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**Potential Mechanisms Behind Changing Survey Catchability in 4RSw
Atlantic Herring**

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Hydroacoustic surveys conducted in late October–early November have been the primary method for assessing Atlantic herring (*Clupea harengus*) in NAFO Division 4RSw since 1991. The first survey series (1991–2002) in 4R produced consistent cohort patterns, while the second series (2009–2022) revealed inconsistencies attributed to changes in survey catchability. Shifts in catchability can decouple survey indices from true biomass, biasing population trend estimates, and are notoriously difficult to resolve without understanding the underlying causes or complementary data sources. This document aims to explore possible physiological and environmental mechanisms and to identify covariates linked to an apparent shift in catchability of herring in 4RSw. We first established the evidence for a delayed fall migration based on landing records and fish telemetry data, showing a 30–60 days temporal mismatch between the median fall acoustic survey date and the date of 50% cumulative landings in 4Rbc from 1991–2022. This shift was not tied to the timing of fall herring spawning. Rather, a delay in landings was associated with lower herring body condition in the fall, suggesting changes in feeding conditions prior to migration into the survey area. Habitat suitability maps suggested that environmental changes do not constrain herring migration into the survey area, but have become increasingly favourable in northern, unsurveyed waters. The complexity of migratory dynamics, together with uncertainties in environmental data, currently limits the establishment of a clearer relationship with the timing of fish landings. Given the available information and the consequences of overlooking changes in survey catchability, we recommend using the temporal mismatch between survey timing and landings as the most suitable covariate to capture these shifts within future stock assessment frameworks.

1. INTRODUCTION

Hydroacoustic surveys have provided the main input for assessing spring and fall Atlantic herring (*Clupea harengus*) in NAFO Divisions 4RSw since 1991 (Figure A1). Conducted in late October–early November to coincide with peak landings, these surveys were initially designed under the assumption that most of the stock was regionally available at that time. The first survey series (1991–2002), conducted every two to three years in 4R, produced relative abundance-at-age patterns consistent with expected cohort attrition (Chamberland *et al.* 2022). In contrast, the second fall series (2009–2022), conducted annually or biennially in 4R and 4Sw, showed inconsistencies when tracking both spring and fall herring cohorts. This contributed to the discontinuation of the fall survey in 2022 and its replacement by a summer acoustic survey initiated in 2019. The inconsistencies in the second fall series appear to be related to changes in survey catchability rather than to observation noise, raising concerns about the reliability of the biomass index to track stock dynamics. These concerns ultimately led to the rejection of the analytical population framework at the November 2020 peer-review meeting and to a recommendation for a full revision of both data inputs and the assessment framework (DFO 2021).

Evidence suggests that changes in fall survey catchability may be linked to shifts in the timing of herring migration. In Divisions 4RSw, herring follow a seasonal north–south migration cycle: after overwintering in the Esquiman Channel, schools migrate northward and inshore in spring, move to and remain in northern areas (4Sw, 4Ra, Strait of Belle Isle) during summer, and then migrate south along Newfoundland’s west coast (mainly 4Rbc) in the fall, where a major purse seine fishery takes place, before returning offshore for the winter (McQuinn and Lefebvre 1995, Émond and Nilo 2025). When the fall acoustic survey was first implemented, it was timed to coincide with the commercial fishery, when herring were believed to have already migrated south into the survey area (4R). However, shifts in the timing of the commercial fishery to a later date since the early 2000s suggest a progressively later fall migration and, therefore, a delayed herring arrival in the survey area within 4RSw (Émond *et al.* 2024). It is hypothesized that a portion of the stock might have remained in the northern areas, which were not covered by the survey in the first period or beginning of the second period (e.g. Strait of Belle Isle). Consequently, the fixed survey window in late October–early November no longer captured the same proportion of the stock during the second survey period (2009–2022), thereby reducing catchability and compromising the reliability of the biomass index for stock assessment.

Spatial and seasonal shifts in fish migration can occur in response to a combination of physiological, environmental, anthropogenic, and ecological factors. Seasonal migrations are influenced by endogenous traits such as age, body size, physical condition, and energy reserves (Thorpe 1994, Brodersen *et al.* 2008, Shaw 2016). Environmental factors like water temperature (Castonguay *et al.* 1999, Tojo *et al.* 2007, Crozier and Hutchings 2014) and food availability (Corten 2000, Broms *et al.* 2012) may likewise affect migrations. Climate change, for instance, has altered sea temperatures and ocean currents, disrupting the spatial and temporal distribution of marine species (Poloczanska *et al.* 2016). For spring-spawning Atlantic herring in the Kiel Fjord (Baltic Sea), empirical studies have shown that they arrive earlier at their spawning grounds in response to warmer winter sea temperatures (Ory *et al.* 2024). Anthropogenic pressures such as overfishing may also interfere with traditional migratory routes by removing experienced older individuals who transmit migratory knowledge (Fernö *et al.* 1998). Ecological factors such as population density and community interactions can likewise affect large-scale migration patterns (Kvamme *et al.* 2003, Shaw 2020, Ono *et al.* 2022).

Understanding the mechanisms driving 4RSw herring migration dynamics is essential for accurately estimating changes in fall acoustic survey catchability and deriving reliable trends in

spawning stock biomass. This document aims to identify processes that might co-vary with shifts in fall survey catchability and could be incorporated into the new population model. We first summarize direct evidence of a shift in fall migration timing based on landings and fish telemetry data (Émond and Nilo 2025). We then evaluated three hypotheses that may explain this shift, the cascading effect hypothesis, the retention hypothesis, and the avoidance hypothesis, by examining physiological parameters relevant to migration timing, including fish spawning phenology and body condition. Finally, we assess environmental drivers of herring spatiotemporal distribution, such as water temperature and prey availability. Together, these analyses aim to clarify the mechanisms underlying altered migration dynamics, inform fall acoustic survey catchability changes, and identify covariates to integrate into the stock assessment framework.

