




Original Article

Intra- and inter-annual variability in the fat content of Atlantic herring (*Clupea harengus*) as revealed by routine industry monitoring

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Fat content indicates individual condition and fuels annual reproductive cycles in many fish species. These cycles, coupled with ecosystem changes, can result in large intra- and inter-annual fluctuations in fat content. However, quantifying this variability is challenging when scientific sampling does not cover the full reproductive cycle. Scottish and Dutch fish processors routinely measure muscle fat content of North Sea autumn-spawning herring (*Clupea harengus*) throughout fishing seasons. We validated these high temporal resolution data by estimating a strong intra-annual signal in fat content, which matched herring reproductive status. Fat content increased from 4.5% 95% CI [0.03, 0.06] to 16.1% 95% CI [0.15, 0.17] during May and June before plateauing and decreasing to 9.1% 95% CI [0.08, 0.10] in September, which coincided with the onset of spawning. We also examined inter-annual variability in the seasonal pattern and the timing and magnitude of peak fat content from 2006 to 2020. Inter-annually, fat content differed from the mean pattern during the feeding or spawning periods in years 2013, 2015–2017, 2019, and 2020. There was no difference in the timing and magnitude of peak fat content between years. Our study validates the scientific use of routinely collected fat content data from pelagic fish processors.

Keywords: between-year variability, *Clupea harengus*, fat content, fish condition, industry sampling, North Sea herring, seasonal variability.

Introduction

Fat constitutes the main energy reserves in teleosts and is used as a reliable indicator of fish condition (Stevenson and Woods, 2006). Following onset of maturity, many fish species undergo annual cycles of feeding, reproduction, and overwintering. Fat is particularly important for capital spawners who finance the energetic cost of reproduction using fat reserves accumulated during relatively short feeding periods (McBride *et al.*, 2015). Inadequate fat reserves in pre-spawning individuals causes lower fecundity, increased atresia, and increased likelihood of skipped spawning (Bucholtz *et al.*, 2013;

Mion *et al.*, 2018; dos Santos Schmidt *et al.*, 2020). Positive associations between spawner condition and stock recruitment suggest these impacts have consequences at the population-level (Marshall *et al.*, 1999). Fat reserves are also used to sustain metabolic activity during overwinter and to fuel lengthy migrations to and from feeding and spawning areas (Slotte, 1999; Gücü *et al.*, 2018).

The reliance on fat reserves during annual cycles results in large intra-annual variability in individual fat content (Lloret *et al.*, 2014). This is especially true of pelagic fish, which accumulate fat in muscle tissue and mesenteries during feeding when maximum fat values are reached. Minimum values are typically associated with the

completion of spawning after these reserves have been utilized for gonad development (Lloret *et al.*, 2014). Many pelagic fish feed on zooplankton and are themselves predated on by larger fish and marine mammals, making them important converters of energy between lower and higher trophic levels (Varpe *et al.*, 2005). Inter-annual variability in pelagic fish condition is often linked to indirect effects of primary production and subsequent zooplankton availability, competition, and sea temperature (Shulman *et al.*, 2005; Brosset *et al.*, 2015; Champion *et al.*, 2020b).

Atlantic herring (*Clupea harengus*) are abundant pelagic forage fish which form distinct stocks in the northeast Atlantic, each separated by time and place of spawning (Parrish and Saville, 1965; Berg *et al.*, 2017). Herring are extreme capital spawners and store fat used for reproduction, migration, and overwintering in their muscle tissue and mesenteries (Bucholtz *et al.*, 2013). Large intra-annual variations in muscle fat content have been found in Norwegian spring-spawning, Icelandic summer-spawning, and western Baltic spring-spawning herring (Slotte, 1999; Óskarsson, 2005; Røjbek *et al.*, 2014). For each of these stocks, fat is highest during feeding and lowest during spawning. A similar pattern has been found for North Sea autumn-spawning herring, which feed in the northern and central North Sea during summer before spawning along a north to south gradient around Shetland, Orkney, Buchan, and the Banks areas from mid-August to October (van Damme *et al.*, 2009; McPherson, 2010; Hufnagl *et al.*, 2015). Fat is accumulated rapidly during May and June before declining steadily in August (Wood, 1958; Iles, 1984; van Damme *et al.*, 2009), however, this seasonal pattern has been estimated using small sample sizes covering limited numbers of years.

Fat contributes to marketability, with fatter fish yielding higher value products (Vogt *et al.*, 2002). Consequently, fat content data is routinely collected by pelagic fish processors as part of standardized quality control procedures. Given muscle fat is of primary relevance to market value, processors typically utilize bioenergetic methods to measure fish fat content (Vogt *et al.*, 2002). Bioenergetic methods indirectly estimate the relative amount of fat stored in one depot or organ (e.g. muscle or mesenteries). Indices derived from bioenergetic methods are more accurate than traditional morphometric (i.e. length–weight) indices and they are also suitable for routine field use (Davidson and Marshall, 2010; McPherson *et al.*, 2011). Newer methods, such as bioelectrical impedance analysis, accurately estimate total body composition (Hartman *et al.*, 2015), however, such methods have yet to be routinely applied to marine fish in the field (Champion *et al.*, 2020a). Bioenergetic methods, therefore, provide reliable estimates of fish stock condition because they can be applied during fishery-dependent sampling.

One example of a bioenergetic method utilized by the fishing industry is the Fish Fatmeter (Distell.com, 2020, Lothian, Scotland). The Fatmeter is a hand-held microwave device that uses the dielectric properties of water to estimate fillet water content. The Fatmeter is programmed to use the inverse correlation between fat and water to estimate muscle fat content (Kent, 1990). Fatmeter data collected by processors in Norway have been used to inform Atlantic mackerel (*Scomber scombrus*) fecundity type and shown to improve the stock's assessment model (Jansen *et al.*, 2021). Pelagic processors in Scotland and the Netherlands also measure muscle fat content of herring and mackerel, however, this data has yet to be scientifically utilized. Data is collected throughout fishing seasons, giving high temporal resolution, and thus, the opportunity to determine both precise long-term and seasonal variability in herring fat content. This is in contrast to scientific surveys, which sample

herring during research vessel surveys at a fixed point in the annual cycle only. As well as informing stock assessments, these industry datasets have potential to provide important insights into changes in biotic and abiotic factors that affect the growth and condition of herring populations. However, before being widely applied scientifically, the datasets require validation to ensure they accurately reflect underlying dynamics in herring bioenergetics.

Here, we aimed to improve precision in the estimation of intra-annual variability in North Sea herring fat content by analysing the high temporal resolution datasets collected by Scottish and Dutch fish processors. We also aimed to validate the accuracy of these industry datasets by determining whether a seasonal pattern in fat content was present and, importantly, whether it was consistent with Atlantic herring annual reproductive cycles widely reported in the literature. If the patterns detected match those expected, then it would indirectly validate the scientific use of routinely collected industry data. A stronger validation would require a comparison between industry and scientific data sampled at the same time and place. However, scientific data does not cover the full reproductive cycle, meaning useful comparisons of intra-annual variability cannot be made. Lastly, given that inter-annual variability in fish fat content can indicate ecosystem changes, we also examined whether the seasonal dynamics and the timing and magnitude of peak fat content varied across recent years (2006–2020).

