Large annual variation in the amount of skipped spawning for female Northeast Arctic haddock *Melanogrammus aeglefinus*

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ABSTRACT

Although the phenomenon of skipped spawning has been described in numerous fishes, time-series are scarce. We used the presence of post-ovulatory follicles in histological gonad slides from females not developing oocytes for Northeast Arctic (NEA) haddock *Melanogrammus aeglefinus* from 2009 to 2012 to construct a length-based statistical model giving the probability that a non - developing female was skipping spawning, as opposed to not being sexually mature. This model was then applied on demographic winter survey data from the Barents Sea from 1989 to 2014. This indicated large annual variation in skipping numbers. Comparing these survey estimates to the total annual ICES stock numbers, we found that skipping peaked in the years 1994–1996 and 2009–2014, when the median yearly estimate of skipped spawners was 20–45 % of all females aged $\geq$ 3 years. In contrast, only $\sim$ 3 % of females at age $\geq$ 3 years skipped spawning in 2007. The proportional representation of skipped spawners at the stock level appeared linked to stock energy reserves with more skipping occurring when energy levels were low. Skipping also became more frequent with increasing population age, i.e. when immatures were less abundant, although the very largest/oldest fish tended to spawn. Because the proportion of NEA haddock that skips spawning is variable and can be high, understanding variation in this phenomenon and its drivers may improve population dynamic models.

1. Introduction

Skipped spawning, i.e. the phenomenon that animals do to not take advantage of every spawning opportunity following initial maturation (*sensu* Rideout et al., 2005), has received attention in marine fish in recent years (e.g. Jørgensen et al., 2006; Rideout et al., 2006; Rideout and Tomkiewicz, 2011; Skjæraasen et al., 2012). There are two main theories as to why skipped spawning occurs, although these are by no means mutually exclusive. The first argues that individuals have insufficient energy reserves to complete maturation and spawning, and therefore skip spawning to build reserves for the next reproductive opportunity, typically the next year in seasonal environments (Rideout et al., 2005). The second theory argues that skipped spawning represents an adaptive strategy for allocating energy towards length growth, which enhances fecundity later in life as well as individual lifetime reproductive success, although it comes at a cost in terms of current reproduction (Jørgensen et al., 2006; Folkvord et al., 2014).

Rideout et al. (2005) reported that skipped spawning had been described in more than 30 species. Since then, it has been reported in a variety of new species including sablefish *Anoplopoma fimbria* (Rodgveller et al., 2016), humpback chub *Gila cypha* (Pearson et al., 2015, 2016), grey mullet *Mugil cephalus* (Fowler et al., 2016), and giant grouper *Epinephelus lanceolatus* (Clua et al., 2015). The observable characteristic that allows the identification of skipped spawning varies from system to system. In populations that migrate to spawning grounds, individuals of adult size or age that stay behind at the feeding grounds are often assumed to skip spawning (e.g, Trotter et al., 2012; Young et al., 2014; Clua et al., 2015; Fowler et al., 2016). In other cases, visual gonad inspection can conclude that ovaries or testes are non-developing but have a distinct appearance from having spawned earlier in life (e.g, (Yaragina, 2010). By making histological sections and investigating these under the microscope, it may be possible to find post-ovulatory follicles in an otherwise non-developing gonad (e.g. Skjæraasen et al., 2009, 2015). For some cold-water teleosts these can

last for more than a year and are then interpreted as an unequivocal identifier of skipped spawning (Witthames et al., 2009) if found at a time when the fish should display maturing oocytes if spawning in the present year.

A common denominator for most investigations into skipped spawning is that they describe one or at most only a few years of data. Often this is sufficient to establish the occurrence of skipped spawning and perhaps estimate population-level frequencies, but often falls short of identifying drivers or the degree of variation between years. This would typically require time-series of some duration in order to sample environmental and trait variation, and thus gain deeper insight and reveal potential correlations.

For the Northeast Arctic (NEA) haddock *Melanogrammus aeglefinus,* an ICES stock name given to a putative population of haddock in the Northeast Atlantic, a short time series covering four years has been established (Skjæraasen et al., 2015). The NEA haddock has its main feeding grounds and nursery areas in the Barents Sea, whereas maturing adults migrate west and south to spawning areas in the Norwegian Sea (Bergstad et al., 1987; Olsen et al., 2010). Spawning occurs from the middle of March to early June, whereafter adults return to the Barents Sea in late summer. Prevailing currents from south transport the early life history stages from the spawning grounds to the Barents Sea nursery areas (Bergstad et al., 1987). There is a distinct cohort effect in the geographical distribution at the feeding grounds in the Barents Sea, with older fish being further west and southwest (Landa et al., 2014). In addition, the distribution both at the feeding grounds and spawning grounds seem to be density dependent (Landa et al., 2014; Langangen et al., 2018), with distributions tending to extend more east and northwards at high densities.