2. METHODS

2.1. DIRECT EVIDENCE FOR CHANGE IN THE TIMING OF FALL MIGRATION

In the fall, both spawning components migrate southward and aggregate along the west coast of Newfoundland, particularly in the vicinity of Bonne Bay (4Rb) and Bay of Islands (4Rc), where a major purse-seine fishery occurs. Over the past two decades, this fishery has progressively shifted later in the season, occasionally extending into January, likely reflecting a delay in the timing of herring migration (Chamberland *et al.* 2022, Émond *et al.* 2024). To characterize this temporal shift, we identified for each year (1985–2024) the date at which 50% of cumulative fall landings had occurred, along with the dates corresponding to 25% and 75% of cumulative landings, representing the central period during which 50% of herring were landed. Commercial landing data for Atlantic herring in Division 4R were obtained from the Zonal Interchange File Format (ZIFF) files produced by DFO’s regional statistics bureau (see Émond *et al.* 2024 for details). For this analysis, we focused on landings in subdivisions 4Rb and 4Rc from mid-September to the end of January to isolate the region and period that best capture the temporal shift in landings.

Given that the timing of the fall acoustic survey has varied across years (1991–2022), and that the timing of the fishery has not followed the same pattern, the first proposed covariate quantifies the temporal mismatch between dates of peak landings and dates of the fall acoustic survey (4R, 1991–2002 and 2009–2022; Émond and Van Beveren In press), using a nonparametric bootstrap approach. Within each year, daily landings were resampled with replacement to generate simulated datasets equal in length to the original dataset, from which the corresponding median landing date was calculated. The difference between this date and the median survey date was computed for each replicate. This procedure was repeated 1,000 times, producing an empirical distribution of annual mismatches, from which the median and 2.5% and 97.5% quantiles were derived.

Changes in the timing of the fishery could result from shifts in fish phenology or in fleet behaviour, influenced by factors such as market or regulatory fishing considerations. We validated that the timing of the fishery reflected the arrival of herring using acoustic telemetry data. Herring acoustic tagging was initiated in 2021. A total of 189 herring were tagged near Blanc-Sablon (subdivisions 4Sw and 4Ra) in September 2021 ($n = 80$) and 2022 ($n = 79$), and in Port-au-Port Bay (subdivision 4Rc) in May 2022 ($n = 30$; see Émond and Nilo 2025 for details). Acoustic tagging detections on the main fishing grounds (subdivisions 4Rb and 4Rc) during the fall and early winter were used to confirm the timing of herring migration. For each year, we identified the date at which tagged herring arrived in this area based on detections at receivers deployed at the mouths of Bonne Bay and Bay of Islands, two bays that account for a large proportion of the landings (Émond *et al.* 2024). These arrival dates were then compared

with the date corresponding to 50% of cumulative landings from the commercial fishery, allowing us to assess whether the timing of the fishery reflects the southward migration of herring. The use of alternative metrics to characterize fishery timing (e.g., based on daily landings or CPUE) was explored but deemed less suitable due to data gaps or high variability.

2.2. POTENTIAL MECHANISMS UNDERLYING THE CHANGE IN THE TIMING OF FALL MIGRATION

A delay in the fall migration and the subsequent arrival of herring into the 4R survey area could result from one or a combination of several processes. Delayed migration from overwintering areas in spring could cascade through the annual migration cycle, leading to a later arrival on the fall spawning grounds (“cascading effect hypothesis”). Alternatively or jointly, favourable summer conditions in northern regions may promote extended residence, causing herring to remain longer in areas not covered by the survey (“retention hypothesis”). Also, unfavourable environmental conditions in southern areas during the fall may discourage migration toward the survey area (“avoidance hypothesis”). Together, these hypotheses provide a useful framework for identifying and testing environmental and biological covariates that may explain temporal changes in migration timing.

2.2.1. Cascading effect hypothesis

Because fishing in the spring and summer has been relatively limited within the last two decades, direct evidence of migration shifts earlier in the year is scarce. A possible delay in spring migration, and its cascading effect into the fall, could be most effectively examined through changes in spawning phenology. Both spring and fall herring migrate from deeper overwintering areas to nearshore regions in spring. Spring herring begin spawning shortly after arrival to these inshore waters, whereas fall herring typically reproduce in August. The timing of fall herring spawning is shaped not only by their return to the spawning grounds, but also by the cumulative effects of earlier seasonal processes, including nearshore migration and summer feeding. Due to the gonadal development of spring spawners occurring partly during a period when few or no samples are collected (late fall to late winter/early spring; Bradford 1993), estimates for this component could not be derived.

Herring samples have been collected since 1965, primarily from commercial fisheries and acoustic surveys (Émond *et al.* 2024), with additional samples obtained opportunistically from other research programs, including DFO’s ecosystem survey in the Estuary and northern Gulf of St. Lawrence (Chamberland *et al.* 2025) and more recent targeted initiatives such as the experimental gillnet survey (Santo *et al.* 2025). Although sample sizes vary among sources, approximately 75% of samples collected each year consist of 30 to 100 randomly selected individuals.