Material and methods

The North Sea herring fishery

The North Sea herring stock supports a multinational fishery and stock status is assessed annually across the North Sea, eastern English Channel, and the Skagerrak and Kattegat (Figure 1; ICES, 2020). The stock comprises two temporally separated spawning components: autumn-spawners, which spawn in the northern and central North Sea between August and October, and winter-spawners, which spawn in the English Channel during December and January (Hufnagl *et al.*, 2015). Both components feed across the entire North Sea during the summer (Berg *et al.*, 2017).

The North Sea herring stock forms the main component of Scottish and Dutch herring fisheries. Dutch freezer-trawler vessels and Scottish refrigerated sea water trawlers catch herring in the northern and central North Sea between May and November each year during the seasonal herring and mackerel fisheries. Dutch freezer-trawlers also fish for herring in the English Channel during December.

Data collection

Sampling procedures

Muscle fat data were collected following landing or hauling of herring catches by Scottish and Dutch trawlers during the seasonal herring and mackerel fisheries between 2005 and 2020. Muscle fat measurements were taken during catch processing by trained personnel as part of routine quality control procedures. As these data were collected for commercial rather than scientific purposes, the time series available for each source was limited by the duration that quality control documentation was retained. This varied between a minimum of 5 years and a maximum of 16 years.

In the Netherlands, processing occurred prior to landing as freezer-trawlers continuously processed hauls of herring onboard during each fishing trip. In Scotland, processing occurred after

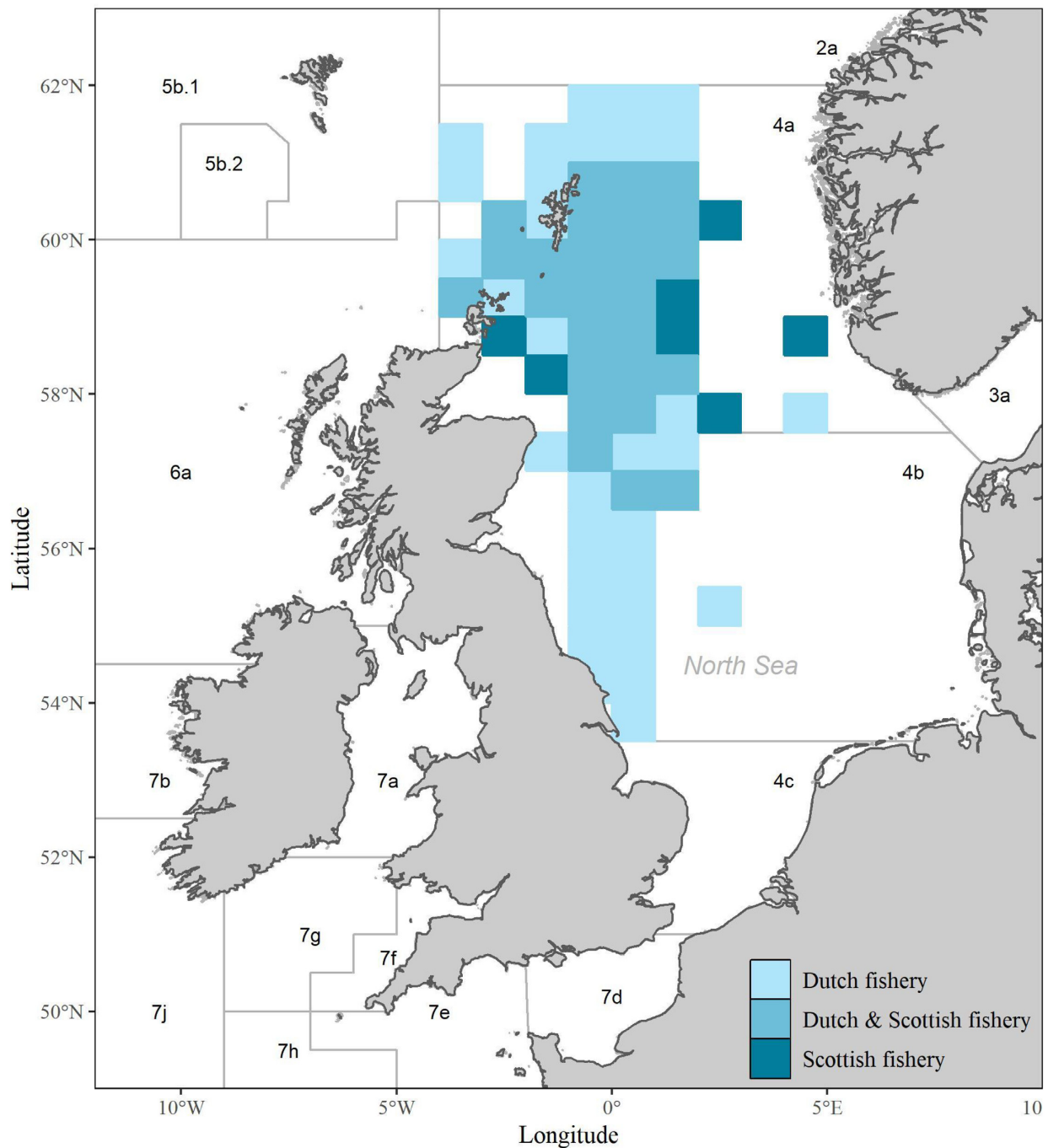


Figure 1. Map of North Sea with the study area indicated by ICES statistical areas 4a and 4b (northern and central North Sea, respectively). Shaded areas are ICES statistical rectangles showing the spatial extent of the Scottish and Dutch North Sea herring fisheries from 2014 to 2020. ICES rectangle information was not available prior to 2014.

landing of herring to factories in Peterhead and Fraserburgh (Supplementary Figure S1). Landings of herring were separated into weight grades (e.g. 170–250 g, 200–250 g, and so on) which differed, and overlapped, between landings based on customer requirements. Proportion of fat within muscle tissue (F) was measured in two to six herring from 20 to 25 kg samples from each weight grade per landing. Some weight grades were sampled up to six times within one landing due to either the large quantity of catch or landings being processed across more than one factory.

In the Netherlands, only the mean weight within each sample was recorded rather than the boundaries of its weight grade.

