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Fat dynamics at the onset of sexual maturation in Atlantic herring *Clupea harengus*: the dual-fuel powering used by 'maatjes' herring

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ABSTRACT: Energetic trade-offs between life-history traits, mediated by body reserves, vary across an individual's life. We quantified 2 fat stores in 3 life stages of Atlantic herring *Clupea harengus* to understand their importance for fuelling growth and reproduction. We determined how the magnitude of both stores changed with body size in immature, maturing virgin, and mature herring using 2 complementary sources of data: (1) validated industry data on muscle fat content in 'maatjes' (assumed here to represent maturing virgins) and mature herring from 2013 to 2021; and (2) scientific data on mesenteric fat index in immature, maturing virgin, and mature herring from 2004 to 2019. Maturing virgin herring had 3% higher muscle fat reserves than mature herring and larger mesenteric fat reserves than either immature or mature herring, illustrating the importance of both fat stores at the onset of sexual maturation. Smaller mature herring had more mesenteric fat than larger mature herring, suggesting that this store is important for fuelling somatic growth. The dual-fuel strategy adopted by maturing virgin herring allows the energetic demands associated with puberty and somatic growth to be met simultaneously. This distinctive allocation strategy contributes to the unique flavour and commercial value of the 'maatjes' herring delicacy.

KEY WORDS: Atlantic herring · Fat content · Life-history · Maatjes · Maturing virgin

1. INTRODUCTION

Limited and highly variable energy budgets require individuals to allocate surplus energy according to trade-offs between growth, reproduction, and survival (McBride et al. 2015). Immature individuals primarily use surplus energy for growth (Lloret et al. 2014); however, energy may also be stored to increase survival during unfavourable ecosystem conditions (Mogensen & Post 2012). Individual growth rates generally slow following sexual maturation, after which a large proportion of energy is used to fuel energetic demands associated with reproduction (Manabe et al. 2018). During periods of low energy availability, short-lived fishes with varying reproductive strategies can maintain population-level reproductive output at the cost of reduced growth and survival (Brosset et al. 2016). Fat is typically the main form of stored energy because it is energy-dense (Anthony et al. 2000) and labile (Lloret et al. 2014).

Atlantic herring *Clupea harengus* is a well-studied pelagic fish rich in omega-3 fatty acids, which contribute to a healthy human diet (Egerton et al. 2020). Herring store fat in both muscle tissue and mesen-

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teries. Mesenteric fat surrounds the intestines and is typically measured using a semi-quantitative index based on visual assessment of its magnitude (van der Lingen & Hutchings 2005). Although subjective and less accurate than biochemical or bioenergetic measures of fat content, fluctuations in the mesenteric fat index are consistent with annual reproductive cycles (van der Lingen & Hutchings 2005), suggesting it is a useful gross indicator of the magnitude of energy stores. Mesenteric fat is also more labile than muscle fat and can be the first store utilised during non-feeding periods (Lloret et al. 2014). Differences in the lability of muscle and mesenteric fat may enable herring to accumulate and utilise these stores selectively depending on the amount of energy required to fuel particular life-history processes (Slotte 1999).

Mature herring rely on both muscle and mesenteric fat to fuel yearly spawning migrations (Slotte 1999) and increase survival over winter when feeding ceases (Óskarsson 2005, Kenyon et al. 2022). Despite these known annual cycles in fat content, it is unclear whether both stores remain equally important throughout adulthood as the growth rate slows. The relative significance of both fat stores in immature herring is similarly unknown. Comparing the magnitudes of muscle and mesenteric fat in immature and mature herring of varying sizes will indicate how these 2 stores are used differentially to fuel growth, reproduction, and survival. Herring at the transition between immaturity and maturity (i.e. maturing virgin) face additional energetic demands associated with reproduction and may therefore use fat stores differently to immature herring that do not need energy for reproduction, or mature herring, which require less energy for somatic growth. To investigate changes in energy allocation across ontogeny, fat dynamics at the transition between immaturity and maturity need to be evaluated.

In most species, it is difficult to unambiguously identify individuals undergoing sexual maturation, and therefore data on maturing virgin fish sampled across space and time are limited. 'Maatjes' herring is a lightly salted and fermented fish product which is particularly popular in the Netherlands (De Boer & Klootwijk 2003, Lyhs et al. 2007). The herring fished to produce maatjes products are assumed to be maturing virgins (ICES 2011), targeted specifically for their high muscle fat content (Lyhs & Björkroth 2008). Maatjes herring are caught by Scottish, Danish, and Norwegian fleets between the end of May and beginning of July in the northern North Sea, before the start of the spawning migration in August. The precise timing and location of the fishery can change between years due to variability in the magnitude of muscle fat; however, it is currently not known what causes these interannual fluctuations. The uniquely high fat content and distinctive body shape of maatjes herring contribute to the flavour and texture achieved during fermentation (Aidos et al. 2001). Due to its commercial value, the muscle fat content of maatjes herring is routinely measured by processing factories to monitor fish quality. Until now, however, these data have not been utilised scientifically. If the assumption is correct that maatjes herring represent the maturing virgin life-history stage, these data provide a novel opportunity to investigate energy dynamics at a critical period during the transition between the immature and mature life stages. Additionally, resolving interannual variability in the magnitude of maatjes muscle fat content is necessary to determine factors affecting fish condition and is relevant to both biologists and the fishing industry.

This study aimed to determine how the magnitude of muscle and mesenteric fat content changes interannually across 3 life-history stages of herring in the North Sea. We combined 2 unique sources of fat content data measured on herring of varying body sizes and life stages (immature, maturing virgin, and mature) collected across highly resolved temporal scales. Specifically, we compared interannual variability in proportion muscle fat content in maturing virgin and mature herring (question 1) and mesenteric fat index across immature, maturing virgin, and mature individuals (question 2). We also investigated how interannual variability in the magnitude of muscle fat changed across weight grades within maturing virgin (question 3) and mature (question 4) herring. Finally, we investigated interannual variability in the mesenteric fat index across weight grades in maturing virgin (question 5) and mature (question 6) herring. A more robust comparison of muscle and mesenteric fat would require samples where measurements of both fat stores had been taken on the same individual. Such data do not currently exist and therefore separate data sets on muscle and mesenteric fat content, from different sources, were combined and analysed.

