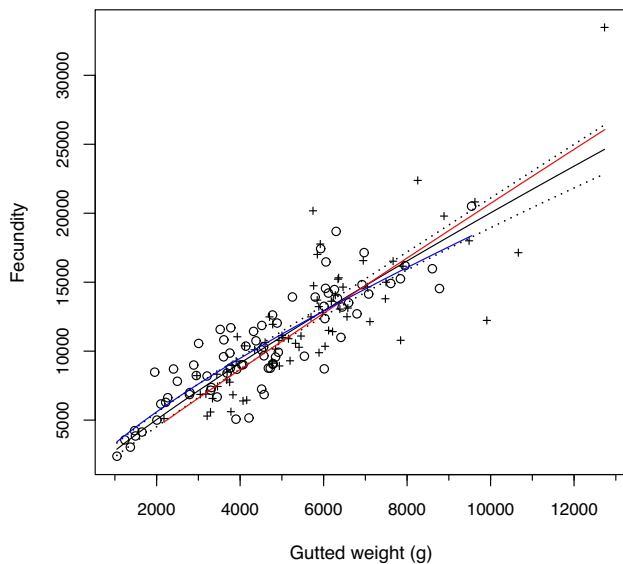


Fig. 5 Potential fecundity versus gutted weight for fish captured in January–June (crosses) and July–October (open circles). Power regression lines (Table 4) for January–June (red line), July–October (blue line), and all data combined (black line) are shown together with 95% confidence intervals for all data combined (dotted line)

Analysis of fish fecundity across 342 species showed that 79% displayed hyperallometric mass scaling of fecundity (Barneche et al. 2018) which equates to the exponent in the $F-L$ relationship being greater than the exponent in the $L-W$ relationship. The significance of a higher $F-L$ exponent is that TEP of a population will increase when the average size of fish within the population increases (Pérez-Rodríguez et al. 2011; Dick et al. 2017). However, the current study showed that the exponent in the $F-L$ relationship for *A. minor* was lower than the exponent in the $L-W$ relationship (Fig. 4; Eq. 4; Table 4). Accordingly, for equal values of SSB, there is a negative relationship between TEP and the

average length of *A. minor* within the stock. Negative relationship between RF and L has previously been documented for *A. minor* in the Barents Sea, for Atlantic wolffish around Iceland and mackerel icefish (*Champscephalus gunnari*) in the South Atlantic Ocean (Gusev and Shevelev 1997; Mili-telli et al. 2015; Gunnarsson 2017).

As previously mentioned, 79% of the fish species included in the study by Barneche et al. (2018) displayed hyperallo-metric mass scaling of fecundity, however, when total repro-ductive energy was assessed by including data on energy content of eggs, 95% of species displayed hyperallometric mass scaling of reproductive energy output as the energy content of individual eggs increases with maternal size. Thus, even if TEP falls with increasing proportion of larger fish, the total reproductive energy output of the population would increase. The result of the current study suggests that this may be the case for *A. minor* as there was a significant correlation between oocyte size and fish size. However, this may be due to larger fish being at a later stage of develop-ment (Kjesbu 1994) rather than having larger eggs. It should be noted that in captive *A. minor* broodstock, no relationship has been found between female length and egg size (Falk-Petersen et al. 1999), however this has not been examined in wild individuals.

Weight was a better predictor of potential fecundity than length. This result is in accordance with findings from other studies of fish fecundity that denote that body weight is a better predictor of fecundity than length (Koops et al. 2004; Rideout and Morgan 2010; McElroy et al. 2016; Kennedy and Ólafsson 2020).

Hepatosomatic index was also included in the final model to predict fecundity, but only explained a small amount of variance, or about 1%, 3%, and 6% for F predicted with weight, F predicted with length and RF , respectively. Relative body condition index was included in the final model to predict F with length and RF , but again, the variance explained was small or 3% and 4%, respectively (Table 3). These results correspond with those of previous studies in which characteristics intended to measure energy reserves or “condition,” added little in comparison to the factors reflecting body size (Óskarsson and Taggart 2006; Alonso-Fernández et al. 2009; Rideout and Morgan 2010; Gunnarsson 2017; Kennedy and Ólafsson 2020). The K_r was included in the final model to predict RF and the relationship was negative. This relationship might be because the fish is losing weight as they approach spawning and therefore RF is increasing while K_r is decreasing (Fig. 6c).