Measurement methods

A total of two bioenergetic condition indices were used to measure F and the full protocol for each is provided in the Supplementary material. Both methods are based on the empirical observation that the proportion of water and fat within herring muscle

Table 1. Outliers removed from the Scottish only and the Scottish and Dutch combined datasets prior to analysis and justification for their removal.

| Analysis | Outlier in | Value | Justification | Number of outliers removed |
|--------------------|------------------------|-------|--|----------------------------|
| Scottish only | Day of year | 314 | Unable to infer seasonal pattern | 1 |
| Both | Year | 2005 | Too few data points to infer seasonal pattern in these years | 1 |
| | | 2011 | | 4 |
| Scottish and Dutch | Proportion fat content | 0.8 | Data entry error | 1 |
| | | 0.001 | | 45 |
| | | 0.005 | | 53 |
| Total | | | | 105 |

tissue is approximately 0.8, and that there is a strong inverse correlation between their magnitudes (Kent, 1990). Onboard Dutch freezer-trawlers, the Distell Fish Fatmeter (FFM-692; Distell.com, 2020, Lothian, Scotland) was used to measure F in four large (> 500 g) or eight small (< 500 g) herring from 22 to 25 kg samples from each weight grade per landing. Factories in Scotland used the evaporation method to measure F using six herring from 20 kg samples from each weight grade per landing (Vogt *et al.*, 2002). Average F values ($\bar{F}_{D,i}$ and $\bar{F}_{S,i}$) were estimated for each sample per landing (i) in both the Dutch (D) and Scottish (S) data. Although the Fatmeter and evaporation methods represent simple indices compared to biochemical methods, F values from both methods correlate well with biochemical indices (Fatmeter: $r = 0.84$; Evaporation: $r = 0.95$; Vogt *et al.* 2002). The methods described also remained consistent throughout the duration of the time series.

Statistical analyses

Data were stored electronically or on paper files which were collated, standardized, and cleaned using R software (R Core Team, 2020, version 4.0.2). Analysis was carried out on data from mature autumn-spawning herring only (i.e. samples caught in the northern and central North Sea; Figure 1). Sub-setting the data to include only mature autumn-spawning herring removed variability from sources other than the annual reproductive cycle and minimized the effect of differing spawning times on fat content. Full details on data cleaning and sub-setting can be found in the Supplementary information.

Since factories are onboard Dutch freezer-trawler vessels, the effect of factory and vessel on $\bar{F}_{D,i}$ is identical. In Scotland, however, factories are onshore and, therefore, vessel and factory may have differing effects on $\bar{F}_{S,i}$ (Supplementary Figure S1). In order to analyse these data sources in combination, we first analysed the Scottish data separately to determine how much variability in $\bar{F}_{S,i}$ is explained by factory and vessel effects. The effect which explained the most variability in $\bar{F}_{S,i}$ was included in the analysis of the data sources combined. Data exploration and analysis was, therefore, twofold: Scottish data only (Response variable: $\bar{F}_{S,i}$) followed by the Scottish and Dutch data combined (Response variable: $\bar{F}_{S \vee D,i}$, where \vee denotes “or”). Data exploration was applied to identify outliers in both datasets, which were subsequently removed (see Zuur *et al.* 2010; Table 1). Table 2 shows the predictors included in the analysis of $\bar{F}_{S,i}$ and $\bar{F}_{S \vee D,i}$ and rationale behind their inclusion. The weight grade of a sample was not included in analyses due to the differential reporting of weight grades between countries.

The Scottish dataset contained 898 observations of $\bar{F}_{S,i}$ collected between 2006 and 2019 (Table 3). The seasonal range of data

extended from days 146 to 257 of the year. Across all years, mean $\bar{F}_{S,i}$ was 0.172 ± 0.032 SD and ranged from 0.15 ± 0.03 SD in 2007 to 0.196 ± 0.02 SD in 2014. The Scottish and Dutch dataset contained 4975 observations of $\bar{F}_{S \vee D,i}$ sampled between 2006 and 2020 (Table 3). From 2014 onwards, herring were mainly caught across the eastern areas of the northern and central North Sea (Figure 1). Catch area was not available prior to 2014. The addition of Dutch data extended the seasonal time range by an average of 56 d across 2015–2019. Across all years, mean $\bar{F}_{S \vee D,i}$ was 0.146 ± 0.042 SD and ranged from 0.128 ± 0.043 SD in 2020 to 0.196 ± 0.02 SD in 2014.

Generalized Additive Mixed Models (GAMMs) were used to estimate intra- and inter-annual trends in $\bar{F}_{S,i}$ and $\bar{F}_{S \vee D,i}$. The average seasonal pattern across all years was fitted with a thin-plate regression spline of day of year and its variation between years as a factor-smooth interaction between day of year (continuous) and year (categorical). This allowed smooth relationships of differing complexity between $\bar{F}_{S,i}$ and $\bar{F}_{S \vee D,i}$ and day of year to be estimated for each year. The Beta error distribution and logit link were chosen because the response variables are proportions bound between 0 and 1.

As well as day of year and year effects, the analysis of $\bar{F}_{S,i}$ included random intercept terms for factory and vessel effects. Trip was not included due to low sample size in the Scottish dataset. The model equation was:

$$\begin{aligned} \bar{F}_S &\sim \text{Beta}(\theta_1, \theta_2) \\ \mu &= \frac{\theta_1}{\theta_1 + \theta_2} \end{aligned} \quad (1)$$

$$\text{logit}(\mu) = \alpha + \beta_{\text{year}} + f(\text{doy}) + f_{\text{year}}(\text{doy}) + \zeta_{\text{factory}} + \zeta_{\text{vessel}}$$

where θ_1 and θ_2 are shape parameters; μ is the mean probability of the response variable; β denotes a fixed effect; f denotes a smoother; doy is day of year (Julian calendar); and ζ denotes a random intercept. Full results from Model 1 can be found in the Supplementary information, however, factory and vessel accounted for 20.1% and 13% of unexplained variation in $\bar{F}_{S,i}$, respectively. Factory was, therefore, included in the model containing the Scottish and Dutch data combined. A separate doy smooth was also fitted for each country in a factor-smooth interaction, allowing differences between measurement methods to be estimated. The model equation was:

$$\begin{aligned} \bar{F}_{S \vee D} &\sim \text{Beta}(\theta_1, \theta_2) \\ \mu &= \frac{\theta_1}{\theta_1 + \theta_2} \end{aligned} \quad (2)$$

$$\text{logit}(\mu) = \alpha + \beta_{\text{year}} + \beta_{\text{country}} + f(\text{doy}) + f_{\text{year}}(\text{doy}) + f_{\text{country}}(\text{doy}) + \zeta_{\text{factory}} + \zeta_{\text{trip}}$$

Concurvity between year- and country-specific doy smoothers and $f(\text{doy})$ was minimized by penalizing their first, rather than second, derivative.