Skjæraasen et al. (2015) reported frequent skipped spawning in the NEA haddock in the years 2009–2012 based on histological analyses and the presence of post-ovulatory follicles. Here we build on these results to principally construct a statistical model for the probability of skipping spawning as a function of length, which we then apply to demographic survey data covering a longer period to estimate the frequency of skipped spawning in the NEA haddock from 1989 to 2014, while accounting for the uncertainty on our original regression. We then test if there is any association between our median yearly estimates of skipped spawning and i) a proxy for energy availability for the stock and ii) a proxy for stock demography, aiming to shed some initial light on the potential underlying causes of skipped spawning for the NEA haddock.

2. Materials and methods

In the following sections, we present the data sources for our study of skipped spawning in NEA haddock from 1989 to 2014 (2.1). Moreover, we present the laboratory analysis on subsampled fish from 2009 to 2012 (2.2) that was used to detect POFs and thereby separate immature fish from skippers. In 2.3 we present the data analysis, i.e., estimation of skipping probability as a function of length based on the subsampling from 2009 to 2012 and the upscaling of these numbers to the population level (2.3.1) for the whole time-series (1989–2014). Finally, we conduct a time-series analysis of the resulting population level data of skipped spawning and we present the covariates used in this analysis in 2.3.2.

2.1. Data collection

Haddock are sampled annually during a winter survey, which takes place at the feeding grounds of the NEA haddock in the Barents Sea in February-March (Fig. 1). We used data from this survey for the years 1989–2014 to investigate the phenomenon of skipped spawning. Since 2000, the winter survey has been a collaboration between the Institute of Marine Research (IMR, Norway) and the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Russia), except

2006–2007 and 2016 when the surveys were conducted with Norwegian vessels only, as it was up until 1999. The survey generally covers the NEA haddock distribution well within our study period (1989–2014), main exceptions are 1997, 1998, and in 2007 when the easterly, Russian part of the Barents Sea was not sampled, and 1999 when sea ice limited access to the same area (Fig. 1). The survey is a combined bottom trawl and a trawl-acoustic survey. At all stations where haddock is found (Fig. 1), individual fish are sampled and combined with acoustic estimates of fish abundances over larger areas (strata) to give population level abundance estimates. At each trawl sampling station, all haddock are measured for length, and for every 5-cm length group the first sampled individual fish are also subjected to more detailed measurement, i.e. it was biologically subsampled (400–1100 fish each year from 1989, Table 1). This subsampling included sexing and a macroscopic coding assigned to the gonad based on its physical appearance: code 1 – immature fish; 2 – developing fish; 3- spawning fish; 4 resting fish; 5 uncertain (this code is typically used if it is difficult to distinguish between 1 and 4). For the years 1989–2014, these gonadal data allowed us to divide fish into those developing (D) gametes for spawning (codes 2 and 3), and those not developing gametes (ND; codes 1, 4, and 5). Since 2001, gonad and liver weights have also been measured as part of the biological subsampling (Table 1). Because haddock store lipids in the liver, relative liver size can serve as a proxy for the individual's energy reserves. In 2009–2012 samples from female gonads (from fish ≥ 35 cm, ≥ 30 cm in 2012, $n = 1386$) were stored on buffered formaldehyde and taken back to the laboratory for image and histological analyses, for which the latter included examining the gonads for presence of post-ovulatory follicles (POFs), an unequivocal marker of past spawning activity (see Skjæraasen et al., 2012, 2015 for further details). Together with two other surveys, the ecosystem survey conducted in the Barents Sea from August to early October and the Russian survey conducted from early October to the end of November, the winter survey provides input to the ICES population model for NEA haddock.

2.2. Laboratory analysis

We conducted detailed laboratory analyses on 1386 individual gonads from female fish sampled in the period 2009–2012. First, we used image analysis to establish which females were developing gametes for the upcoming spawning season ($n = 534$) and which ones were not ($n = 852$). The majority ($n = 1011$) of these female gonads were subsequently processed for histology using standard protocols for resin embedding (Technovit 7100), producing 4 mm sections stained with 2% toluidine blue and 1% sodium tetraborate. Each of these histological sections was inspected in the microscope and presence or absence of POFs was noted. Detection of a POF in a ND gonad ($n = 755$) is unequivocal evidence of past spawning activity in a fish that will not spawn the current year, i.e. skipped spawning. Based on the histological sections, ND females were thus subdivided into skippers (POFs present) and immatures (POFs absent). See Skjæraasen et al. (2012) and Skjæraasen et al. (2015) for further details.