Hepatosomatic index was included in all final models to predict fecundity and a positive relationship between fecun-dity and HSI was detected in all instances (Table 3). The HSI decreased from January to May before stabilising, indicating that the weight loss in liver was proportionally lower than in carcass weight at least from July to October (Fig. 6a). Liver

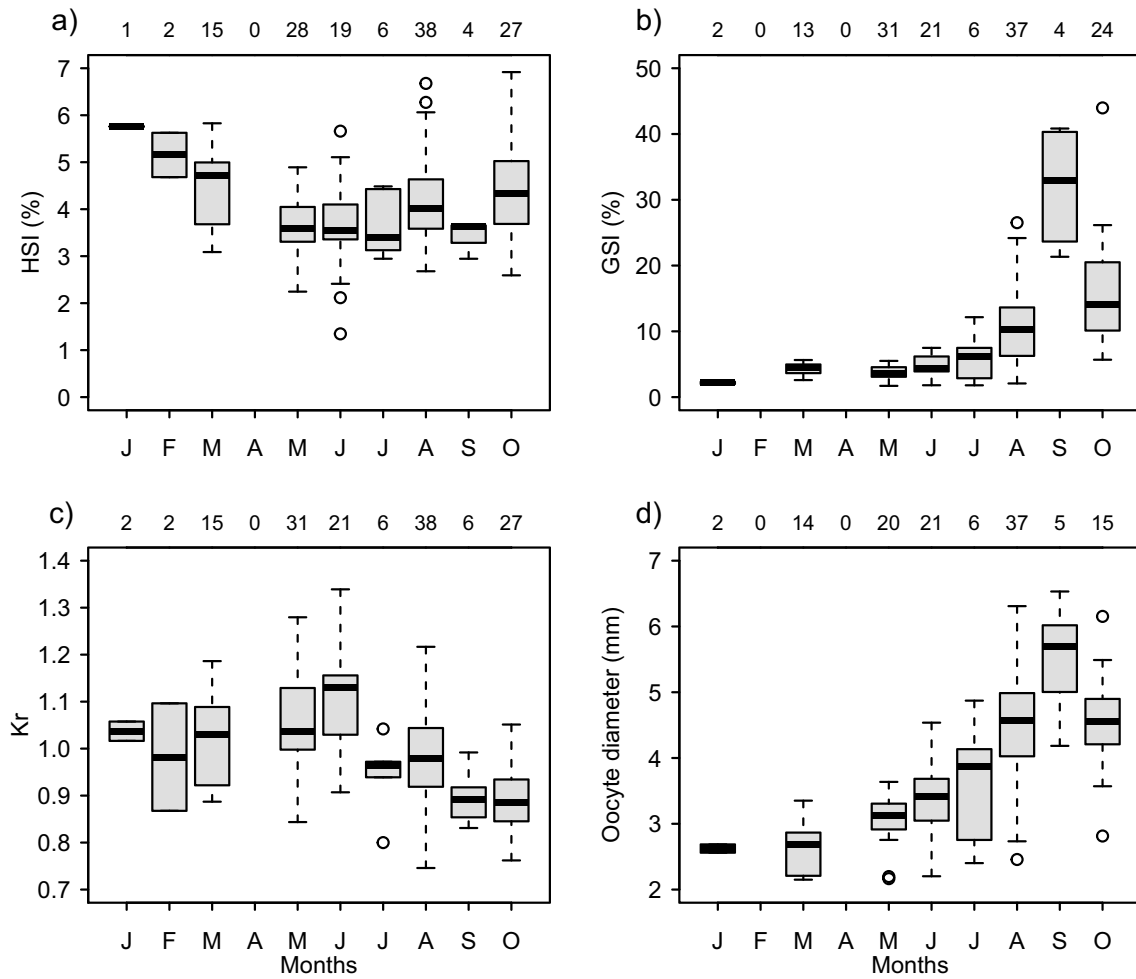


Fig. 6 Monthly variation of **a** hepatosomatic index (*HSI*), **b** gonadosomatic index (*GSI*), **c** relative condition (K_r) and **d** average oocyte diameter. The number of fishes used for the calculation of each of these variables is indicated on the top of the individual figures for each month

Fig. 7 Evolution of the oocyte diameter by day of the year. The black line represents predicted values from linear regression where both mean of total length (*L*) and hepatosomatic index (*HSI*) were used with day of the year. The grey lines represent predicted values from liner regression where one standard deviation were either subtracted from *HSI* and *L* or added (Table 2). The dotted lines represent 95% confidence interval estimated when mean values of *L* and *HSI* were used