2. MATERIALS AND METHODS

2.1. Maatjes herring

The assumption that maatjes herring are maturing virgins can be traced back over 200 yr. After its establishment in 1809, the UK Fishery Board graded and branded barrels of cured herring according to strictly enforced standards (Jones et al. 2016). 'Matties' (an anglicisation of the Dutch word 'maatjes') were the smallest herring, measuring between 22.2 and 23.5 cm long. These herring were understood to be 'maiden herring [with] undeveloped reproductive organs, [...] caught in May and June' (Smith 1902, p. 5). At the International Fisheries Exhibition in 1883, it was stated that 'matties are the finest condition of the fish, when all the food goes to form [its] fattening properties' (Munro 1883, p. 39). Other herring grades were reserved for larger fish with fully developed gonads. This definition of maatjes herring used by the fishing industry remains largely unchanged.

In present times, the maatjes fishing season commences only when muscle fat content reaches approximately 16–20% (Lyhs & Björkroth 2008). Prior to 2000, maatjes herring were predominantly fished by Dutch vessels; however, they are now exclusively caught by Scottish, Danish, and Norwegian fleets. In 2021, the distribution of maatjes herring shifted northwards, and, in 2022, the season started 3 wk earlier than usual (Garrett & Pinnegar 2022). Fishers and fish processors hypothesise that this could have been due to a change in February sea temperatures experienced by maatjes herring earlier in the same year (M. Pastoors pers. comm. with industry).

2.2. Herring data sources

Biological data on herring fat content (muscle and mesenteric), life-history stage (immature, maturing virgin, and mature), and weight (wet weight in g) were compiled from 2 sources: commercial sampling from Scottish and Dutch fleets and scientific surveys conducted by Norway. Commercial samples were caught in the northern and central North Sea, with maatjes herring primarily caught in the northeastern North Sea (Fig. 1). The scientific surveys were also carried out in the northeastern North Sea, meaning that data on muscle and mesenteric fat content in maturing virgin herring were collected from the same place and time of year (summer) across all years (Fig. 1).

Data on muscle fat content in maturing virgin and mature herring were collected at pelagic processing factories located in Scotland, the Netherlands, Norway, and Denmark by trained fishing industry personnel from 2013 to 2021. Data were collected on herring caught during the seasonal North Sea herring fishery between May and July each year. Muscle fat measurements were taken during catch processing as part of routine quality control procedures. Dutch freezer-trawler vessels have processing factories onboard; thus, hauls of herring were continuously processed during each fishing trip prior to landing. Herring were also caught by refrigerated seawater trawlers before being landed and processed at onshore factories in Scotland, Norway, and Denmark. During processing, all herring were separated into weight grades (e.g. 170–250 g, 200–250 g, and so on) which differed, and overlapped, between fishing trips based on customer requirements. Up to 6 samples, each weighing between 20 and 25 kg, were taken from each weight grade per fishing trip. In the Netherlands, Norway, and Denmark, the mean weight of fish per sample, rather than the weight grade, was recorded. In Scotland, only the weight grade was recorded. In all countries, muscle fat content was measured in 2–6 herring from each sample.

Data on mesenteric fat content in immature, maturing virgin, and mature herring from 2004 to 2019 were collected during the Norwegian part of the herring acoustic survey (HERAS). HERAS is coordinated by

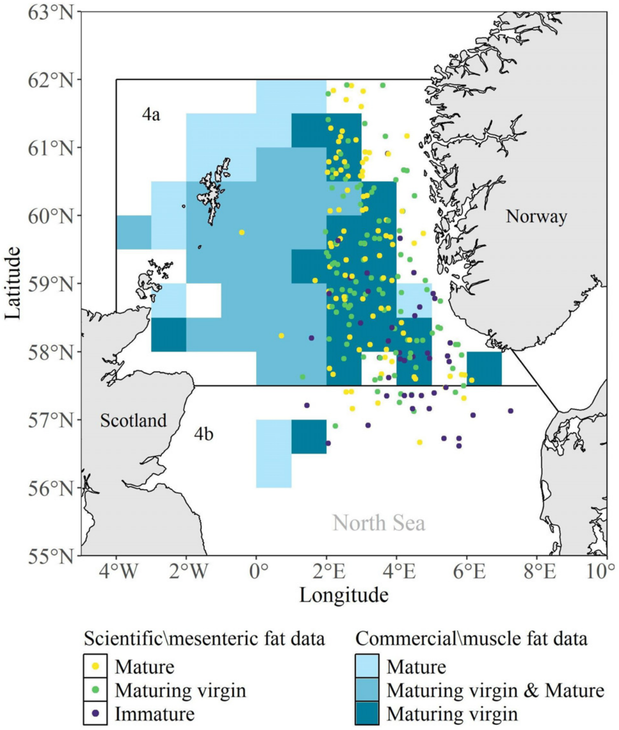

Fig. 1. North Sea study area indicated by ICES Areas 4a and 4b. Shaded areas are ICES statistical rectangles showing locations where mature and maturing virgin Atlantic herring used in this study were caught by Scottish and Dutch vessels. No area information was available for commercial samples caught prior to 2014. Points represent haul locations during Norwegian HERAS surveys and colours indicate locations where the majority of samples were mature, maturing virgin, or immature