All samples were processed at the Maurice Lamontagne Institute (MLI) to determine total length (± 1 mm), total weight (± 1 g), sex (male, female or unknown/undetermined), gonad weight (± 0.1 g), gonadal maturation stage (macroscopic scale from 1 to 8), and age (0 to 11+), the latter assessed through otolith extraction and examination. Individuals were assigned to a spawning component (spring or fall) based on their gonad maturity stage and sampling date (McQuinn 1987, 1989).

The gonadosomatic index (*GSI*) was used to examine the spawning phenology of herring in Divisions 4RSw and was calculated as:

$$(\text{eq. 1}) \ GSI = \frac{W_g}{W_t} * 100$$

where W_g is the gonad weight (g) and W_t is the total weight (g) of individual fish. Because data availability was low in some years, data were grouped into 4-year periods. The mean daily GSI was then fitted with a bell-shaped function:

$$(eq. 2) f(GSI) = d * \exp\left(-\frac{(GSI-\mu)^2}{2\sigma^2}\right)$$

where d is the amplitude (height of the curve), μ is the mean (peak), and σ is the standard deviation describing the width of the curve. A mixed-effects model (R package *nlme*, Pinheiro *et al.* 2024) was applied, with the 4-year period included as a random effect. Alternative functional forms (e.g., double-logistic, gamma, log-normal, and skew-normal) were tested to account for a slight asymmetry in the GSI distribution, but none provided an improved model fit based on Akaike's Information Criterion (AIC) and visual assessment, nor did they affect the main conclusions of the analysis. To assess temporal changes in the timing of spawning, the means (μ) of the fitted curves, representing the estimated peak spawning dates, were estimated and plotted over time with the 95% confidence intervals estimated with a nonparametric bootstrap procedure.

2.2.2. Retention hypothesis

Herring may remain longer in their summer feeding areas, some of which extend beyond the dates of the acoustic survey. Evidence supporting this possibility includes herring detections in summer and fall acoustic survey strata sampled only during some periods (4Sw in 2009–2022 and the Strait of Belle Isle in 2021–2022), as well as sporadic herring catches by harvesters along the Labrador coast. Retention in feeding areas is likely influenced by environmental conditions and may be reflected in fish physical condition. For instance, a reduction in prey abundance, quality, or both could force herring to feed for a longer period to rebuild energy reserves necessary for overwintering, potentially resulting in lower body condition during the fall. Conversely, favourable conditions could promote extended residence in northern areas, thus leading to higher body condition. Energy reserves are also shaped by non-trophic factors such as temperature, which affects metabolic rates and therefore the energetic costs of maintenance and movement. To provide a more comprehensive view of stock changes, we examined temporal trends in fish body condition with the relative condition factor (Kn) of Le Cren (1951) which was estimated as:

$$(eq. 3) Kn = \frac{W}{aL^b}$$

W is the somatic weight (g), L the total length (mm), and a and b are the parameters of the logarithmic weight-length relationship. Kn was calculated separately for each spawning component and year. Because the estimated length-weight exponents are very close to the isometric values ($b = 2.97$ and 3.01 for spring and fall herring, respectively), interannual differences in the length structure of the sampled population are unlikely to introduce meaningful bias in mean Kn . Because the temporal variations in Kn were similar across ages 2–11+ (Figure B1), values were pooled annually for each spawning component. We calculated the mean Kn for spring- and fall-spawning herring collected in the northern feeding area (4Ra and 4Sw) during the summer months (July–September) and in the more southern area (4Rbc) where herring migrate during fall months (October to December). We then examined the relationship between mean Kn values and the date corresponding to 50% of cumulative landings in the fall/early winter commercial fishery.

2.2.3. Avoidance hypothesis

Assessing environmental changes is key to understanding shifts in herring habitat suitability or migration, as it can provide evidence supporting either the retention hypothesis or the avoidance hypothesis. Specifically, we asked whether northern summer or southern fall environmental conditions have changed in correspondence with changes in fall migration. Therefore, we developed a spatial distribution model to quantify the relationship between herring density and environmental variables, and to assess changes in habitat suitability at different spatiotemporal scales.

2.2.3.1. Environmental variables

Several environmental factors could influence the timing of herring migration, such as water temperature and salinity, seasonal plankton production, and water mass traits (Fernö *et al.* 1998). Among these, water temperature and zooplankton availability are considered key variables that may affect the migratory behaviour of herring (Broms *et al.* 2012).

We derived monthly (September–December) temperature estimates for 1999–2023 from the Global Ocean Physics Reanalysis (GLORYS12v1) model, provided by the EU Copernicus Marine Service Information (<https://doi.org/10.48670/moi-00021>). The dataset features a horizontal resolution of $1/12^\circ$ (~8 x 8 km grid cells) and a vertical resolution of 50 depth levels spanning from -5500 m to the surface. We calculated the average temperature in the 0–50 m layer (T0_50), the minimum temperature within the water column (Tmin), and the bathymetry (the water depth relative to sea level) with the estimates of GLORYS12v1 product. The T0_50 variable was chosen based on acoustic survey data consistently locating herring within this depth range (Figure D1), capturing realized vertical habitat use. Tmin was included as a threshold indicator, given that herring have been observed to avoid water colder than 1-2 °C in other regions (Fernö *et al.* 1998, Broms *et al.* 2012, Melle *et al.* 2020). Bathymetry was considered essential for identifying suitable adult and larval habitats, as it affects substrate availability and hydrodynamic stability (Standaert *et al.* 2024).