2.3. Data analysis

Our goal was to calculate the yearly abundance of skipped spawners for the NEA haddock and estimate what proportion this constituted of the total stock while taking into account both uncertainties in our estimates of skipped spawners and also in the total stock size reported by ICES. To the former, we constructed a statistical model based on the POF-sampling years that estimates the probability of a female being a skipped spawner based on the potential proxies body length and energy reserves (relative liver size). We then applied the resulting relationship to the whole time-series of demographic and phenotypic data from the winter survey (see *Calculation of skipped spawning* below), and then scaled this up to the annual stock numbers published by ICES (ICES,
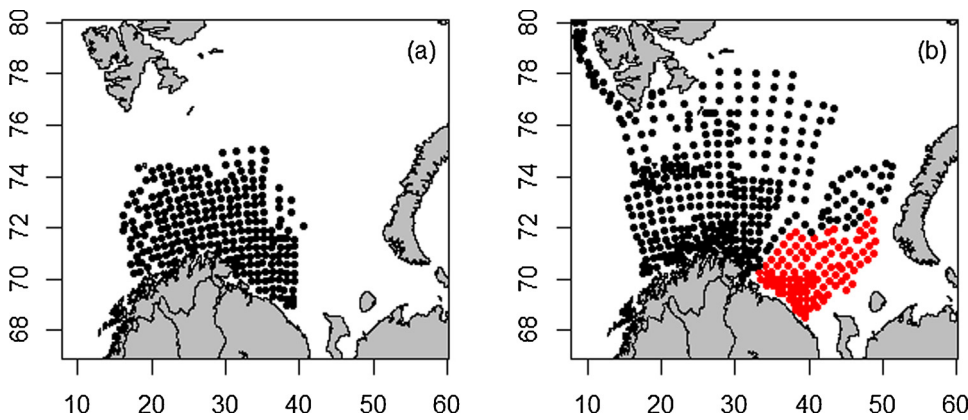
Fig. 1. The IMR-PINRO winter survey. Sampling stations for (a) 1999 and (b) 2014. Black symbols indicate stations sampled by Norwegian vessels, while red symbols denote stations sampled by Russian vessels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 1
Number of female haddock for which there exist a macroscopic maturity stage code and gonad weights in the different years.

Year	Macrocopic maturity stage (n)	Gonad weight (n)
1989	443	
1990	416	
1991	447	
1992	450	
1993	524	
1994	530	
1995	598	
1996	483	
1997	330	
1998	344	4
1999	290	
2000	446	
2001	582	171
2002	586	377
2003	661	378
2004	718	420
2005	777	435
2006	711	414
2007	679	409
2008	937	367
2009	1016	361
2010	958	522
2011	897	429
2012	728	467
2013	709	376
2014	1029	572

2019) to determine levels of skipped spawning at the stock level and across time. We also evaluated the relative role of stock energy reserves and demography (age) in influencing the annual value estimated for skipped spawning by constructing two yearly proxies representing each of these facets and regression them against our yearly median estimates of females skipping spawning (see *Proxies of skipped spawning* below).

2.3.1. Calculation of skipped spawning

By combining the information from length distributions at each sampling station during the winter survey and the corresponding biomass estimate from the acoustic survey taken at other times of the year, biologically subsampled fish are given an index value ($A_{i,y}$) which in effect translates to an abundance estimate (reported as units of 1000 individuals). This allows scaling up from individual-level observations to stock-level estimates. In brief, the winter survey survey includes a dedicated, extensive bottom trawl sampling programme with more than 100 geographical locations, i.e. trawl stations, sampled annually (Fig. 1). At each trawl station the biological sub-sampling is stratified into 5-cm length groups with one sampled specimen per said length group. Individual information, i.e., length, weight, age (from otoliths), sex, liver weight, gonad weight, and maturity stage, is collected from

the sampled individuals. It is this information that was subsequently used to characterize the estimated population present here. To up-scale this biometric information from the individual to the population level, statistical weighting factors, w_j, were assigned to each single fish observation. These weighting factors were calculated as the inverse of the sampling probability, i.e. the inclusion probability (Horvitz and Thompson, 1952). Hence, the probability of sampling a given fish was set equal to the probability of the trawl sample itself, swept area relative to total survey area, multiplied with the probability of being sub-sampled from the catch in question. This weighting principle was used in all analyses below. Further details about this procedure are given in the supplementary materials of (Skjæraasen et al., 2012) and (Skjæraasen et al., 2015) and therefore not reiterated here.

We calculated the total abundance (N) in year y of the three maturity categories immature ($N_{I,y}$), skipping ($N_{S,y}$), and developing ($N_{D,y}$) fish. The latter category is simply the sum of all abundance indices for all fish in category D (macroscopic code 2 and 3). In order to separate between immature and skipping fish, we also need additional information on the probability of a given ND fish skipping spawning. To get this, we started by estimating the overall likelihood of a ND fish being a skipped spawner versus an immature as a function of the potential linear predictors *length* and *relative liver weight* (hepato-somatic index, $HSI = $ Liver Weight·Total Weight^{-1}·100 %). We fit this model using only the data from the years with histology analyses of POFs, 2009–2012. First, we employed the following initial logistic regression model;

$$P_{skip} \sim Length*HSI \tag{2}$$

where P_{skip} is the likelihood of a ND fish being a skipped spawner, *Length* is the total length (cm) of the fish and *HSI* is relative liver weight. The initial model allowed an interaction between these explanatory terms. Each individual measurement was assigned a weighting factor, w_i, according to the abundance of this length class at that specific trawl station (this is linked to, but not the same as the index value for the same fish described below; for details see electronic supplement to (Skjæraasen et al., 2015)). We then simplified the initial model using the Aikaike Information Criterion corrected for small sample sizes ($AICc$,) with the of use of the *dredge* command of the *MuMIn* (Barton, 2016) library of R to find the model with the lowest $AICc$ score.