the International Council for the Exploration of the Sea (ICES) and is carried out annually in June and/or July to determine the abundance and distribution of herring and sprat *Sprattus sprattus* in the North Sea (ICES 2015). Six countries participate in HERAS. However, we used data from Norway (Institute of Marine Research, Bergen) because this is currently the only country that measures mesenteric fat of herring sampled during HERAS. The Norwegian HERAS covers the eastern half of the northern North Sea (2–6° E, 56.5–62° N; Fig. 1) (ICES 2015). Sampling was carried out along parallel transects with random starting points. Species allocations of acoustic records were confirmed by taking targeted and periodic hauls using bottom and pelagic trawls, allowing biological data to be collected (ICES 2015). Haul locations are shown in Fig. 1, and sampling dates from 2004 to 2019 can be found in Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m763p115_supp.pdf. Generally, 50 herring were sampled per haul and the fat content (mesenteric fat index), length (to nearest 0.5 cm below), weight (wet weight in g), age (otolith extraction), sex, maturity stage (macroscopic staging; Table S1), stomach fullness, and vertebrae count were recorded.

2.3. Life-history staging

Muscle fat data collected by the fishing industry were separated into maturing virgin and mature samples based on the week of the year they were caught and the factory in which they were processed. Maatjes herring (i.e. herring assumed to be maturing virgins) were targeted specifically by Scottish, Danish, and Norwegian fishing industries in Weeks 21–27 of the year in the northern North Sea (Fig. 1). Specific onshore processing facilities are required to produce maatjes herring products. In Scotland, maatjes herring were landed by 5 vessels to 2 onshore factories during the first 5 wk of the North Sea herring fishery (Weeks 22–27 of the year approximately; M. Buchan pers. comm.). All remaining herring samples within the Scottish data set were categorised as mature and were caught between June and November. Data from onshore factories in Norway and Denmark were collected on maatjes herring exclusively and were therefore categorised as maturing virgin samples. All herring processed onboard Dutch freezer-trawler vessels were categorised as mature because these vessels do not have the facilities to produce maatjes herring products onboard. Herring sampled onboard freezer-trawlers were caught between mid-May and December.

During the Norwegian part of the HERAS survey, macroscopic maturity staging was used to assess the maturity of herring samples. Trained technicians sexed each herring sampled from hauls and assigned a maturity stage using an 8-point maturity scale based on the visual appearance of the gonads (Table S1) (ICES 2011). Maturity stage 1 samples were categorised as immature; maturity stage 2 samples were categorised as maturing virgin; and maturity stage 3–8 samples were categorised as mature (Table S1). Although maturity stage 2 is termed 'immature b' using the Norwegian macroscopic maturity scale (Table S1), this stage is the equivalent of 'maturing virgin' in the standardised European herring maturity scale (ICES 2011). Both stages are characterised by larger gonads, which are transparent but have a hint of colour, compared to the first maturity stage of either scale.

2.4. Fat measurement methods

2.4.1. Muscle fat content

The proportion of fat in herring muscle tissue (F) was measured within processing factories using 2 bioenergetic condition indices. Both methods are based on the empirical observation that the proportion of water and fat within herring muscle tissue totals approximately 0.8 and that there is a strong inverse correlation between their magnitudes (Kent 1990). Onboard Dutch freezer-trawlers, the Distell Fish Fatmeter (FFM692; Distell.com) was used to measure F in 4 large (>500 g) or 8 small (<500 g) herring from 22–25 kg samples from each weight grade per fishing trip (Distell.com). Onshore factories in Scotland, Norway, and Denmark used the evaporation method to measure F using 6 herring from 20 kg samples from each weight grade per fishing trip (Vogt et al. 2002). Average F values ($\bar{F}_i$) were then estimated for each sample (i) per fishing trip. The consistency between fat content values obtained using the Distill Fish Fatmeter, and the evaporation method was tested in Kenyon et al. (2022). No significant difference between these measurement methods was found, confirming they are comparable. Full muscle fat measurement protocols can be found in Text S1.

2.4.2. Mesenteric fat index

During the Norwegian part of the HERAS survey, the mesenteric fat content of each herring sampled from hauls was visually assessed by a trained technician.

The magnitude of fat surrounding the mesentery (i.e. intestines) was measured using a 4-point semi-quantitative index (Fig. S2) (van der Lingen & Hutchings 2005). The index has the following values with no units: 1 (no fat); 2 (narrow band of fat); 3 (some fat); and 4 (abundant fat). The protocol described remained consistent throughout the time series.

2.5. Statistical analysis

During the HERAS survey, data were collected across multiple herring stocks, including Norwegian spring-spawning, western Baltic spring-spawning, and North Sea autumn spawning (NSAS) herring. To allow comparison between the commercial and scientific data sources and to remove the effect of differing spawning times on fat content, analyses were carried out on data from NSAS herring only. NSAS herring were selected in the scientific data using mean vertebrae count per sample and age class (ICES 2018). Age classes in the survey data were defined using the number of winter rings (wr) on the otolith and were categorised as 1wr, 2wr, 3wr, and 4+wr. Age-structured samples with a mean vertebral count of between 56.5 and 57.2 were classified as NSAS herring because this is the assumed population range of mean vertebral count for NSAS herring (ICES 2018). Commercial data were assumed to contain samples of NSAS herring exclusively because fishing locations occurred in the northern and central North Sea (Fig. 1).

Commercial data were subset by day-of-year to allow accurate comparison between life-history stages and fat stores, thereby minimising the complication of temporal variability. Table 1 describes the commercial and scientific data subsets used to address each of the 6 research questions. Data exploration was applied to each subset to identify outliers, which were subsequently removed (Table 1) (Zuur et al. 2010). Across all subsets, 45 commercial samples from Scotland had no minimum weight value for their weight grade. To increase the precision of these weight grades, the year-specific weight at minimum landing size (20 cm) was used as the minimum boundary of the weight grade (Council of European Parliament 2019). The weight at 20 cm was estimated using a general linear model applied to the scientific HERAS data with log-transformed weight as the response variable and an interaction between log-transformed length and year as an explanatory variable (Fig. S3). Further details on cleaning of the commercial data can be found in Text S2.