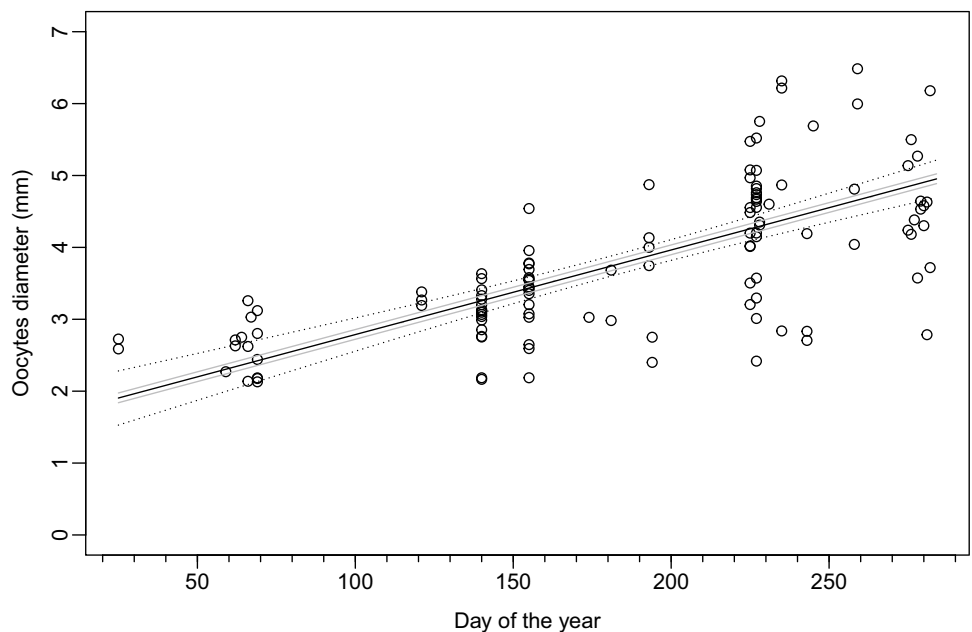


Table 5 Number of pre-spawning and spent female spotted wolffish (*Anarhichas minor*) from commercial catch and the Icelandic Autumn Groundfish Survey (AGFS) by month

Month/AGFS	Pre-spawning	Spent	Date range	Ratio spent (%)
August	40	7	13–22*	18
September	17	72	1–24	80
October	0	41	7–29	100
November	0	91	8–30	100
October AGFS	38	101	1–17**	72

Data range for samplings dates, Ratio spent (%) percentage of spent females from total number of pre-spawning and spent females caught

*Only for spent

**Only for pre-spawning

or body condition indices are presumed to reflect the energy reserves of the fish, but these different indices are not equivalent measure of bioenergetic condition (Pardoe et al. 2008). Protein and lipids, which can be both utilised for energy are stored differently in different species e.g. in Atlantic cod (*Gadus morhua*), most of the energy reserved for oocyte production, in the form of lipids, are stored in the liver while proteins are stored in the carcass (Black and Love 1986; Lambert and Dutil 1997). Whereas, in many flatfish species the liver is small, with little fat content and the main storage of lipids and protein is in the carcass (Tyler and Dunn 1976; Dawson and Grimm 1980). The mean hepatosomatic index of *A. minor* was about 4 which is between that of Atlantic cod and many flatfish species, such as winter flounder (*Pseudopleuronectes americanus*), which indicates that *A. minor* is storing proportionally more lipids in its liver than many flatfish species but less than Atlantic cod (Tyler and Dunn 1976; Pardoe et al. 2008). Despite *A. minor* using muscle

as an energy store for lipids, the effect of K_r on fecundity was low. Part of the reason for this may be that the muscle water content may be variable between individuals which could mask the effect of condition i.e. some individuals with a high K_r , may simply have a high water content in their muscle (Lloret et al. 2014). In some species, the influence of body condition and hepatosomatic indices on fecundity peaks several months before spawning or at the beginning of vitellogenesis (Skjæraasen et al. 2006; Kennedy et al. 2007). This was not detected in the present study i.e., time did not influence the effect of condition on fecundity, perhaps due to low sample size during early vitellogenesis (Table 1).