Table 2. Predictors included in the analysis of the Scottish only and the Scottish and Dutch combined datasets and rationale for their inclusion.

| Variable | Analysis | Details | Type | Impact on response variable |
|-------------|--------------------|---|-------------------|---|
| Day of year | Both | Scottish dataset: 146–257 Dutch dataset: 138–330 | Continuous | Annual reproductive cycles |
| Year | Both | Scottish dataset: 2006–2010, 2012–2019 | Categorical fixed | Ecosystem changes and unbalanced sampling |
| Trip | Scottish and Dutch | Dutch dataset: 2015–2020 Unique identifier assigned to each fishing trip | Random | Particular area fished during a trip |
| Vessel | Scottish | Unique identifier assigned to each vessel | Random | Scottish dataset: skipper fishing preferences Dutch dataset: skipper fishing preferences and technician teams |
| Factory | Both | Unique identifier assigned to each processing factory | Random | Scottish dataset: technician teams Dutch dataset: skipper fishing preferences and technician teams |
| Country | Scottish and Dutch | Scotland or the Netherlands | Categorical fixed | Dutch dataset: skipper fishing preferences and technician teams Different measurement methods used between countries and unbalanced sampling |

Table 3. Mature North Sea herring (*Clupea harengus*) sample sizes per year and country in the Scottish and Dutch combined dataset with available months, days of year, vessels, and factories. Vessel and factory are the same in the Netherlands hence only one is shown. All Scottish observations shown constituted the Scottish only dataset apart from the single observation in November 2017 (day 314), meaning the sample size for this year in the Scottish only dataset was 132.

| Year | Country | Months | Days of year | Number of vessels | Number of factories | Sample size |
|-------|-------------|----------------------------|--------------|-------------------|---------------------|-------------|
| 2006 | Scotland | June–August | 157–240 | 9 | 1 | 32 |
| 2007 | Scotland | July–September | 184–253 | 6 | 1 | 14 |
| 2008 | Scotland | July–August | 184–240 | 6 | 2 | 15 |
| 2009 | Scotland | July–August | 188–238 | 8 | 2 | 15 |
| 2010 | Scotland | June–September | 153–249 | 11 | 2 | 29 |
| 2011 | | | | | | |
| 2012 | Scotland | May–September | 146–247 | 9 | 2 | 80 |
| 2013 | Scotland | June–September | 157–245 | 9 | 2 | 77 |
| 2014 | Scotland | June–August | 154–227 | 7 | 3 | 54 |
| 2015 | Scotland | June–August | 155–239 | 5 | 3 | 126 |
| | Netherlands | July–October | 190–291 | | 2 | 92 |
| 2016 | Scotland | May–September | 152–249 | 9 | 3 | 82 |
| | Netherlands | July–October | 184–304 | | 7 | 427 |
| 2017 | Scotland | May–September and November | 150–314 | 7 | 3 | 133 |
| | Netherlands | June–November | 173–322 | | 6 | 530 |
| 2018 | Scotland | May–September | 150–257 | 5 | 3 | 157 |
| | Netherlands | June–November | 157–330 | | 12 | 1 240 |
| 2019 | Scotland | June–September | 155–254 | 6 | 2 | 85 |
| | Netherlands | May–November | 138–328 | | 10 | 976 |
| 2020 | Netherlands | May–November | 138–309 | | 10 | 811 |
| Total | | | | | | 4 975 |

For each year (y) and country, maximum predicted $\hat{F}_{S \vee D, i}$ values ($\max \hat{F}_{S \vee D, y}$) and the predicted timing (day of Julian calendar) of these maximum values ($\hat{J}_{S \vee D, y}$) were computed from Model 2. These metrics were used as response variables to model their inter-annual variability for each country. These models were specified as:

$$\begin{aligned} \max \hat{F}_{S \vee D} &\sim \text{Beta}(\theta_1, \theta_2) \\ \mu &= \alpha + \beta_{\text{country}} + f_{\text{country}}(\text{year}) \end{aligned} \quad (3)$$

$$\begin{aligned} \hat{J}_{S \vee D} &\sim \text{Normal}(\mu, \sigma^2) \\ \mu &= \alpha + \beta_{\text{country}} + f_{\text{country}}(\text{year}) \end{aligned} \quad (4)$$

Parameter names $\theta_1, \theta_2, \mu, \sigma^2, \alpha, \beta, f$, and ζ are recycled and not shared between models. The weight of each $\max \hat{F}_{S \vee D, y}$ and $\hat{J}_{S \vee D, y}$ value was determined by the normalized precision of its prediction, meaning values estimated with higher precision contributed more to the model log-likelihood, i.e.

$$\text{Weight}_k = \frac{SE_k^{-2}}{\bar{x}(SE^{-2})}, \quad (5)$$

where SE_k^{-2} is the precision of k th value; and $\bar{x}(SE^{-2})$ is the mean precision across all values. Coefficients of Model 2 were simulated 10000 times and $\hat{J}_{S \vee D, y}$ values were extracted for each simulation.

Table 4. Results from the GAMM analysing the Scottish and Dutch combined dataset ($\hat{F}_{S \vee D, i}$). e.d.f is the effective degrees of freedom and represents the complexity of the fitted smooth for each term. Smooth terms containing a colon (:) represent factor-smooth interactions and their associated values quantify the difference between the smooth for each factor level and the “s(day of year)” smooth term.

| Smooth terms | e.d.f | Chi-square | p-value |
|----------------------------|-------|------------|---------|
| s(day of year) | 19.89 | 249.7 | < 0.001 |
| s(day of year):2006 | 0.003 | 0.001 | 1.000 |
| s(day of year):2007 | 2.652 | 16.32 | 0.051 |
| s(day of year):2008 | 0.003 | 0.002 | 0.531 |
| s(day of year):2009 | 0.044 | 0.049 | 0.311 |
| s(day of year):2010 | 0.483 | 1.075 | 0.245 |
| s(day of year):2012 | 0.005 | 0.001 | 1.000 |
| s(day of year):2013 | 5.238 | 205.4 | < 0.001 |
| s(day of year):2014 | 0.011 | 0.008 | 0.442 |
| s(day of year):2015 | 11.49 | 315.7 | < 0.001 |
| s(day of year):2016 | 14.96 | 237.1 | < 0.001 |
| s(day of year):2017 | 13.18 | 13.83 | < 0.001 |
| s(day of year):2018 | 4.449 | 11.94 | 0.130 |
| s(day of year):2019 | 34.01 | 367.4 | < 0.001 |
| s(day of year):2020 | 14.27 | 88.73 | 0.042 |
| s(day of year):Netherlands | 0.021 | 0.019 | 0.002 |
| s(day of year):Scotland | 10.80 | 103.9 | 0.098 |
| s(factory) | 15.82 | > 1 500 | < 0.001 |
| s(trip) | 346.4 | 4 248 | < 0.001 |

The distribution of $\hat{F}_{S \vee D, y}$ values allowed 95% CIs of the estimates to be calculated using 0.025 and 0.975 probability quantiles (Wood, 2017).

All analyses were carried out in R (R Core Team, 2020, version 4.0.2) using the *mgcv* package and *gam* function (Wood, 2017). Normality of residuals, homogeneity of variance between deviance residuals and linear predictors, and number of basis functions were checked using the *gam.check* function from *mgcv*.