The logistic regression has the following general form:

$$\log(\frac{p}{1-p}) = \alpha + \beta x \tag{3}$$

where $\alpha + \beta x$ is the so-called linear predictor of the logistic regression. In our case the final model fit based on Eq. (2) with p then denoting the probability that a fish was skipping spawning as a function of the predictors retained in the final regression. To estimate the uncertainty in the probability of a certain fish to skip spawning as a function of the selected predictors, we performed a non-parametric bootstrap of the

logistic regression. The bootstrap was performed by resampling the individual fish data that had available POF information from the years 2009–2012 1000 times with replacement using the *boot* library in R (Canty and Ripley, 2019). We then allowed the uncertainty associated with the regression to propagate to the estimates of abundance of skipping fish by performing the upscaling to the population level (see below) independently for each bootstrap sample.

The abundance of developing ($N_{D,y}$), skipping ($N_{S,y}$), and immature ($N_{I,y}$) females in year y was calculated as

$$N_{D,y} = \sum_{i=1}^{N_y} A_{i,y} d_{i,y} \tag{4}$$

$$N_{S,y} = \sum_{i=1}^{N_y} A_{i,y} p_{skip,i,y}(1 - d_{i,y}) \tag{5}$$

$$N_{I,y} = \sum_{i=1}^{N_y} A_{i,y}(1 - p_{skip,i,y})(1 - d_{i,y}) \tag{6}$$

where N_y is the total number of sampled fish in year y, $d_{i,y}$ describes the developmental status of the fish i and has value 1 if the fish is developing gonads for spawning (i.e. macroscopic code 2 or 3) and 0 otherwise (i.e. macroscopic code 1, 4, or 5), and $p_{skip,i,y}$ is the estimated probability that the non-developing fish i was a skipped spawner in year y as inferred from the statistical model based on its length and liver weight (Eq. (2)). $A_{i,y}$ is the aforementioned abundance index for fish i in year y, i.e. the index derived from combining length distributions at each sampling station with acoustic data giving a numerical estimation of the abundance of this individual's phenotype in the population (for further description see (Skjæraasen et al., 2012, 2015). We only focused on fish $\geq$ 20 cm given that fish below this size generally are not sexed or macroscopically staged. Further, because (Skjæraasen et al., 2015) did not examine females < 30 cm for POFs, fish staged as ND below this length were considered immature. Some indexed fish lacked information about sex and/or gonadal stage (< 1 % of the total index across years). The index values for these fish were assigned based on 5-cm length-group probabilities calculated by pooling all data across all sampling years where both sex and staging information were available.

ICES report the estimated numerical abundance of NEA haddock for ages 3 and above annually. To estimate the occurrence of skipped spawning at the population level we calculated the ratio of annual number of skipping fish ($N_{S,y}$) to the total annual stock numbers by age published by ICES (ICES, 2019) and denoted this the proportion of the population of females $\geq$ 3 years that where skipping spawning or $Skip_{pop}$. Given that the ICES stock numbers are published for both sexes combined this number was divided by two to get the assumed number of females. We estimated the uncertainty in this ratio by assuming independence between $N_{S,y}$ and total annual stock numbers and by combining the bootstrap samples for $N_{S,y}$ with a set of random samples (1000) of total stock numbers drawn from the confidence interval of the estimated stock size as reported by ICES (ICES, 2019).

Note that the present approach of calculating the numbers of skipped spawners is slightly different from the approach used on the same data in (Skjæraasen et al., 2015). There, image analysis and histology were first used to classify females into D and ND females, after which a discriminant analysis suggested that relative gonad size, *GSI*, could be used to accurately discriminate between D and ND. It was then found that the GSI classification closely matched the macroscopic classification in 2010–2012, and thus the macroscopic classification was used for the whole dataset for these years (Skjæraasen et al., 2015). For 2009 GSI values were used to classify females into ND and D fish (Skjæraasen et al., 2015). Length- (or age-) group specific proportions of fish developing, skipping, or being immature were then extrapolated to all data pertaining to that particular length (or age)-group for each year. Fish of size below the sampling range, $\leq$ 35 cm in 2009–2011 and $\leq$ 30 cm in 2012, were excluded when estimating the annual number of

skipped spawners in (Skjæraasen et al., 2015).

2.3.2. Proxies of skipped spawning

As outlined in the introduction, one hypothesis is that individual length or energy reserves affect the likelihood of skipping spawning. To tentatively evaluate these hypotheses, we first compared the hepato-somatic index of ND and D females in the winter survey by an ANOVA test. We then constructed two proxies; one proxy for stock energy levels (E_y) and one proxy for stock age ($\bar{a}_y$). These proxies were then regressed against the proportion of skippers at the stock level ($Skip_{pop}$). The values for $Skip_{pop}$ were $\sin^{-1}$ square root transformed before conducting the regression. Given that we *a priori* expected the years with no coverage in the Russian part of the Barents Sea to produce lower estimates of skipped spawners, we first performed the above regression including all years, and then by excluding the years 1997–1999, and 2007. The proxies themselves were constructed in the following way;