Generalised additive mixed models (GAMMs) were used to estimate variability in the magnitude

Table 1. Subsets of commercial data on muscle fat content and scientific data on the mesenteric fat index used in this study. The life-history stage(s), weight range, days of year, years, number of outliers removed, sample size, and response variable of each of the 6 subsets are also indicated. *F*: proportion muscle fat content; *M*: mesenteric fat index

Research question	Model number	Fat depot	Life-history stage(s)	Weight range (g)	Day-of-year range	Years	Outliers removed	Sample size	Response variable
How does the magnitude of muscle fat differ between maturing virgin and mature herring?	1	Muscle	Maturing virgin Mature	67–250 65–323	145–190 150–190	2013–2021 2014–2020	0 2	877 935	$\bar{F}_1$
How does the magnitude of mesenteric fat differ between immature, maturing virgin, and mature herring?	2	Mesenteric	Immature Maturing virgin Mature	6–198 19–300 31–419	178–212 178–212 178–212	2004–2019 2004–2019 2004–2019	0 0 0	878 969 3327	M_2
How does the magnitude of muscle fat within maturing virgin herring change interannually and across weight values?	3	Muscle	Maturing virgin	67–250	145–190	2013–2021	0	862	$\bar{F}_3$
How does the magnitude of muscle fat within mature herring change interannually and across weight values?	4	Muscle	Mature	63–345	182–213	2013–2020	2	1993	$\bar{F}_4$
How does the magnitude of mesenteric fat within maturing virgin herring change interannually and across weight values?	5	Mesenteric	Maturing virgin	19–300	178–212	2004–2019	0	969	M_5
How does the magnitude of mesenteric fat within mature herring change interannually and across weight values?	6	Mesenteric	Mature	31–419	178–212	2004–2019	0	3327	M_6

of both muscle and mesenteric fat content across life-history stages, years, and weight values. GAMMs were chosen because data exploration revealed non-linear relationships between variables. Each of the 6 research questions outlined in Table 1 was addressed using a separate statistical model which was fitted to the corresponding subset of data. Models 1 and 2 estimated differences in interannual variability of muscle and mesenteric fat reserves between life-history stages using an interaction between year (continuous) and life-history stage (categorical). For Models 3–6, a smooth interaction between year and weight was used to estimate variability in muscle and mesenteric fat reserves within maturing virgin and mature herring. In models where muscle fat content was the response variable ($\bar{F}_{1,3-4}$), factory was included as a random intercept term and the beta error distribution and logit link were chosen because muscle fat was measured as a proportion with values between 0 and 1. In models where the mesenteric fat index was the response variable ($M_{2,5-6}$), an ordered categorical distribution was chosen such that the probability of an observation coming from each of the 4 categories was estimated. Statistical analyses were carried out using the 'mgcv' package (Wood 2017) in R (v.4.0.2) (R Core Team 2020). Uniformity and dispersion patterns were checked by visual assessment of the residuals using the 'DHARMa' package (Hartig 2024). A full description of the models fitted and associated model equations can be found in Text S3.

3. RESULTS

3.1. Interannual variability in muscle fat content (Model 1)

Maturing virgin herring had significantly higher muscle fat content than mature individuals ($p = 0.003$). The mean proportion of muscle fat content (response variable: $\bar{F}_1$) was 0.186 (95% CI: [0.166, 0.208]) in maturing virgin herring and 0.156 (95% CI: [0.144, 0.17]) in mature herring. Significant non-linear trends over time in muscle fat content were found in both maturing virgin and mature herring (maturing virgin: effective degrees of freedom [edf] = 7.843, $p < 0.001$; mature: edf = 5.556, $p < 0.001$; Fig. 2). Muscle fat content was significantly different between maturing virgin and mature herring in 2014 and 2020 (Fig. 2). In maturing virgin herring, there was high variability in muscle fat content from 2013 to 2015, after which the magnitude of fat was relatively stable (Fig. 2). In mature herring, the proportion of muscle fat content increased from 0.14 in 2014 to 0.178 in 2016, approaching a similar magnitude as maturing virgin individuals of the same year. Between 2016 and 2020, fat content in mature herring decreased gradually to