Results

Model 2, which analysed variability in $\hat{F}_{S \vee D, i}$ (hereafter, referred to as fat content), explained 88.7% of deviance. Effective degrees of freedom (i.e. measure of smoother complexity), Chi-square values, and *p*-values for each smooth term of Model 2 are shown in Table 4. There was a significant non-linear seasonal pattern in fat content (e.d.f = 19.89, *p* < 0.001), which was consistent with annual reproductive cycles of North Sea herring. Fat content increased from 0.045 on day 138 (late May) to 0.161 on day 178 (late June; Figure 2). Fat content remained relatively constant until day 205 (late July), coinciding with the summer feeding period. Fat content then declined gradually throughout August and September from 0.158 on day 205 to 0.091 on day 262 (mid-September), coinciding with the migration and spawning periods. Fat content then remained relatively constant, ranging between 0.091 and 0.097, until day 302 (late October) after which it declined to 0.053 on day 330 (late November), coinciding with the start of overwinter (Figure 2).

Year-specific smoothers for 2013, 2015–2017, 2019, and 2020 were significantly different from the mean effect of day of year (Figure 3; Table 4). However, each year-specific smooth displayed a rapid increase in fat content between days 138 and 204. On average, in all years apart from 2015, fat content plateaued between days 160 and 225. In 2015, fat content reached a pronounced peak on day 204 before declining rapidly. Fat content also declined rapidly in 2017 following a plateau between days 160 and 235. The decline in other years was more gradual. Fat content generally increased slightly

or plateaued immediately following spawning. However, in 2015, fat content in both countries declined gradually following spawning while in 2019 it increased steadily. Country-specific smoothers were not significantly different from the mean effect of day of year (Netherlands: e.d.f. = 0.021, *p* = 0.002; Scotland: e.d.f. = 10.8, *p* = 0.098), however, fat content was higher in Scotland than the Netherlands across all day of year and year values for which there was data (Figure 3). Significant differences in fat content were found between factories and trips (*p* < 0.001 for both effects; Table 4).

$\max \hat{F}_{S \vee D, y}$ (hereafter, referred to as maximum fat content) ranged from 0.22 in 2008 (Scotland) to 0.16 in 2020 (Netherlands), with a mean of 0.186 ± 0.017 SD (Figure 4). Scotland had higher maximum fat content values across all years for which there was data for both countries (Figure 4). In the Dutch data, maximum fat content increased slightly between 2006 and 2012 before declining slowly until 2020 (e.d.f. = 2.68, *p* = 0.01; Figure 4). There was no relationship between maximum fat content and year in the Scottish data (e.d.f. = 1.89, *p* = 0.38; Figure 4). Since there were no Dutch data available prior to 2015 and no Scottish data available in 2020, estimated trends for these years followed those of the other country and were, thus, omitted from Figure 4. $\hat{J}_{S \vee D, y}$ (hereafter, referred to as timing of maximum fat content) ranged from day 161 in 2017 (Scotland) to day 217 in 2016 (Netherlands), with a mean of $194 \pm SD 14$ d (Figure 5). There was large uncertainty in the Scottish data in 2007, 2013, 2016, 2017, and 2019 which correspond to years when there was a larger increase in fat content following spawning (Figure 5). In the Netherlands, the timing of maximum fat content advanced by approximately 10 days between 2015 and 2020, however, this change in timing was not significant (e.d.f. = 2.93, *p* = 0.18; Figure 5). There was no trend in the timing of maximum fat content in the Scottish data (e.d.f. = 1, *p* = 0.85; Figure 5). The generation of 10000 simulations of Model 2 coefficients revealed bimodal distributions in the timing of maximum fat content across years in both countries (Figure 6). This could indicate the presence of two peaks in fat content occurring on days 170 and 200 of years 2006, 2008–2012, 2014, 2018, 2020. In 2007, 2013, 2016, and 2019,

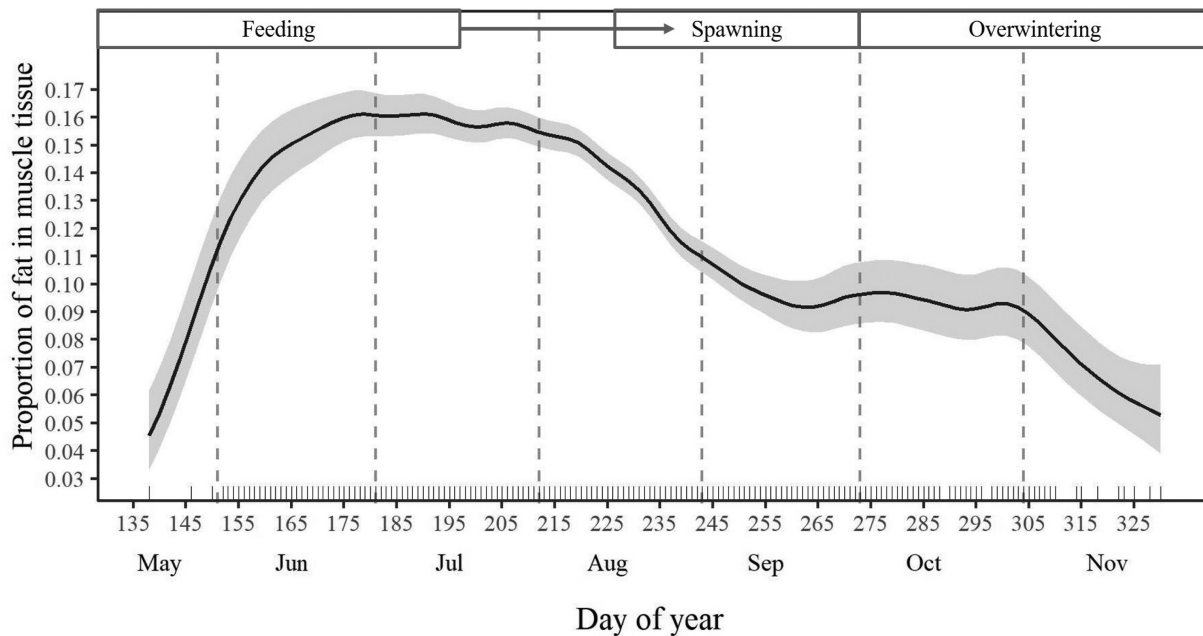


Figure 2. Fitted smooth function for day of year for the analysis of $\bar{F}_{SVD,i}$ with 95% CIs and the timing of feeding, spawning, and overwintering periods indicated (van Damme *et al.*, 2009; McPherson, 2010; Hufnagl *et al.*, 2015). The arrow represents the spawning migration. The vertical bars along the x-axis are a “rug plot” that represents the distribution of observed data across the full range of day of year values.

these peaks are smaller and further apart, with the second peak occurring around day 310. In 2017 and 2019, the first peak occurred earlier than in other years around day 160. In 2015, there was a single pronounced peak in both countries around day 200.