In many species, fecundity decreases during ovary development due to a portion of the oocytes becoming atretic, this is known as downregulation, and refines the number of developing oocytes to bring fecundity in line with available energy reserves (Kurita et al. 2003). If ovary development is synchronized across the population, then it would be expected to see differences in fecundity at different points in time. However, none of the time variables, year, month, day of the year or period, were included in any final model to predict fecundity. This suggests that there was no temporal difference in fecundity indicating that levels of atresia were low. Although we did not assess atresia directly i.e., using histology, we assumed that atresia can be deduced indirectly using changes in fecundity over time. However, as sample sizes were low, it may be that such effects could not be detected. Many species typically exhibit an “atretic window” during development where atresia is at its highest intensity (Kjesbu et al. 1998; Óskarsson et al. 2002; Kennedy et al. 2007; Skjæraasen et al. 2013). Whether *A. minor* exhibit such a window is unknown, but in Atlantic wolffish the atresia primarily occurred during May–June when the mean oocyte diameter is about 2.1 mm and 2.7 mm,

Fig. 8 Location of capture of pre-spawning and spent female spotted wolffish (*Anarhichas minor*) from the annual autumn groundfish survey (AGFS) (filled circles) from 2006 to 2023. Crosses indicate stations where no pre-spawning or spent individuals were caught. Open circles show locations of spent individuals captured in the commercial fishery in October in the period 2008 to 2022

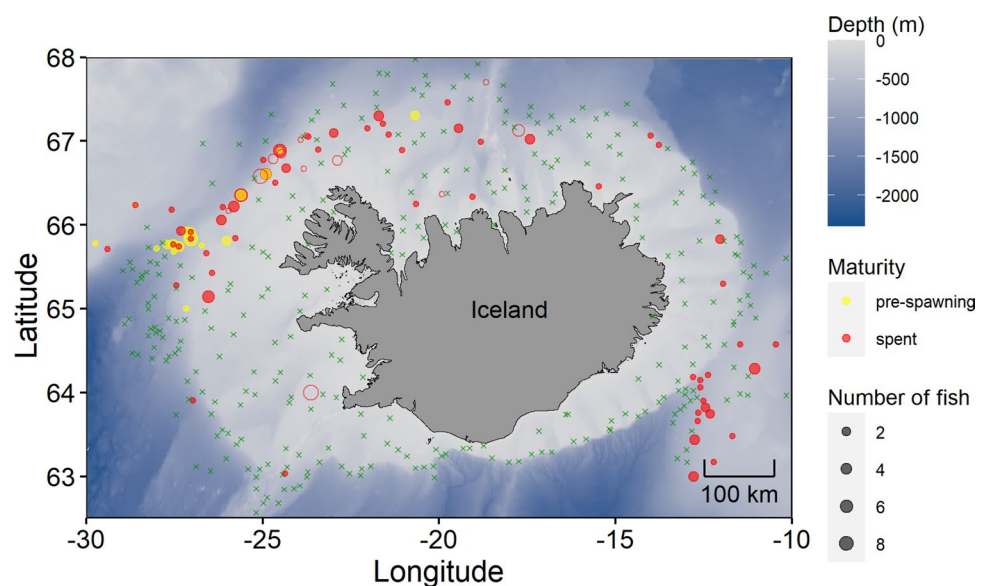
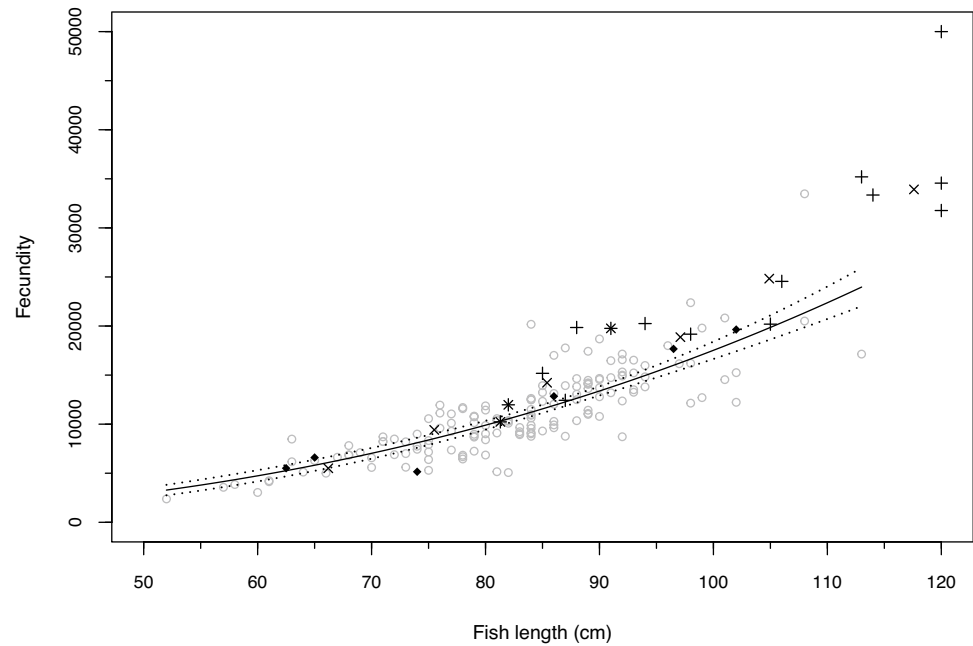