We first calculated the stock-level weight-at-age anomaly (E_y) for each year y on a relative scale. E_y was calculated to reflect how the weight-at-age of fish in a given year compared to the long-term average. A value of 0.1 indicates that fish were 10 % heavier that year compared to the long-term median, whereas a value of –0.1 indicates that fish weighed 10 % less that year. E_y was calculated by using the ICES stock assessment numbers (ICES, 2019; Table 4.6 (stock weight-at-age) and 4.13 (stock numbers-at-age)) in the following way

$$E_y = \frac{\sum_{a=3}^{a_{max}} N_{a,y} \left(\frac{m_{a,y} - \bar{m}_a}{\bar{m}_a} \right)}{N_y} \tag{7}$$

where $N_{a,y}$ is the abundance of fish in age class a in year y, $m_{a,y}$ is weight at age for age a in year y, and $\bar{m}_a$ is the median weight at age a during our study period. N_y is the total abundance of fish aged $\geq$ 3 in year y. We used the ICES numbers given that these should reflect the annual values for the whole stock and not just the fish present in the Barents Sea during the winter survey.

Mean stock age, our proxy of demography, was calculated as ($\bar{a}_y$);

$$\bar{a}_y = \frac{\sum_{a=3}^{a_{max}} a N_{a,y}}{N_y} \tag{8}$$

where a denotes age. All analyses and graphs were made with the use of R v 3.13 (R CoreTeam, 2016) using the base, *ggplot2* (Wickham, 2016), *MuMIn* (Barton, 2016) and *boot* (Canty and Ripley, 2019) libraries.

3. Results

3.1. Skipped spawning

The selected logistic regression model included *length* as the only significant explanatory variable of the likelihood of a ND female being a skipped spawner based on the POF observations (Table 2, Fig. 2a,b). Based on the winter survey data, the proportion of D females generally increased with female length (Fig. 2c,d). However, there was some variation in these proportions between years, especially in the larger length groups (Fig. 2c). Also, the proportional representation of immature, skipping, and developing females from the winter survey in the Barents Sea varied considerably through our study period (Fig. 2d). In terms of absolute abundance, skipping females were particularly abundant in two periods, 1994–1996 and 2008–2014 (Fig. 3a).

Table 2
Logistic model fit. Length was centered at the mean observed (44.5 cm) in the analyses.

| Variable	Estimate	SE	df	z-value	p
Intercept	1.00920	0.26235	753	3.847	< 0.001
Cen Length	0.25686	0.05314	753	4.834	< 0.00001
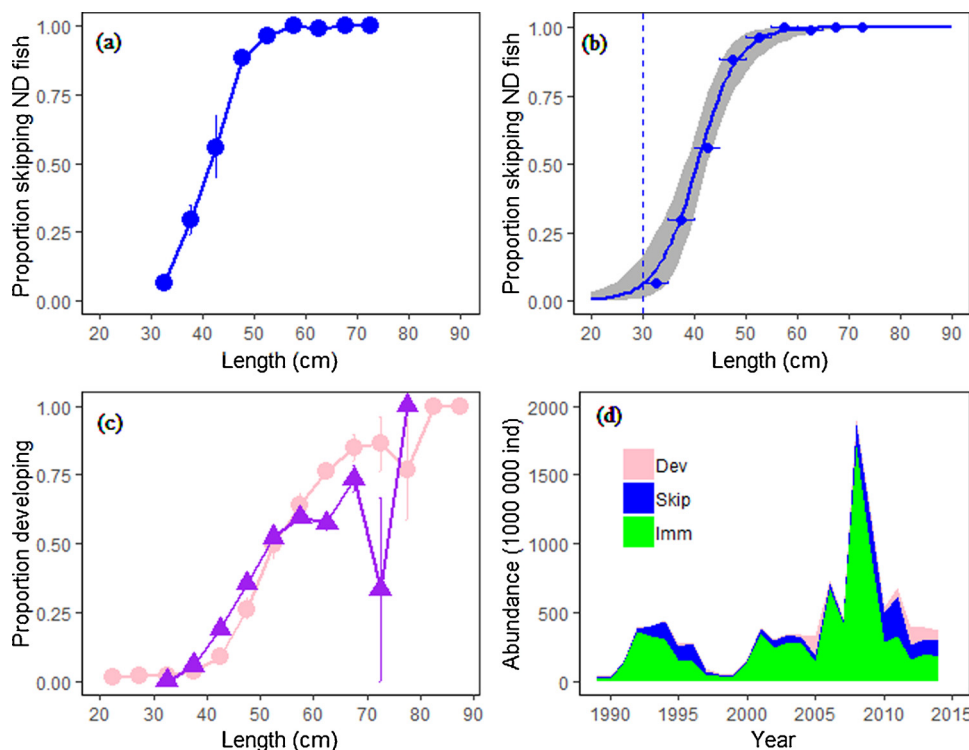
Fig. 2. (a) Observed proportions of ND females from the winter survey in the Barents Sea that were skipped spawners (i.e. non-developing but had reproduced before) in our sampling years 2009-2012, based on the presence of post-ovulatory follicles (POF). Points represent the mean value across years for every 5 cm length group from 32.5 cm while error bars represent variance. (b) Fitted probability line for results of the logistic regression given in Table 2. Note that we only had post-ovulatory follicle (POF) observations for fish ≥ 30 cm and values given below these lengths are extrapolated from the statistical model. In the calculation of skipped spawners all fish below this length were deemed immature. Points represent the actual average proportions calculated for each 5 cm length group, given as the median value for that length group with horizontal error bars indicating the maximum and minimum size fish in each length group. Shaded area indicates uncertainty of estimated line as determined from bootstrap analyses. (c) Proportion of females from the winter survey in the Barents Sea developing gonads at length: i) in our sampling years 2009-2012 (triangles, purple line); and ii) in the whole study period 1989-2014 (circles, pink line). Symbols represent mean values and error bars the variance. (d) Estimated abundances of immature, skipping and developing females in the Barents Sea using phenotypic data from the winter survey 1989-2014 and the statistical model to separate non-developing fish into immatures and skipped spawners. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