Discussion

Intra-annual variability

This study utilized herring fat content data associated with high (i.e. daily) temporal resolution collected by Scottish and Dutch processors. The detailed analysis of such large-scale industry data on North Sea herring fat content has not previously been undertaken. We aimed to validate the accuracy of such data by determining whether estimated intra-annual patterns reflected annual reproductive cycles of North Sea herring. We found a strong intra-annual signal in fat content which matched the expected pattern of accumulation and utilization previously reported for northeast Atlantic herring stocks (Wood, 1958; Slotte, 1999; Óskarsson, 2005; van Damme *et al.*, 2009; Røjbek *et al.*, 2014). Fat content increased and reached a maximum between May and June during feeding as excess fat became stored in the muscle tissue. It then declined during August and September as herring migrated to spawning grounds, metabolizing fat stores to provide energy for movement and gonad development. Low fat content values were estimated during spawning and overwintering periods after fat stores had been depleted. This intra-annual pattern did not differ between countries, despite the fact that Scottish and Dutch processing factories used different measurement methods. The consistency between these data sources has not previously been demonstrated and confirms they are comparable.

Our results are consistent with Wood (1958), who found the fat content of whole North Sea herring increased from 9.2% in May to 22% in July before declining in September to 13.9% and

increasing slightly again in October and November. Wood (1958) concluded the secondary increase resulted from post-spawning herring taking advantage of relatively abundant food resources. However, these conclusions are based on low sample sizes (2–5 herring) for May, October, and November. van Damme *et al.* (2009) also found autumn-spawning herring fat content increased from May to June before declining in September, however, the seasonal pattern was resolved at a monthly resolution with no samples obtained following spawning. Our study contained 177 samples in May, October, and November across 7 years, with daily temporal resolution throughout the summer months. Fat content increased from 4.5% in May to 16.1% in late June/early July before declining in August and September to 9% and even further in November to 3%. Other studies on herring fat content dynamics have largely been carried out on Norwegian spring-spawning, Icelandic summer-spawning, and western Baltic spring-spawning stocks (Slotte, 1999; Óskarsson, 2005; Røjbek *et al.*, 2014). These stocks differ in the timing of their annual cycle throughout the year, particularly the spawning period. Therefore, seasonal dynamics in fat content also differ between stocks. However, the accumulation of fat during feeding and its subsequent utilization during spawning and overwintering periods (regardless of the time of year they occur) is synonymous across stocks (McPherson, 2010). The consistency between our results and previous findings (Wood, 1958; Slotte, 1999; Óskarsson, 2005; van Damme *et al.*, 2009; Røjbek *et al.*, 2014) demonstrate that fat content data routinely collected by pelagic processors in the northeast Atlantic accurately capture underlying dynamics in herring bioenergetics. Our study also estimates these dynamics with high precision previously unattainable from scientific sampling.

Intra-annual variability of pelagic fish fat has commercial implications, with market value of “oily” species such as herring being partly influenced by muscle fat content. These implications may be stock-dependent due to differing rates of fat utilization between

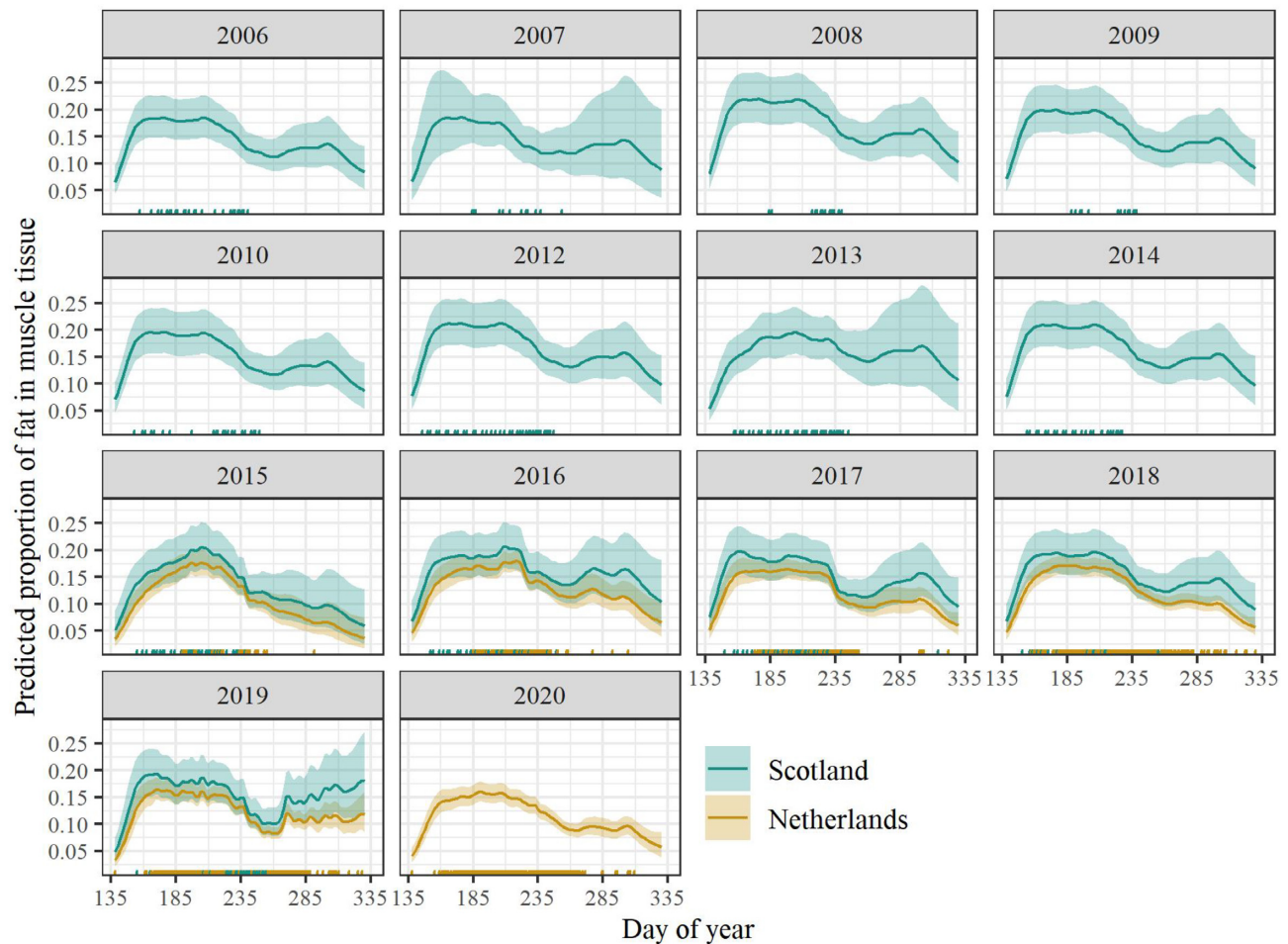


Figure 3. Predicted seasonal pattern in proportion muscle fat content ($\bar{F}_{S \vee D, i}$) from 2006 to 2020, with 95% CIs. The vertical bars along the x-axis are a “rug plot” that represents the distribution of observed data.