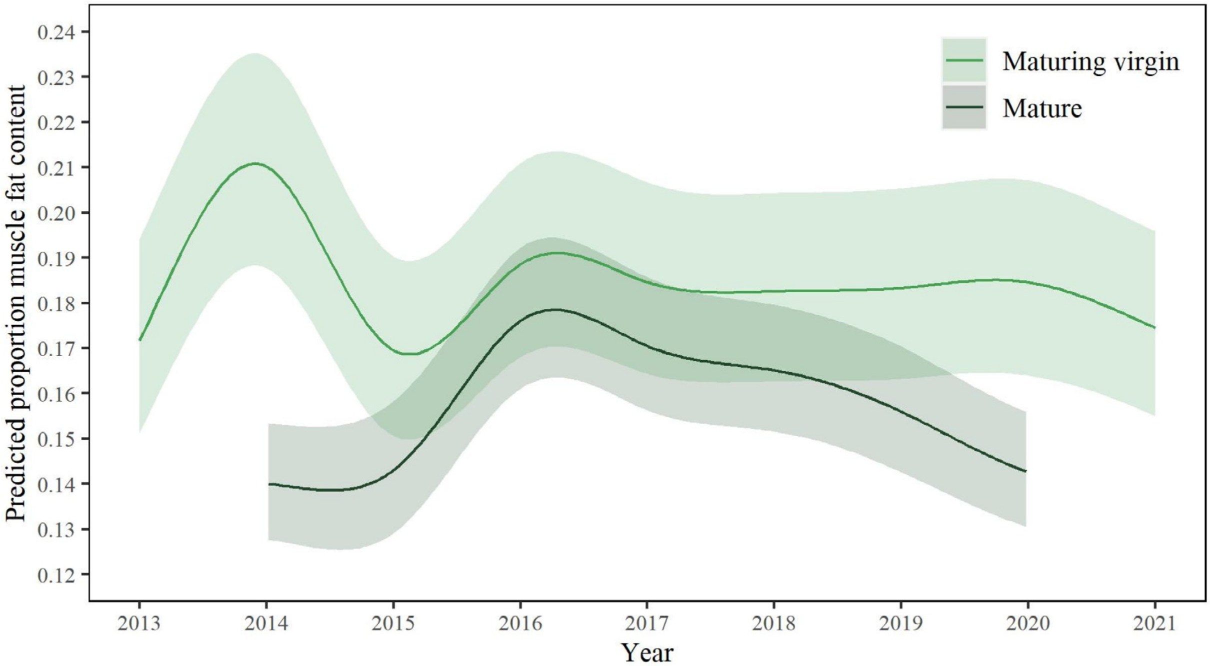

Fig. 2. Smooth effect of year on the proportion muscle fat content for each maturing virgin and mature life-history stages of Atlantic herring. Lines: predicted proportion muscle fat content; shading: 95% CI around the prediction

0.143, diverging from the stable trend in maturing virgin herring (Fig. 2). There were significant differences in fat content values measured between factories ($p < 0.001$). Overall, Model 1 accounted for 74% of the deviance.

3.2. Interannual variability in mesenteric fat content (Model 2)

There was no significant difference in the mesenteric fat index (response variable: M_2) between immature and mature herring ($p = 0.152$); however, maturing virgin herring had a significantly higher mesenteric fat index than either immature or mature individuals ($p < 0.001$). Both immature and mature herring were most likely to have a mesenteric fat index of 3 (Probability [Pr] = 0.467 and 0.473, respectively) while maturing virgin herring were most likely to have an index of 4 (Pr = 0.544).

Interannual trends in the mesenteric fat index of immature herring were significant and non-linear (edf = 10.5, $p < 0.001$). The probability of herring having a mesenteric fat index of 4 fluctuated widely between years, from an average of 0.97 in 2007 to 0.04 in 2019 (Fig. 3). Immature herring were unlikely to have a mesenteric fat index of 1 across the time series (Pr = 0.04), apart from in 2019, when the highest probability of 0.37 occurred (Fig. 3).

A significant and non-linear trend in the mesenteric fat index was found in maturing virgin herring (edf = 12.3, $p < 0.001$; Fig. 3). The probability of having a mesenteric fat index of 1 or 2 was generally very low (0.02 and 0.08, respectively); however, in 2019, the probabilities reached a maximum of 0.14 and 0.35, respectively (Fig. 3). On average, the probability of maturing virgin herring having a mesenteric fat index of 3 or 4 was 0.36 and 0.54, respectively.

Mature herring also showed significant, non-linear trends in the mesenteric fat index (edf = 13.9, $p < 0.001$). The mesenteric fat index was highest in 2007 and lowest in 2009 (Fig. 3). The index remained relatively constant in all other years (Fig. 3). The average probability of mature herring having a mesenteric fat index of 3 or 4 was 0.47 and 0.25, respectively. Model 2 explained 10.8% of the deviance.

3.3. Effect of weight and year on muscle fat content (Models 3 and 4)

For maturing virgin herring (response variable: $\bar{F}_3$), there was a significant, non-linear relationship between muscle fat content and year, which varied

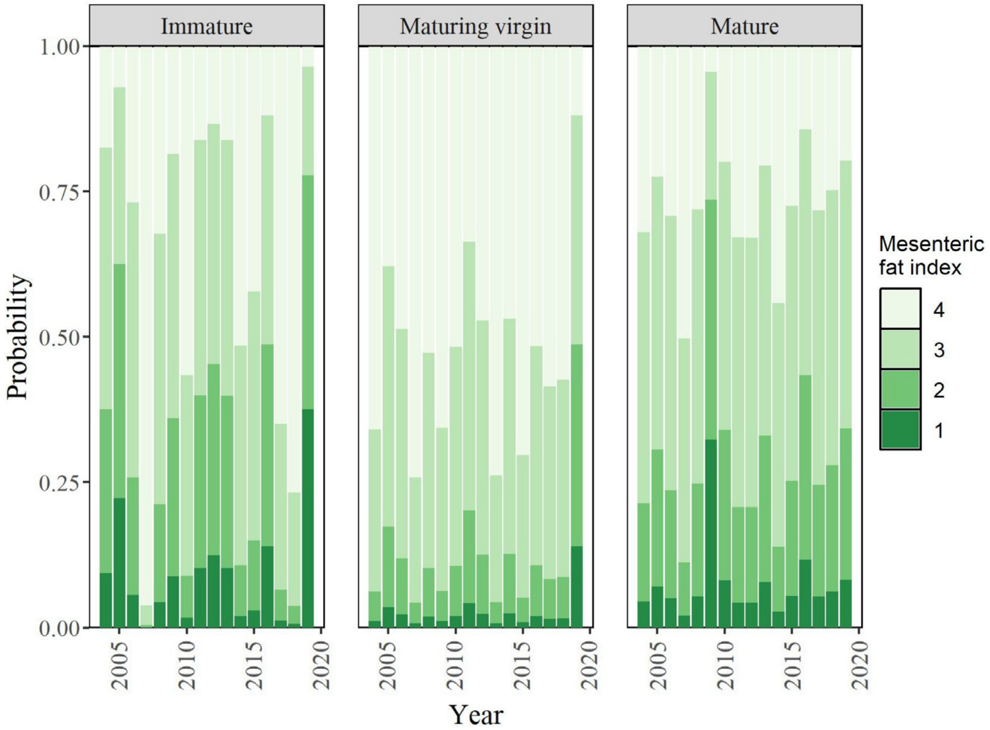

Fig. 3. Predicted probability of Atlantic herring in life-history stages immature, maturing virgin, and mature having a mesenteric fat index of 1, 2, 3, or 4 across years