Calanus copepods are the dominant prey item in the diet of Atlantic herring, with other possible preys including fish larvae and eggs, euphausiids and mysids (Darbyson *et al.* 2003, Randall *et al.* 2022). For our analyses, we focused on the late developmental stages (copepodite stages IV–VI) of three species of *Calanus* (*C. finmarchicus*, *C. hyperboreus*, and *C. glacialis*). The 1999–2020 time series presented in Plourde *et al.* (2024) were extended with the 2021–2023 data from Canadian and U.S. oceanographic monitoring programs (AZMP from DFO, Mitchell *et al.* 2002; EcoMon from NOAA, Northeast Fisheries Science Center). Plourde *et al.* (2024) developed and validated zero-altered Gamma (ZAG) models to predict species-specific *Calanus* abundance (N/m^2), which were then converted into biomass (mg/m^2) to account for variations in individual body weight across species and years. We updated these species-specific *Calanus* distribution models (SDM) up to 2023 following the same approach and validation as Plourde *et al.* (2024). *Calanus* spp. biomass predictions were made at a monthly-yearly temporal scale using the GLORYS12v1 spatial grid ($1/12^\circ$). We used the predicted biomass (mg/m^2) of the three *Calanus* species for the full 1999–2023 period.

2.2.3.2. Herring density

A first series of acoustic surveys, aimed at estimating herring biomass during the fall, was completed in October and November of 1991, 1993, 1995, 1997, 1999, and in September 2002. A second series was conducted in October and November of 2009, 2010, 2011, 2013, 2015, 2017, and from 2019 to 2022 (Figure A1, Figure A2). Spatial survey coverage changed over time, with NAFO subdivision 4Sw included during the second period and two strata within the

Strait of Belle Isle added in 2021–2022. Although the annual fall survey biomass index is restricted to 4R data to maintain temporal consistency, all available strata from 2009 until 2022 were used here to characterize habitat suitability in order to maximize spatial coverage and capture the full range of environmental conditions associated with herring distribution.

The methodological details and results of the first series of acoustic surveys (1991–2002) are presented in McQuinn and Lefebvre (1999) and the second series (2009–2022) in Émond *et al.* (2024) and Beaudry-Sylvestre *et al.* (2024). Briefly, the hydroacoustic survey took place at night, in accordance with known diurnal cycles of herring (McQuinn and Lefebvre 1999), and followed a systematic stratified design comprising a maximum of fourteen strata. Not all strata were sampled each year due to operational limitations. Within each stratum, parallel transects were oriented perpendicular to the coastline, and their starting position was randomly reassigned each year. Transects were generally spaced at a target interval of 5 nautical miles; however, when survey time was limited or in response to weather conditions and operational constraints, spacing was occasionally increased to 7.5 or 10 nautical miles. Strata covered the main physical characteristics of the available habitat documented from scientific surveys and commercial catches, and included depths ranging from 8 to 250 m. The vessels used for the fall survey were equipped with a hull-mounted, split-beam SIMRAD EK60 or EK80 echosounder operating at up to five frequencies (38, 70, 120, 200, and 333 kHz). Conductivity, temperature, and depth profiles (CTD) were collected at the beginning of each stratum and used to adjust the sound speed and absorption coefficient during data collection for that stratum. Biological herring samples were collected by a second accompanying fishing vessel equipped with a purse seine or pelagic trawl net. A maximum of 100 herring were randomly selected from each haul, and each individual was measured (± 1 mm) and weighted (± 1 g).

We processed the raw volume backscattering strength (S_v : dB re 1 m⁻¹) using the standard approach outlined in McQuinn *et al.* (2005). The classification of herring targets in the acoustic data followed the procedure outlined in Beaudry-Sylvestre *et al.* (2024), which separates acoustic signals from fish with and without swimbladder based on differences in S_v across the 38, 120 and 200 kHz frequencies. Most acoustic signals classified as swimbladdered fish were considered to be herring. Echograms were subsequently scrutinized by the analyst to remove non-herring targets or reassign acoustic signals to the appropriate category (swimbladder or nonswimbladder) when necessary. Backscattering strength was integrated into cells 2 m deep and 25 m apart using the CH2 software (Simard *et al.* 2000) from 2009 to 2020 and Echoview 13 in 2021 and 2022 (Myriax Pty, Ltd., Hobart, Tasmania, Australia). The backscattering strength attributed to herring was then converted to density (kg/m²) using estimates of target strength per unit length determined from the equation of Ona (2003) for Atlantic herring at 38 kHz, and further converted to target strength per unit weight (McQuinn and Lefebvre 1999). Average fish length and weight were obtained from all available biological samples. Herring density estimates were calculated without distinguishing between the two spawning stocks (i.e., spring and fall spawners).

Herring density estimates (kg/m²) were available at a vertical resolution of 2 m (depth) and a horizontal resolution of 25 m for each transect ($n = 7,544,523$). For the spatial distribution analysis, we first summed densities across the entire water column (i.e., all 2 m depth cells). Then, to reduce spatial autocorrelation (herring schools may extend up to 200 m horizontally, Weber *et al.* 2009) and to align with environmental data, we averaged densities following the GLORYS12v1 spatial grid (1/12°). This resulted in a final dataset of 1,764 observations.

2.2.3.3. Data exploration and preprocessing

Prior to model fitting, we conducted an exploratory data analysis following the protocol of Zuur *et al.* (2010). Outliers were identified using Cleveland dotplots (Cleveland 1993). Collinearity among explanatory variables was assessed using the Variance Inflation Factor (VIF), and variables with $VIF > 3$ were excluded (Zuur *et al.* 2010). Pairwise scatterplots and Pearson's correlation coefficients (r) were also examined to ensure that highly correlated variables ($r > 0.70$) were not included simultaneously. The three *Calanus* species (*C. finmarchicus*, *C. hyperboreus*, and *C. glacialis*) showed strong intercorrelation ($r = 0.80$ – 0.91) and were therefore pooled into a single total biomass variable. *Calanus* spp. biomass was also highly correlated with bathymetry ($r = 0.91$, Figure C1). Both *Calanus* biomass and bathymetry exhibited right-skewed distributions and were log-transformed [$\log(x)$, base e] to improve normality.