stocks. We found the rate of decline in fat content between the end of the feeding period (mid July) and beginning of the spawning period (mid September) was 0.11% per day for North Sea herring. Over the same time frame in Norwegian spring-spawning herring, Slotte (1999) found percentage muscle fat content declined by 0.03% per day. The faster rate of decline found in our study can be explained by the need for North Sea herring to mobilize fat stores immediately following feeding to prepare for spawning. Remaining fat stores are then gradually utilized during overwinter. Conversely, Norwegian spring-spawning herring gradually utilize mesenteric fat stores during migrations and overwinter before depleting muscle fat during the spawning migration in spring. During a captive tank experiment, McPherson (2010) found total fatty acids in both the muscle and mesenteries of adult North Sea herring decreased during gonad development, however, the relative utilization of these fat depots throughout the annual cycle remains unknown. Our study confirms muscle fat is utilized during the pre-spawning, spawning, and overwintering periods of North Sea herring. However, observational data having similar degree of intra-annual resolution on mesenteric fat would need to be analysed to evaluate how this fat store in North Sea herring is utilized throughout the year in relation to muscle fat.

Inter-annual variability

The effect of day of year on fat content was similar across all years, indicating the annual reproductive cycle has a large influence on seasonal fat dynamics each year in adult herring. Coherent seasonal patterns in fat content due to annual reproductive cycles have been reported in several other species and are common in capital spawners (Lloret *et al.*, 2014). In most years, fat content increased slightly after spawning. As Wood (1958) hypothesized, this secondary rise may result from secondary feeding opportunities. This could be particularly beneficial to herring which spawn first in August around Orkney and Shetland, as zooplanktonic prey may still be available during late summer. Icelandic summer-spawning herring are known to have two feeding periods, temporally separated by one overwintering and one spawning period (Óskarsson, 2008). Opportunistic feeding following spawning could allow North Sea herring to overwinter in better condition, reducing mortality during this critical period (Gücü *et al.*, 2018). Inter-annual changes during the feeding period in 2015–2017 and 2019 could be due to variability in zooplankton seasonal cycles. Changes in the spatial and/or temporal overlap between the herring population and food availability could cause slight fluctuations in fat accumulation during feeding (Corten, 2000; Mackas *et al.*, 2012).

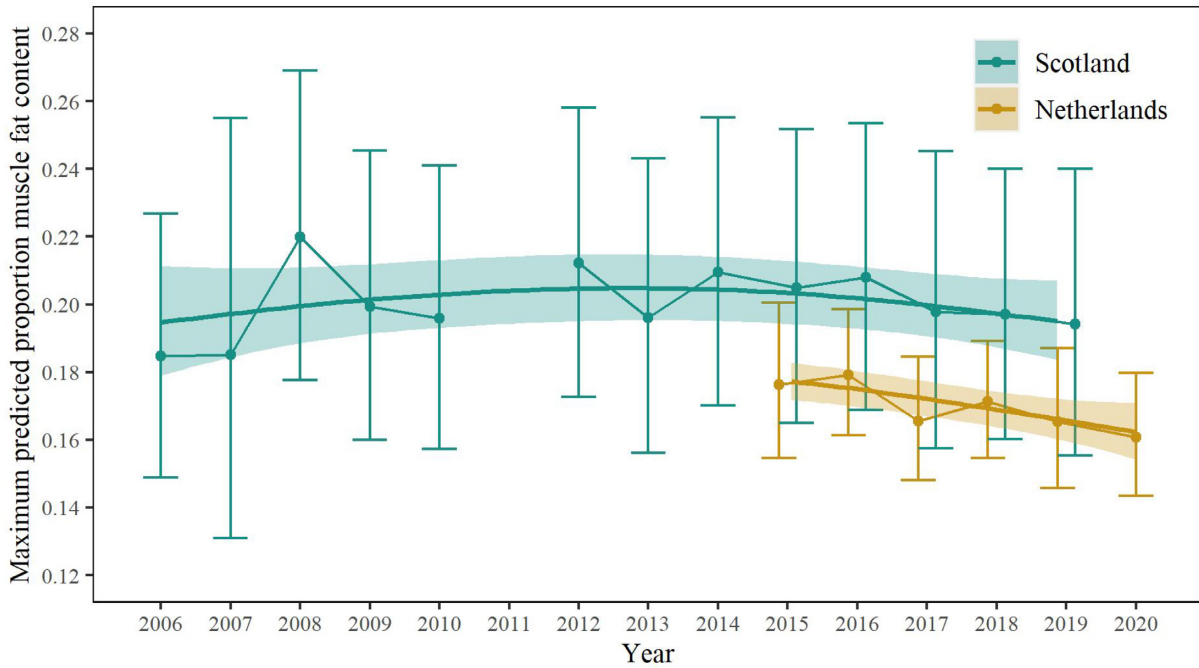


Figure 4. Maximum proportion muscle fat content ($\max \hat{F}_{S \vee D, y}$) and fitted smooth function of year from 2006 to 2020 across both countries, with 95% CIs.

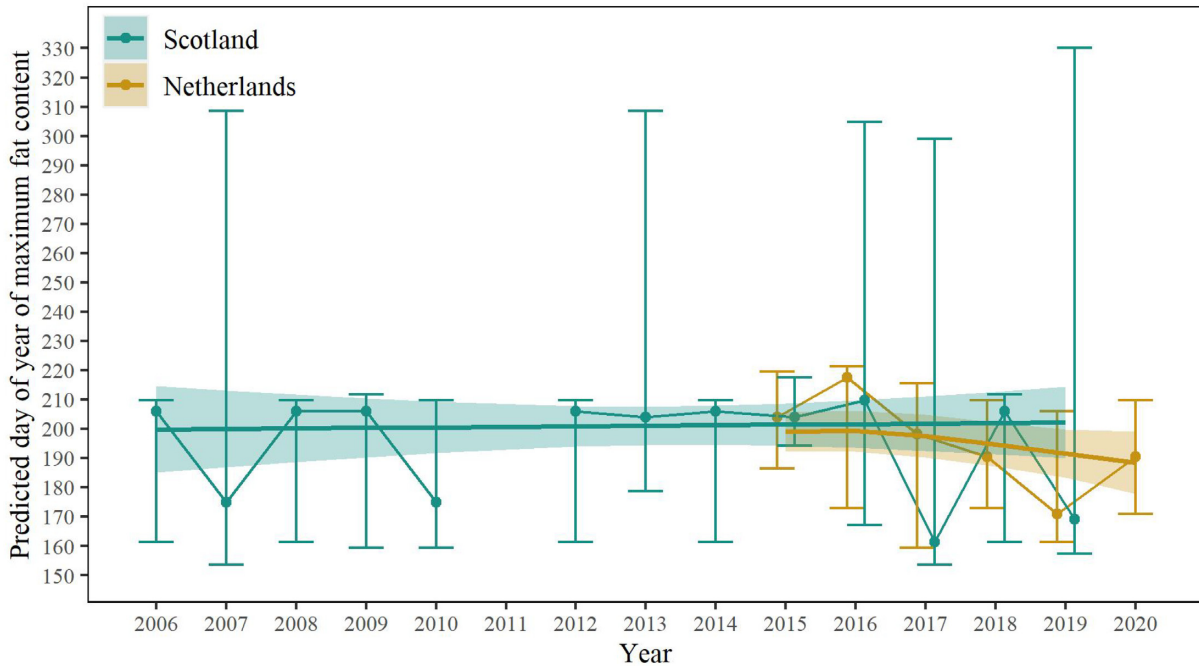


Figure 5. Day of year of maximum proportion muscle fat content ($\hat{J}_{S \vee D, y}$) and fitted smooth function of year from 2006 to 2020 across both countries, with 95% CIs.