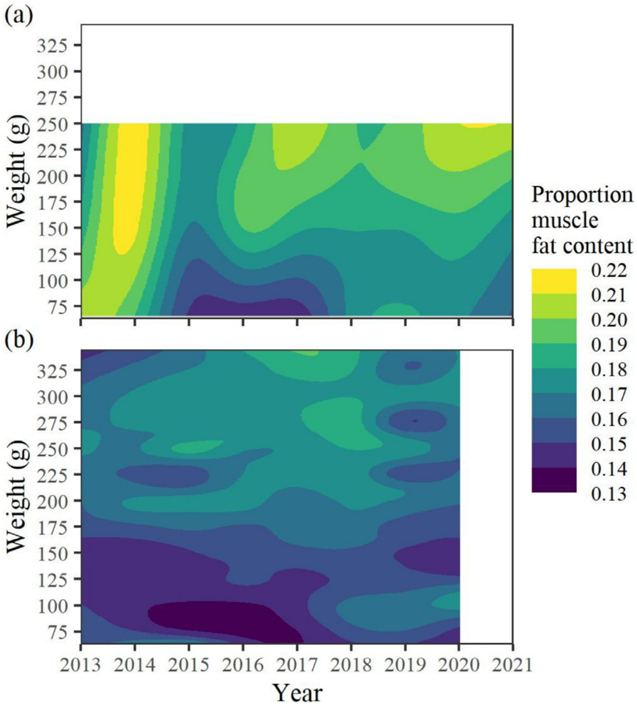

Fig. 4. Predicted interannual variability in the proportion muscle fat content across weight values for (a) maturing virgin and (b) mature Atlantic herring

across weight values (edf = 23.4, $p < 0.001$; Fig. 4a). Weight ranged between 66.5 and 250 g; however, very low and high values (<100 and >230 g) were not recorded in all years. Where weight values were missing in certain years, the proportion of muscle fat content was predicted using Model 3 (Fig. 4a). In 2013, muscle fat content was high across all weight values (approximately 0.21). Between 2014 and 2017, muscle fat content was lower in lighter (<150 g) herring and higher in heavier (>149 g) herring (0.14 and 0.2, respectively). Thereafter, muscle fat content increased slightly in lighter individuals to 0.17 while remaining the same in heavier herring (Fig. 4a). This model explained 45.1% of the deviance.

In mature herring, there was a significant, nonlinear relationship between muscle fat content and weight, dependent on year (response variable: $\bar{F}_4$; edf = 79.22, $p < 0.001$; Fig. 4b). Weight in mature herring ranged between 63.1 and 345 g. Mature individuals heavier than 300 g or lighter than 100 g were not available in 2013 and, before 2015, there were no mature individuals heavier than 325 g. Muscle fat content at these weights was predicted from Model 4. In individuals weighing more than 150 g, fat content remained relatively constant between 2013 and 2017 (0.16–0.18) before increasing slightly in 2018 and declining again until 2020 (Fig. 4b). Muscle fat content was lower in lighter herring (<150 g) than in heavier herring (>149 g) between 2013 and 2018 (0.14; Fig. 4b). After 2018, muscle fat content in herring weighing less than 150 g increased slightly to 0.17–0.18. This model explained 77.5% of the deviance.

3.4. Effect of weight and year on mesenteric fat content (Models 5 and 6)

Interannual trends in mesenteric fat content of maturing virgin herring were dependent on weight (response variable: M_5; edf = 39.5, $p < 0.001$; Fig. 5a). Across all years, maturing virgin herring of all sizes were very unlikely ($\Pr < 0.1$) to have a mesenteric fat index of 1 or 2, apart from in 2004–2006, when the probability of light herring (<100 g) having a mesenteric fat index of 2 was approximately 0.7. In all other years, mesenteric fat content fluctuated between indices 3 and 4. In 2010, there was a decrease in mesenteric fat content in herring weighing more than 150 g. Fat content then gradually increased between 2011 and 2019. Herring weighing less than 150 g had a high mesenteric fat content ($\Pr(M_5 = 4) > 0.8$) across all years with the exception of 2004 and 2019, when the probability of having an index of 2 and 3, respectively, increased (Fig. 5a). Model 5 explained 25.3% of the deviance.

In mature herring, there was a significant and nonlinear relationship between mesenteric fat index and weight, which was dependent on year (response variable: M_6; edf = 57.24, $p < 0.001$: Fig. 5b). In general, mature herring weighing more than approximately 250 g had low mesenteric fat content, with $\Pr(M_6 = 1) > 0.9$ in most years. Exceptions occurred in 2004 and 2013, when the probability of having an index of 2 or 3 increased (Fig. 5b). Conversely, mature herring weighing less than 250 g had a high probability (>0.5) of having a mesenteric fat index of 4 across most years. During 2009, the probability was greater than 0.9 (Fig. 5b). Model 6 explained 10.8% of the deviance.