The response variable (herring density) exhibited a few outliers, as revealed by the Cleveland plot (Figure C2). To reduce the influence of these extreme values, we applied winsorization by capping outliers at a predetermined threshold corresponding to the 0.995 quantile (Aguinis *et al.* 2013, Kwak and Kim 2017). The density variable was also right skewed, and 2.61% of observations were zeros. We thus applied a Generalized Additive Model (GAM) with a Gaussian distribution to characterize the spatial distribution of herring, using log-transformed density values [$\log(x)$, base e] for presence-only data (density > 0 , $n = 1718$).

2.2.3.4. Model fittings

We fitted GAMs using thin-plate regression splines for environmental covariates and a cubic regression spline for the temporal effect (year), with basis dimensions set to $k = 4$ – 5 to limit overfitting. Spatial structure was modelled using a two-dimensional thin-plate tensor product smoother, $te(\text{latitude}, \text{longitude})$, and an spatiotemporal interaction term, $ti(\text{latitude}, \text{longitude}, \text{year})$, to capture integrated spatial and temporal variability. Model fitting was performed using restricted maximum likelihood (REML) in the *mgcv* package in R (Wood 2025).

A suite of candidate models was developed to identify which explanatory variables—namely, temperature ($T0_{50}$ and $Tmin$), bathymetry (depth), and food biomass (*Calanus* spp)—were the most likely ecological drivers of variability in herring density. Model selection was based on the lowest AIC value among the predefined candidate models. We also computed ΔAIC and AIC weights (ω_i), where models with $\Delta AIC \leq 2$ were considered to have substantial support relative to the most parsimonious model (where it has a ΔAIC of 0, Burnham and Anderson 2002), and ω_i indicated the relative likelihood of each model within the candidate set (Vandekerckhove *et al.* 2015).

2.2.3.5. Model validations

We verified normality of residuals using normal quantile-quantile plots, the homogeneity of residuals by plotting residuals vs. fitted values, against each covariate in the model, and the accuracy of predictions against observations (Quinn and Keough 2002, Zuur *et al.* 2010). We used variograms to assess spatial independence of residuals (Schabenberger and Pierce 2001). We evaluated the model performance and the adjustment through a suite of quantitative metrics, i.e., the explained deviance, the adjusted R-squared coefficient (R^2_{adj}), and the Mean Absolute Error (MAE, accuracy of the predictions compared to the observed values) by performing a cross-validation procedure using 70% of the data into a calibration set (to estimate model parameters) and 30% of the data into a validation set (to assess the quality of the fit).

Characterizing long-term seasonal changes in herring habitat suitability required projecting beyond the temporal window of observed conditions. Therefore, both interseasonal model robustness and interannual projection skill were assessed. We first visually confirmed that the

model results were not meaningfully different from an analogous model using the shorter summer acoustic survey dataset collected in August 2019–2023 (not reported in the present document). We then assessed the predictive performance of the species distribution model using the forecast skill approach (Kell *et al.* 2016). To do so, we iteratively excluded the final year of the time series, generated habitat suitability predictions for that year, and compared them to the observed values. This procedure was repeated while successively excluding the most recent years, up to the limit imposed by the spline’s basis dimension (k) in the GAM. Forecast accuracy was evaluated using the relative error (RE), calculated as:

$$\text{(eq. 4) } RE = \frac{\text{predicted value} - \text{observed value}}{\text{observed value}} \times 100$$

2.2.3.6. Predictions and habitat suitability mapping

We estimated herring habitat suitability (HS) for the areas (Labrador, Strait of Belle Isle, 4Ra-Sw, and 4Rbc) and months (September–December) of interest, over the period 1999–2023. This allowed us to understand how environmental drivers shape where herring can occur and how habitat suitability changed in both surveyed and unsurveyed areas (Strait of Belle Isle before 2021 and coast of Labrador) over the entire survey period. Relevant changes were expected primarily north of the study area rather than south (e.g., 4Rd, 3Pn) or into deeper, more offshore waters, given the rising water temperatures and modifications in prey availability. The northeastern coast of Newfoundland was also considered a potentially suitable habitat, but was excluded from the analysis, as it is occupied by a distinct herring stock (3KLPs) and recently tagged herring in 4RSw (see section 2.1) were not detected in this area. Deeper waters were likewise excluded from consideration because acoustic data show no evidence of a shift in vertical distribution; herring depth distribution appears to have remained stable over time (Figure D1).

Habitat suitability was computed from the predicted density field of the Gaussian GAM. Predictions were made on a regular spatial grid using environmental covariates only (T0_50, Tmin, and *Calanus* biomass), with the spatiotemporal interaction term excluded because it captures survey-specific residual patterns that cannot be reliably extrapolated. Predicted densities were bias-corrected for log-normal bias, log-transformed, and rescaled to a 0–1 HS index. We performed all statistical analyses using R software version 4.4.1 (R Development Core Team 2024).