We found no difference in the timing and magnitude of peak fat content between years. This contradicts other studies which have found considerable inter-annual fluctuations in fish stock condition resulting from changes in prey species availability (Shulman *et al.*, 2005; Brosset *et al.*, 2017). Herring feed mainly on *Calanus* copepods (Raab *et al.*, 2012), the abundance of which in the North Sea has declined over the duration of our study period

(Capuzzo *et al.*, 2018). Inter-annual variability in the timing and magnitude of peak fat content perhaps did not reflect these changes in prey abundance due to the presence of two peaks in fat content each year. These peaks could be due to the presence of two sub-populations of North Sea herring (those which spawn first in August around Orkney and Shetland and another which spawns in September around Buchan and the Banks areas), which fishers

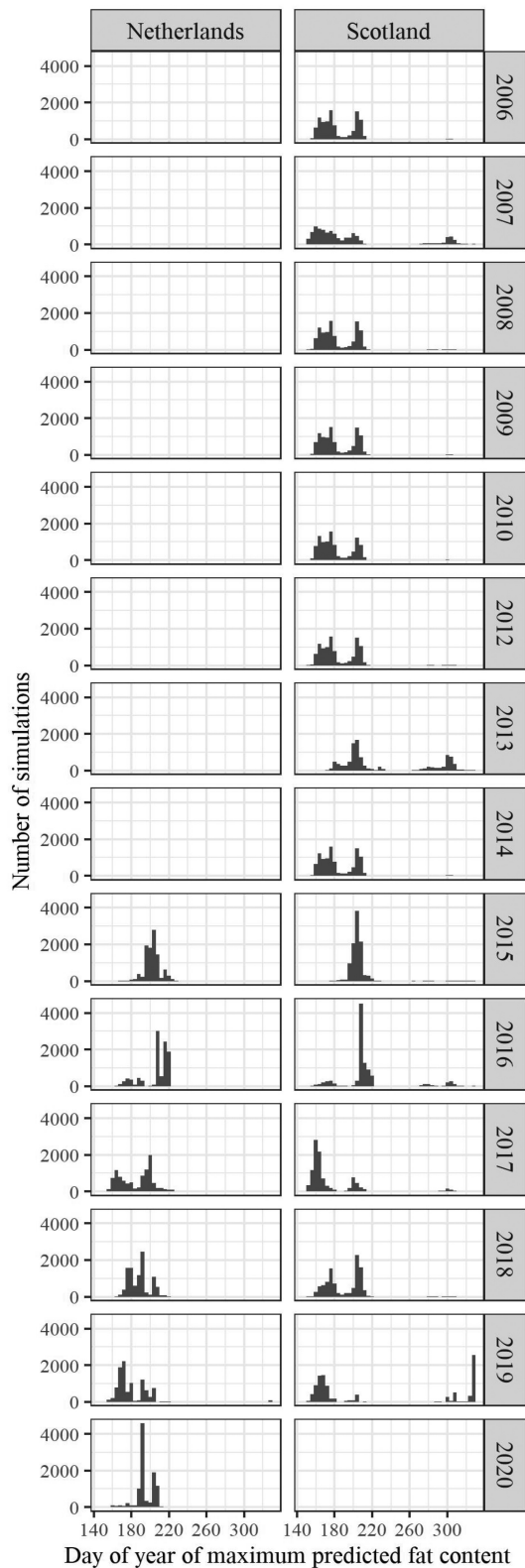


Figure 6. Distributions of the day of year of maximum proportion muscle fat content resulting from 10000 posterior simulations from Model 2 (response variable: $\bar{F}_{S \vee D, i}$) for each year and country.

follow along a north to south gradient. Wood (1958) found temporal differences in the utilization of fat between North Sea autumn-spawning and winter-spawning herring, however such differences within only autumn-spawners as found in this study have not previously been reported. Another possible explanation could be the targeting of juvenile herring by both countries during June. These herring have not yet invested fat reserves for maturation and so have a particularly high muscle fat content. The second peak occurs when adult herring are targeted later in the season during July. Although an effort was made to remove immature herring from our dataset based on weight, it is possible that larger than average immature herring remained in the analysis causing the first peak in mean fat content during June.

Application of industry data

Our study validates routinely collected fat content data from fish processing factories and estimates intra-annual variability in herring fat content with high precision. To our knowledge, there are no comparable population-level datasets on species bioenergetics which cover broad spatio-temporal scales with high resolution. Such industry datasets can have wide scientific applications due to their ecological value. For example, the sensitivity of fat content to biotic and abiotic factors experienced by individuals mean it can reliably indicate food consumption (Shulman *et al.*, 2005), ecosystem status (Latour *et al.*, 2017), and habitat quality (Schloesser and Fabrizio, 2019; Champion *et al.*, 2020b). These applications may also benefit fisheries management decisions. Pelagic fishes provide an important ecological function through trophic transfer of energy. Since fat is known to impact reproductive potential and is in turn influenced by food availability, industry datasets can provide useful insights into factors affecting stock dynamics, such as recruitment (Jansen *et al.*, 2021). Additionally, knowledge of inter-annual variability in the seasonal pattern of fat content could inform pelagic fishery harvesting decisions (Lloret *et al.*, 2014). Both the Scottish and Dutch pelagic fisheries produce different products depending on the magnitude of muscle fat content (Aidos *et al.*, 2002). For example, adult herring are caught immediately following the feeding period to obtain maximum muscle fat content for filleted products. Predicting when herring muscle fat content will be highest year to year can allow fisheries to optimize the value of their catch before fat content declines during the onset of spawning (Mello and Rose, 2005). Ultimately, continued and systematized monitoring of fat content and other biological properties by fishing industries across the northeast Atlantic can serve as a valuable bioindicator of changes in commercially important fish species and their ecosystems.

Supplementary material

Supplementary material is available at the ICES/JMS online version of the manuscript.

Data availability statement

Anonymized data underlying this article will be shared upon reasonable request to MP or SM with permission from the data owners listed in the Acknowledgements.

Authors' contributions

SK, MP, SM, and CTM conceived the ideas and designed the methodology; SM and MP facilitated access to the data; SK and MP collated the data; SK and TC analysed the data; and SK led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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