4. DISCUSSION

Due to their commercial relevance, most research on maatjes herring has focused on optimising by-products and storage methodologies (Aidos et al. 2001, Lyhs & Schelvis-Smit 2005, Lyhs et al. 2007). Our study highlighted the biological relevance of maatjes herring based on their assumed representation of a critical life-history stage: the transition between immaturity and maturity (i.e. maturing virgin). Using a unique combination of commercial and

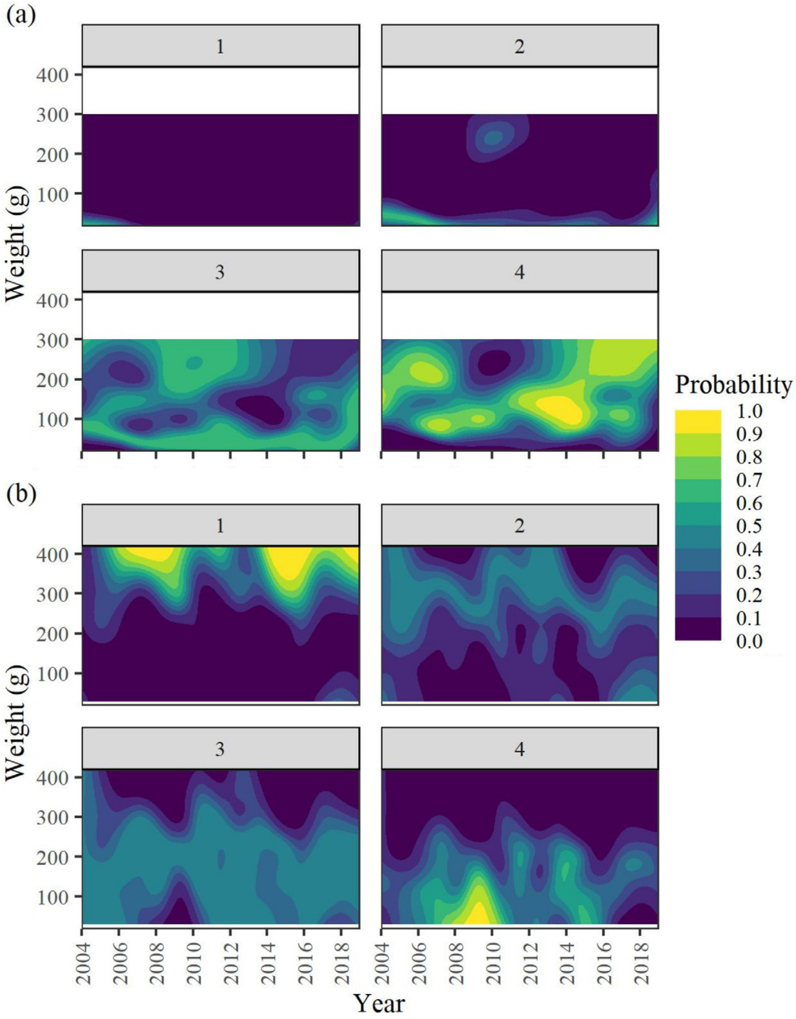

Fig. 5. Predicted probability of (a) maturing virgin and (b) mature Atlantic herring having a mesenteric fat index of 1, 2, 3, or 4 across years and weight values

scientific data collected across large and highly resolved spatio-temporal scales, we found that store-specific measurement of fat content provides an unambiguous biomarker of maturation. Fat dynamics during the transition between immaturity and maturity are distinct from preceding and subsequent life-history stages. In June, maturing virgin herring have on average 3% higher muscle fat content than mature herring. Additionally, in July, maturing virgin herring are most likely to have a mesenteric fat index of 4, while both immature and mature herring are most likely to have an index of 3. These results suggest that maturing virgin herring rely heavily on both muscle and mesenteric fat stores, implying that the energetic demands of first-time spawning (detailed below) require a dual-fuel allocation strategy.

Methods currently used to identify first-time spawning in iteroparous fish are indirect. For example, it has been proposed that the presence of 'spawning zones' on Atlantic cod *Gadus morhua* otoliths can indicate the occurrence of first maturation (Denechaud et al. 2021). However, differences in otolith features between spawners and immatures may not always be present (Irgens et al. 2020) and spawning zone formation may be slow and inconsistent during the years following first maturation (Denechaud et al. 2021). Additionally, the identification of otolith spawning zones can be highly subjective and variable between readers and time periods (Denechaud et al. 2021). These limitations highlight the ambiguity in attributing the presence of otolith 'spawning zones' to precise spawning events (Irgens et al. 2020). Given that maatjes herring have a distinctive body shape (Aidos et al. 2001), presumably due to the presence of large mesenteric fat reserves, our results suggest that first-time spawning herring can be identified using the non-destructive assessment of muscle fat content and body shape. This study is therefore the first to distinguish maturing virgin iteroparous fish unambiguously using a physiologically based index of fat content. Measuring both muscle and mesenteric fat content in individual fish may be a useful method for determining first maturation in other small pelagic species, such as sprat and European sardine *Sardina pilchardus*. Caballero-Huertas et al. (2023) found variable fat reserves in immature sardines across Mediterranean populations. Once mature, variability in muscle and mesenteric fat throughout the annual reproductive cycle also differed between populations. However, fat content at the first onset of sexual maturation was not analysed (Caballero-Huertas et al. 2023).

Accumulating 2 large fat stores at the onset of sexual maturation may be a physiological fitness strategy which maximises reproductive success in herring. This hypothesis assumes that maturing virgin herring face critical trade-offs between energetic demands. Maatjes herring were sampled in the summer months (June and July) from across the northern North Sea, and efforts were made to only include NSAS herring in the analyses. In June and July, NSAS herring feed offshore before beginning their spawning migration along the east coast of the British Isles (van Damme et al. 2009, Hufnagl et al. 2015). Maturing virgin herring shoal together while feeding before adopting the spawning migration routes of older year classes (Corten 2000). After spawning, herring migrate to overwintering grounds, where they remain until the following spring when they return offshore to feed (van Damme et al. 2009, Hufnagl et al. 2015). Thus, in June and July, maturing virgin herring require sufficient fat reserves to fuel their first spawning migration, gonad maturation, and overwintering survival. Additionally, they require energy for continued somatic growth (Martin et al. 2017). Given these competing energetic demands, it is reasonable to assume that trade-offs between physiological processes are optimised when the maximum amount of fat is available.