3. RESULTS AND DISCUSSION

3.1. DIRECT EVIDENCE FOR CHANGE IN THE TIMING OF FALL MIGRATION

Timing of 50% cumulative herring landings in NAFO subdivisions 4Rb and 4Rc (west coast of Newfoundland) during the fall–early winter fishing season (September 15–January 25) was variable over the years (Figure 1). From 1985 to 1997, landings occurred progressively earlier in the season (late November to early October), followed by a shift toward later timing up to 2023 (mid-December). This amounted to an overall delay of roughly two months in the timing of peak landings over the past three decades. A sharp decline was observed in 2024; however, no fishing activity was recorded after November because there were no herring in the region, making it impossible to conclude that landings had returned to earlier levels.

A temporal mismatch (days) between the median date of the fall acoustic survey and the date of 50% cumulative herring landings in 4Rbc was documented from 1991 to 2022 (Figure 2). The initial acoustic surveys (1991–2002) were, with the exception of 2002, always conducted within

three weeks of the central landing date (50% cumulative herring landings), whereas the second acoustic series typically occurred 30 to more than 60 days before the central herring landings date.

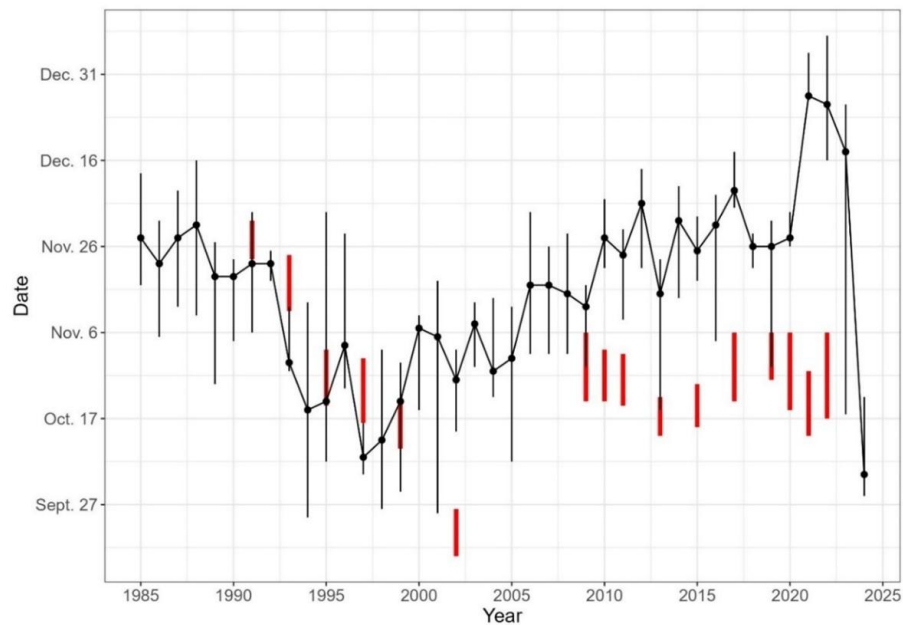


Figure 1. Timing of 50% cumulative herring landings in NAFO subdivisions 4Rb and 4Rc (west coast of Newfoundland) during the fall-early winter fishing season (September 15–January 25), 1985–2024. Black vertical bars mark the 25% and 75% cumulative landing thresholds. Red vertical bars denote the acoustic survey date ranges.

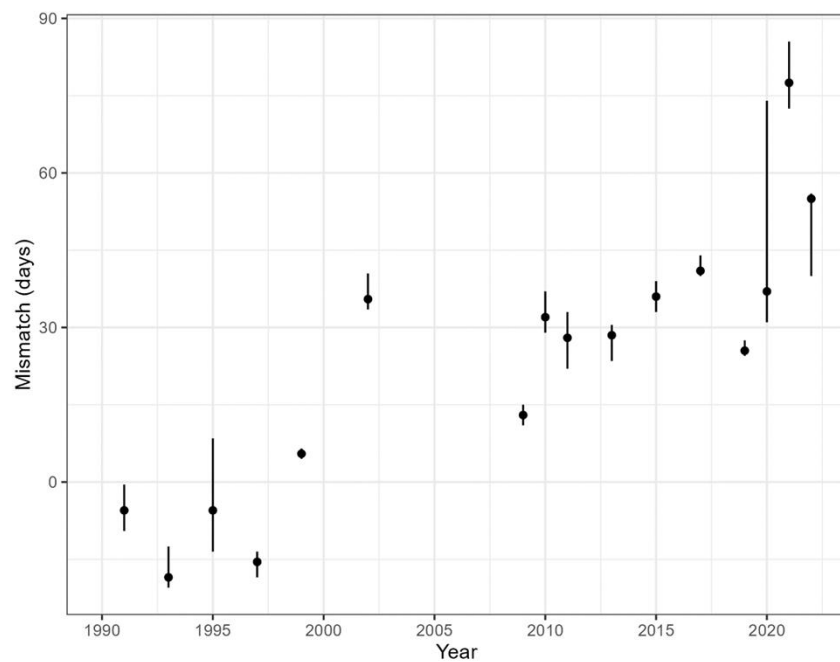


Figure 2. Temporal mismatch (days) between the fall acoustic survey median date and the date of 50% cumulative herring landings in 4Rbc (see Figure 1), 1991–2022. Negative values indicate that the survey preceded the midpoint of the fishing season, and positive values indicate it occurred afterward. Vertical bars represent the 2.5% and 97.5% bootstrap quantiles.

Fish telemetry data indicated that the timing of the fishery aligned closely with the seasonal migration of herring along Newfoundland's west coast. Specifically, 142 out of 189 herring were detected and acoustic detections of tagged herring showed that they arrived in the Bay of Islands (4Rc) from mid-to late November, followed by later arrivals in Bonne Bay (4Rb) from late November to late December (Table 1). These arrival periods coincided with the timing of peak landings in both areas (Figure 3). This correspondence supports the use of 50% cumulative landings as a reliable indicator of migration timing.