3.2. Population level occurrence and proxies of skipped spawning

We found that the proportion of females ≥ 3 years that were skipped spawners ($Skip_{pop}$) varied significantly between years even when accounting for the uncertainty in the estimated numbers of skippers and in the stock estimates themselves. The highest median yearly estimates were found in 1996 and 2011 (40–45 %) and the lowest in 2007 (∼3 %) (Fig. 3b). D females had significantly larger

livers than ND females for all years where this information was available (p < 0.0001, Fig. 4). The population level occurrence of skipped spawning (median estimate) was negatively related to relative weight at age, as reduced to the single annual value E_y (p < 0.001, Table 3, Fig. 5a), and positively associated with mean age (p < 0.05, Table 3, Fig. 5b). Combined, these two variables explained 35 % of the variation observed in skipped spawning at the stock level (Table 3). When excluding the years when the easterly Russian part of the Barents Sea was
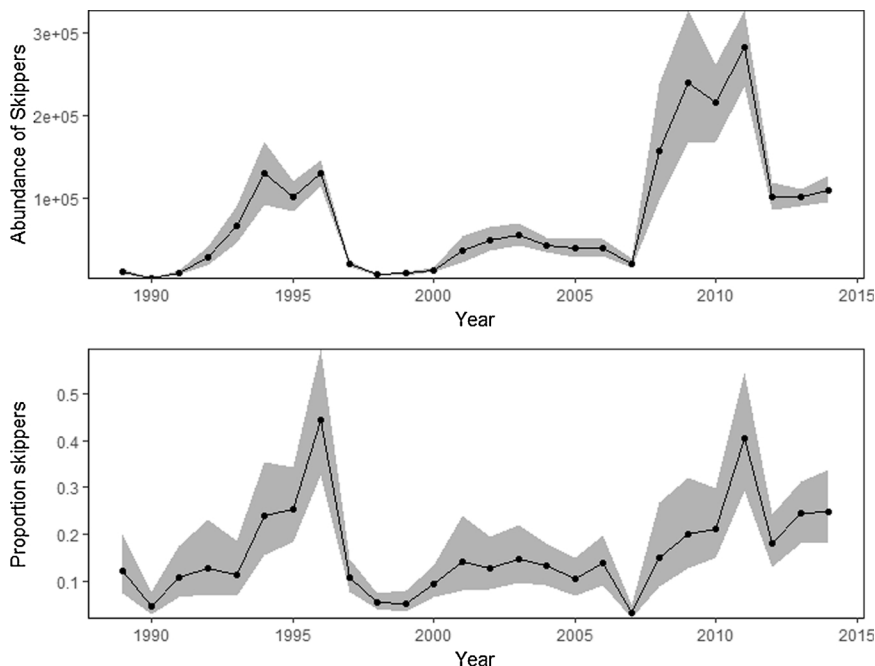
Fig. 3. (a) Total yearly abundance of skipping female haddock as calculated from the winter survey. (b) Calculated proportion (by abundance) at the population level that are skipping spawning. All numbers consider only female haddock of age ≥ 3 years. Shaded areas represent bootstrapped confidence intervals.
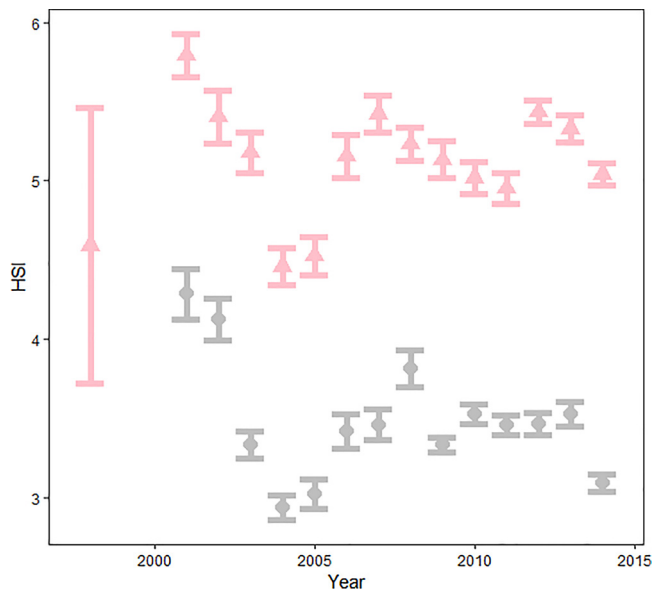
Fig. 4. Relative liver weight (HSI) of females developing (D; triangles) and not developing oocytes (ND; circles) for the upcoming spawning period. Data source [HYPHEN] the winter survey. Symbols represent mean values and error bars the variance.

not sampled (1997–1999 and 2007), both relationships were still statistically significant, and the amount of variation explained increased to 56 % (Table 3).