The different energetic demands faced by maturing virgin herring mean their fat reserves can be allocated in multiple ways. Since adult herring rely on muscle fat to fuel the spawning migration (Kenyon et al. 2022), it may be that maturing virgin herring also use muscle fat to fuel their first migration to spawning grounds. Under this scenario, the large amount of mesenteric fat accumulated could be utilised to survive overwintering. Alternatively, given its lability (Slotte 1999), mesenteric fat may be relied upon to fuel the first spawning migration while muscle fat provides a more stable energy source for overwintering. This second allocation strategy is supported for several reasons. Firstly, in Norwegian spring-spawning herring, adults initially rely upon mesenteric fat in the lead-up to spawning before switching to muscle fat (Slotte 1999). Secondly, the physical constraints within the abdominal cavity mean that there may be insufficient space for both mature gonads and large mesenteric fat reserves. Therefore, maturing virgin herring may be mechanistically required to convert mesenteric fat into energy used for the spawning migration or gonad development early on in the spawning season. Thirdly, our study found that mesenteric fat was generally important for maturing virgin herring of all sizes (45–300 g) while muscle fat reserves appeared to be slightly larger in heavier (>150 g) than in lighter (<150 g) maturing virgin herring. Overall, these results suggest that mesenteric fat is the more important reserve for herring undergoing the onset of maturation because it is present in large amounts compared to immature and mature stages and is typically the first reserve to be both accumulated and metabolised. By contrast, muscle fat becomes a secondary and opportunistic store for maturing virgin herring to accumulate, perhaps increasing their survival chances over winter.

The importance of mesenteric fat appears to extend beyond first maturation. Mature herring sampled in July were on average likely to have a mesenteric fat index of 3; however, this was highly dependent on their individual weight. Lighter (<250 g) mature herring had a higher mesenteric fat index (3 or 4) than heavier (>250 g) mature herring (mesenteric fat index of 1 or 2). The decreasing amount of mesenteric fat with increasing size suggests this fat reserve is important for fuelling growth. Other possible explanations may be a prolonged or delayed spawning season in older herring or the effect of processes such as senescence. To accurately disentangle these effects, data on both the magnitude of fat stores and age would need to be analysed. The change in muscle fat content with weight was less apparent; however, mature herring above ~200 g had slightly larger muscle fat reserves than those below ~200 g. Thus, it appears that as herring become larger and reach maturity, they switch from primarily using mesenteric fat to relying (almost entirely in the case of mature herring) on muscle fat. This switch in energy allocation implies that these fat stores are used differentially across life-history stages depending on the energetic demands faced (Martin et al. 2017). While this study did not analyse muscle fat content in immature herring, it is clear that mesenteric fat is important for this pre-reproductive life-history stage. Immature herring had an average mesenteric fat index of 3; however, this fluctuated widely between years. Given that growth and survival are the main energetic demands of immature fish (Mogensen & Post 2012), this study shows that mesenteric fat is important for fuelling either or both of these processes.

Interannual variability in the magnitude of both muscle and mesenteric fat was evident in maturing virgin and mature herring. Given that the comparisons between life-history stages and fat stores were made on herring sampled at the same time of year (with the exception of maturing virgin herring), interannual variability can presumably be attributed to changes in feeding conditions, mediated by sea temperature and density-dependent prey abundance (Yaragina & Marshall 2000, Casini et al. 2006, Sandeman et al. 2008). Herring in the North Sea primarily feed on *Calanus* copepods, the abundance of which was relatively high in 2009 (Capuzzo et al. 2018). Mesenteric fat of small mature herring was also high in 2009 while herring stock biomass was relatively low (ICES 2018). Between 2010 and 2013, northern North Sea temperatures were slightly cooler than average but were followed by larger temperature anomalies in 2014 (DEFRA 2019). In 2014, the magnitude of muscle fat in maturing virgin herring peaked while mature herring had the smallest magnitude of muscle fat, indicating that temperature may have differential effects on herring condition depending on life-history stage. The difference in fat content between maturing virgin and mature herring did not appear between 2015 and 2019. Varying interannual patterns in fat content between maturing virgin and mature herring may reflect degrees of feeding success and/or spatial overlap in feeding areas.

In this study, we assumed that maatjes herring represent the maturing virgin life-history stage based on historic and contemporary evidence from the fishing industry. Future research should aim to validate this assumption using histological evidence. We also assumed that herring caught onboard freezer-trawler vessels were mature. While these vessels do not have maatjes processing facilities onboard, the possibility that herring of the maturing virgin stage are caught but processed for fillets cannot be ruled out. The misclassification of maturing virgin herring as mature samples would have increased the estimated muscle fat content of mature herring. Therefore, any inaccuracies would have produced conservative effect sizes. We also acknowledge that the use of a semi-quantitative scale as an index for the magnitude of mesenteric fat is subjective (van der Lingen & Hutchings 2005). Weighing the mesenteric fat would provide a more precise measurement of its magnitude, but these data are not routinely collected.

Taking advantage of a unique combination of data, this study has shown the importance of 2 fat stores for the onset of first maturation in herring, a phenomenon that we term the dual-fuelling strategy. We provide new knowledge on the importance and dynamics of fish bioenergetics that determine growth and reproduction. This insight was made possible due to the routine sampling by industry of a critical life-history stage represented by maatjes herring. Continued systematic monitoring of fat content in both mature and maturing virgin herring by industry will result in the formation of a unique long-term data set on herring bioenergetics. Such data could provide valuable insights into the trophic and environmental drivers of herring condition. Given that the timing of the maatjes herring season is dependent on the magnitude of muscle fat, links between fat content and food availability could be used to predict herring quality and thus inform the start of the maatjes season. High-resolution data sets on fish fat content can also be used to inform bioenergetic models which often rely on simplistic assumptions about energy allocation and lipid storage dynamics (Rose et al. 2024). Similarly, an extended time series of fat content in commercially and ecologically important species can improve understanding of life-history adaptation in response to climate change (Thunell et al. 2023).

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