Table 1. Range of arrival dates of acoustic-tagged herring detected in Bonne Bay (4Rb) and Bay of Islands (4Rc) during the 2021–2022 and 2022–2023 fishing seasons with dates of 50% cumulative landings (25–75%).

Fishing season	Date of arrival		50% cumulative landings (25–75%)
	Bonne Bay (4Rb)	Bay of Islands (4Rc)	
2021–2022	2021/12/22–2022/01/10	2021/11/30–2022/01/30	2021/12/31 (2021/12/30–2022/01/10)
2022–2023	2022/11/30–2022/12/19	2022/11/10–2023/01/09	2022/12/29 (2022/12/16–2023/01/14)

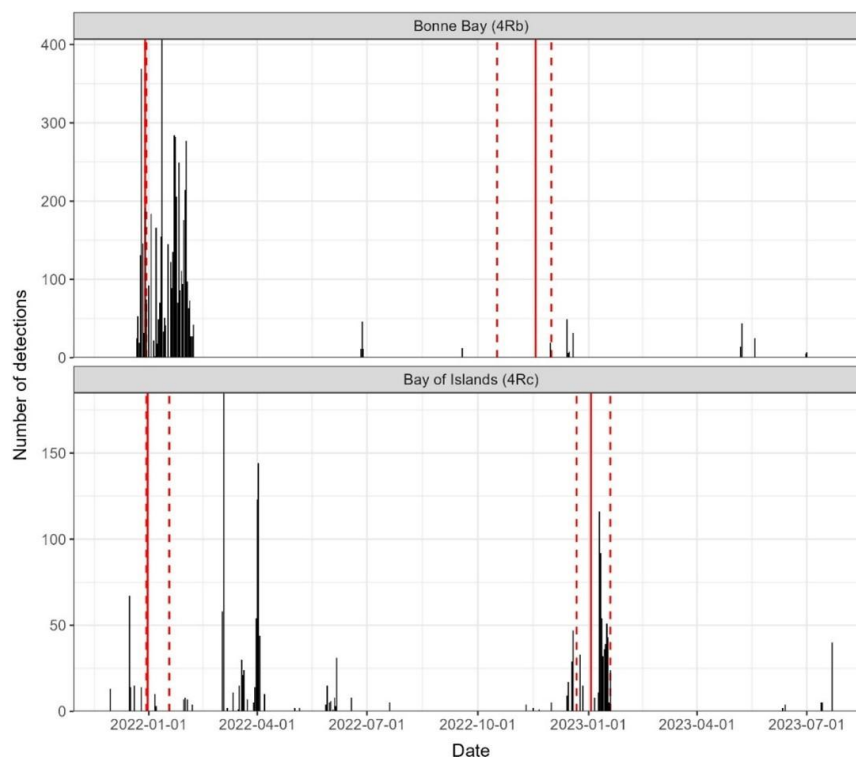


Figure 3. Daily acoustic detections of herring in Bonne Bay (4Rb) and Bay of Islands (4Rc). Vertical red lines denote when 25% (dashed), 50% (solid), and 75% (dashed) of landings were reached in each area during the fall/early winter fishery.

3.2. POTENTIAL MECHANISMS UNDERLYING THE CHANGE IN THE TIMING OF FALL MIGRATION

3.2.1. Cascading effect hypothesis

The GSI was used to assess gonadal development among mature individuals and to estimate the timing of spawning. For fall spawners, gonadal development typically began in early May, peaked in August, marking the onset of spawning, and generally ended in early November (Figure 4). The day of the year on which the GSI reached its peak in fall-spawning herring has shifted only slightly over time, occurring just a few days earlier in recent years (e.g., 2022–2025) compared to historical observations (e.g., 1970–1973), illustrating that the timing of spawning has remained relatively stable (Figure 5).