4. Discussion

By using demographic data and a detailed dataset on gonad histology, we infer the temporal dynamics of skipped spawning in female Northeast Arctic (NEA) haddock. Our results suggest considerable inter-annual variation in the relative amount of skipped spawning, with more than a 10-fold difference between years in the median yearly estimates. We also find links to potential drives of skipped spawning, particularly energy reserves.

Our study represents an important contribution towards increased understanding of skipped spawning by presenting a long time-series of skipped spawning in a gadoid fish. Studies on time-series of skipped spawning are scarce, with the exception of the work (Yaragina, 2010) on skipped spawning in NEA cod. Our analysis of the long time-series of skipped spawning in NEA haddock suggests that skipped spawning is negatively associated with stock energy reserves, implying that fewer fish skip spawning in years where fish are on average in good condition. Insufficient energy reserves have been proposed as one reason as to why skipped spawning may occur (Rideout et al., 2005, 2006; Rideout and Tomkiewicz, 2011), hereafter referred to as 'energy-constrained skipped spawning'. Like the present study (Fig. 4) it was found that females developing oocytes had significantly larger livers than females skipping spawning, a pattern that fits with 'energy-constrained skipped

spawning'for both NEA cod (Skjæraasen et al., 2012) and NEA haddock (Skjæraasen et al., 2015). These latter studies principally compared liver energy reserves of fish within the same year. Given that the lipid energy required to fuel vitellogenesis (Tyler and Sumpter, 1996) is drawn from the liver in gadoids (Lambert and Dutil, 1997), a buildup of liver energy is a prerequisite for female gadoid spawning. This leads to an alternative hypothesis: fish may have a big liver because they are prepared for spawning, rather than vice versa. Cause and effect may therefore be difficult to establish from these data, as noted by (Skjæraasen et al., 2015). The present results using an annual proxy of weight-at-age compared to the long-term average based on several surveys at different times of the year, therefore offers a more comprehensive view of the drivers of skipped spawning. On face value, our results indicate that low energy reserves lead to more skipped spawning and a possible link to density - dependent effects. When a stock is large in terms of numbers or biomass, there can be stronger competition for food, spawning sites, or during early phases of the life cycle. Density-dependent growth is commonly applied to marine teleosts to study variation in growth patterns and linked to phenomena such as maturation schedules (Forrester, 1995; Caley et al., 1996; Rose et al., 2001). It was also suggested to affect the number of female NEA cod participating in spawning (Skjæraasen et al., 2012). Given that there was a strong signal of weigh-at-age in our analysis, a study of effects of population biomass on energetics and skipped spawning would likely be informative. If there exists information about food abundance and experienced temperature, one could go a step beyond correlation towards truly understanding the underlying causation of skipped spawning. It should also be noted that if haddock have experienced good growth conditions and on average are long for their age in a given year, then the weight-at-age would be high, as well as the likelihood of skipped spawning among non-developing fish (as found by our regression on individuals with POF observations). The pattern of less skipped spawning can therefore not alone conclusively inform about the underlying mechanisms of skipped spawning but suggests interesting links with individual and stock-level size and energy reserves that need to be investigated further. There may also be considerable merit in looking further at individual level data on weight, length and energy reserves and not only population level proxies as done presently.

An alternative hypothesis for the drivers of skipped spawning, derived from life history considerations, is based on the observation that fecundity increases with size in fish. Hence, spending resources on growth will lead to larger size and higher fecundity in all future breeding seasons, at the cost of no reproduction in the season that is skipped. This can be referred to as 'life history-driven skipped spawning' (Jørgensen et al., 2006; Jørgensen and Fiksen, 2006; Shaw and Levin, 2013). It assumes that evolutionary considerations and trade-offs are the drivers of skipped spawning. Logically, whether to spawn or skip spawning is exactly the same life history distinction as whether to sexually mature or stay immature, a problem for which there is a wealth of empirical (e.g., Charnov, 1982; Trippel, 1995; Roff, 2002) and theoretical literature (e.g., Williams, 1966; Roff, 1984). In the evolutionary model for skipped spawning in cod, high food was predicted to lead to increased skipped spawning – the logic was that individuals would make the most of the good feeding conditions and

Table 3

Selected linear regression models for the proportion of skipped spawning at the population level as a function of population age ($\bar{a}_y$) and energy reserves (E_y). For the *Full Coverage* analysis, data from 1997-1999 and 2007 was omitted since the Russian part of the Barents Sea was not sampled during the winter survey in those years.