Fig. 9 Fecundity of present study compared to other studies. The open circles (o) are data collected during the present study; (+ and *) represent data from the Barents Sea from Maslov (1944) and Gusev and Shevelev (1997), respectively; (♦) represent combined data from the Barents Sea to west Greenland (Beese and Kändler 1969) and (*) from Canada, (Templeman 1986). The line represents the power function correlation ($F=0.134 \times L^{2.559}$, $R^2=0.74$) of data in present study and the broken black lines represent the 95% confidential interval



respectively (Gunnarsson 2017; Marine and Freshwater Research Institute (Iceland), unpublished data). If, *A. minor* have a window at a similar size, then this could explain the lack of downregulation as there were only a small number of fish at this stage of development. In addition, from June to October, synchronization on ovary development was low as indicated by the wide range of OD in these months (Fig. 6d). Atresia in, *A. minor* has been confirmed in captive fish but was only found in first-time spawners (Dupont Cyr et al. 2018). It certainly could be the case that, with, *A. minor*, there is little or no atresia. The magnitude of atresia within a species varies greatly and can depend on factors such as food availability, area and year, it also likely to vary across species due to life-history characteristics specific to each species (Tyler and Dunn 1976; Kjesbu et al. 1998; Óskarsson et al. 2002; Kennedy et al. 2008; Skjæraasen et al. 2013; McElroy et al. 2016).

Extrapolating oocyte sizes backwards suggests that vitellogenesis in, *A. minor* begins in December. Therefore, the duration of vitellogenesis would be in the range 8–10 months. This is a rather prolonged period for vitellogenesis compared to e.g., Atlantic wolffish or Atlantic cod where duration of vitellogenesis is about 4–6 months, but similar to lumpfish (*Cyclopterus lumpus*) where vitellogenesis is at least 8 months (Tveiten and Johnsen 1999; Yaragina 2010; Gunnarsson 2017; Kennedy and Ólafsson 2020).

Based upon the *GSI* and OD, data from commercial and AGFS catch, spawning appears to occur during August to October with peak of spawning in September. Spawning in August and September agrees with Gunnarsson et al. (2008) who documented spawning fish which were caught in the commercial fishery in August and September.

However, of the mature fish landed from the fishery during 20th of September to November, all of them were spent despite pre-spawning fish being caught in AGFS during October, which is like the results in present study (Table 5). This mismatch between the fishery and the surveys suggest that maturity stages are not homogenously distributed through the population and given the mobility of the fishery, and the uncertainty around the migration timing and routes, it is difficult to be certain when the “main” or “peak” spawning occurs. Spawning season at Iceland begins later than in Russia, Norway and Canada, where spawning is mainly in July–August (Barsukov 1959; Østved 1963; Templeman 1986), but according to this study the main spawning in Iceland is from middle of August to middle of October.

In conclusion, there was a negative relationship between relative fecundity and length in July–October. There was no evidence to suggest intra- or inter-annual differences in fecundity, indicating little or no atresia during vitellogenesis in *A. minor* and thus estimates of fecundity collected at different points during vitellogenesis or different months of the year can be combined. Hepatosomatic index and condition had relatively small influence on fecundity. Spawning season is from middle of August to middle of October.

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Author contributions ÁG designed the study, carried out the laboratory work, analysed the data and wrote the first draft. JK participated in the analysis of data and writing of the manuscript, BE performed the statistical analysis of the data and participated in the writing. ARG data handling and reviewing the manuscript.

Data availability The data used in the current study is available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethical approval The sampling was carried out in strict accordance with the relevant Icelandic legislation on animal welfare for Welfare of Experimental Animals. The authors therefore declare that all applicable international, national and/or institutional guidelines for sampling, care, and experimental use of organisms for the study have been followed.

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