	Variable	Estimate	S. E.	t	p-value
All years	*Intercept*	0.06214	0.149889	0.041	0.96729
(R^2-adjusted =	$\bar{a}_y$	0.088183	0.032917	2.679	0.01340
0.35)	E_y	−0.694400	0.208993	−3.323	0.00296
Full coverage years (R^2-adjusted = 0.56)	*Intercept*	−0.01374	0.12412	−0.111	0.912994
	$\bar{a}_y$	0.09902	0.02735	3.620	0.001822
	E_y	−0.75810	0.16715	−4.535	0.000226
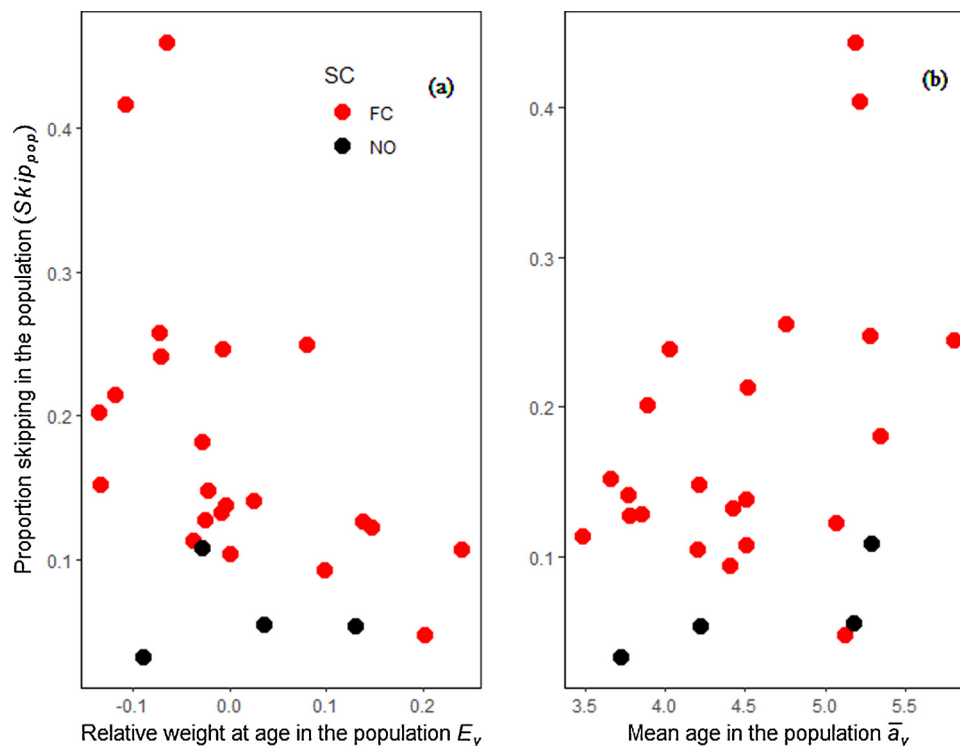
Fig. 5. Proportion skipping in the population ($Skip_{pop}$) plotted against (a) the observed relative weight at age compared to the long-term average, represented by the proxy for population energy reserves (E_y) and (b) mean age in the population ($\bar{a}_y$). Red dots denotes years were the winter survey used to estimate the number of skipped spawners had full coverage (Russian and Norwegian data) and black dots years where coverage was limited to the Norwegian part of the Barents Sea, see also Fig. 1. All numbers consider only female haddock of age ≥ 3 years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

not spend time away at the spawning grounds (Jørgensen et al., 2006). Temperature could also play an important role, as it is generally positively correlated with individual growth rate (Brown et al., 2004) but its effects on skipped spawning might be more complicated. If food is abundant, digestion and growth may be faster, but if food is scarce, metabolic losses may increase with temperature and starvation become a more imminent threat.

Our analysis also suggests a link to population demography in that relatively more skipping occurred when the average fish in the population was older. This makes logical sense in that a population dominated by very young fish will consists of mostly juveniles and hence immature fish, whereas a population of older fish will include more individuals that have spawned at least once and thus are potential skippers. Life history theory predicts that the adaptive advantage of skipping spawning decreases as fish get older (Jørgensen et al., 2006). Thus, we would perhaps expect a sigmoid or even parabolic relationship between population mean age and the likelihood of skipped spawning. We could find no indication of such patterns in the statistical analysis of our data. However, it is noteworthy that even in the winter survey data, clearly biased towards non-migrating, non-spawning fish, the very largest females tended to spawn (Fig. 3). Whether it is possible to trace life history predictions at the individual level in aggregated population patterns is also unclear as there are many compounded processes and observational uncertainties.

In this study, we used abundance estimates from the winter survey and compared this directly to the annual population estimates published by ICES (2019) to estimate population level frequencies of skipped spawning. It seems unlikely that large numbers of non-spawning fish would leave the Barents Sea feeding grounds, thus making it fair to assume that most skipping females are present in the Barents Sea at the time of the winter survey. As previously mentioned, together with two other surveys, the winter survey provides input to the ICES population model. This implies that the winter survey estimates,

and the ICES estimates are not truly independent. Despite this issue there is reason to believe that the general trends found in the present work are not spurious but represent important dynamics affecting reproduction in this stock. The large interannual variation in the numbers of females skipping spawning appears related to stock energy reserves, and by combining insights from multiple species and stocks it may be possible to further disentangle the underlying mechanisms that affect skipped spawning and its contribution to recruitment variation in fish.

CRediT authorship contribution statement

Declaration of Competing Interest

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.

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