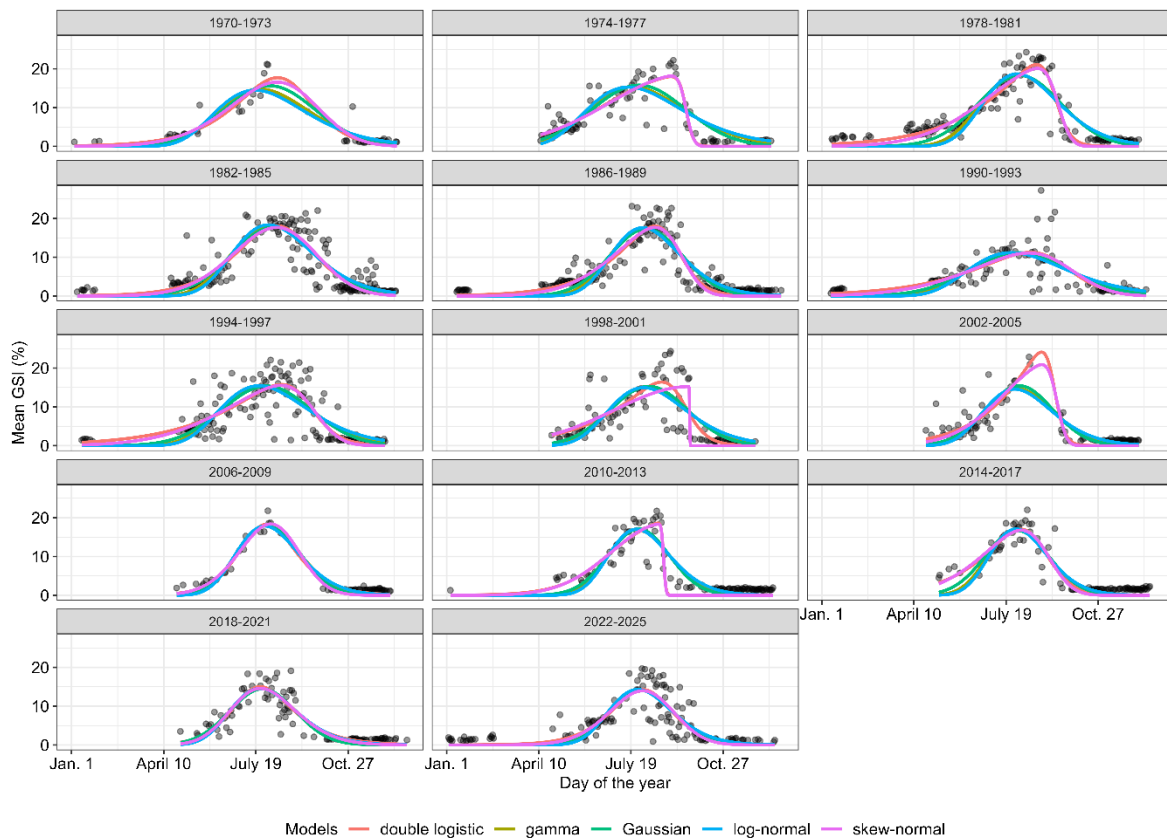


Figure 4. Annual variation of the daily mean gonadosomatic index (GSI) per 4-year period for fall spawning herring. The colour lines represent the functional forms (i.e., double-logistic, gamma, gaussian, log-normal, and skew-normal) assumed when fitted to the data.

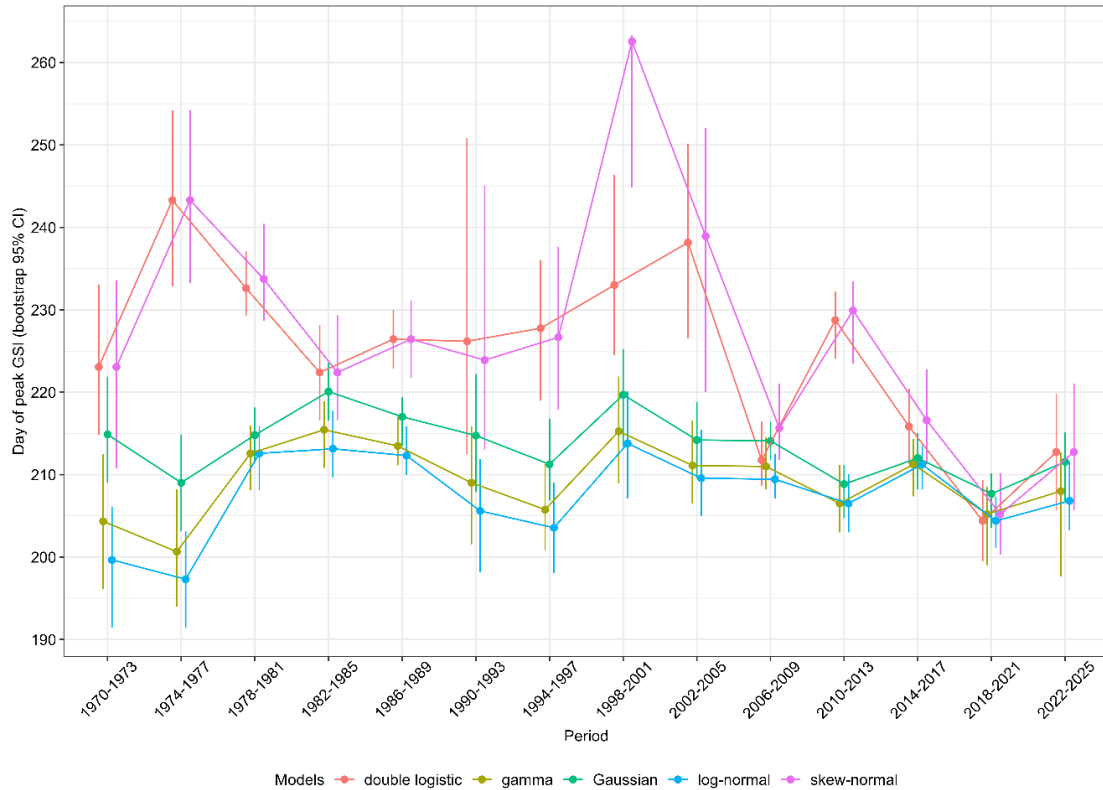


Figure 5. Day of year of peak GSI for fall spawners (bootstrap 95% confidence intervals).

3.2.2. Retention hypothesis

Analyses of herring body condition across northern summer feeding areas (4Ra–4Sw, July–September) and post-feeding (4Rbc, October–December) were conducted to assess whether changes in physical condition support extended residency in the northern areas and match environmental changes. Fish in better condition are predicted to migrate earlier than those in poor condition (Heim *et al.* 2016).

Le Cren's relative condition index for spring- and fall-spawning herring during feeding and post-feeding decreased from 1980 to 2024, and was particularly low after 2010 in subdivisions 4Rbc (Figure 6). The persistent decline across seasons and stock components suggests insufficient energy accumulation driven by environmental factors rather than by life-history changes (e.g., spawning-related costs). Such reduced energetic reserves may delay the onset of fall migration and be reflected in the progressively later timing of landings.

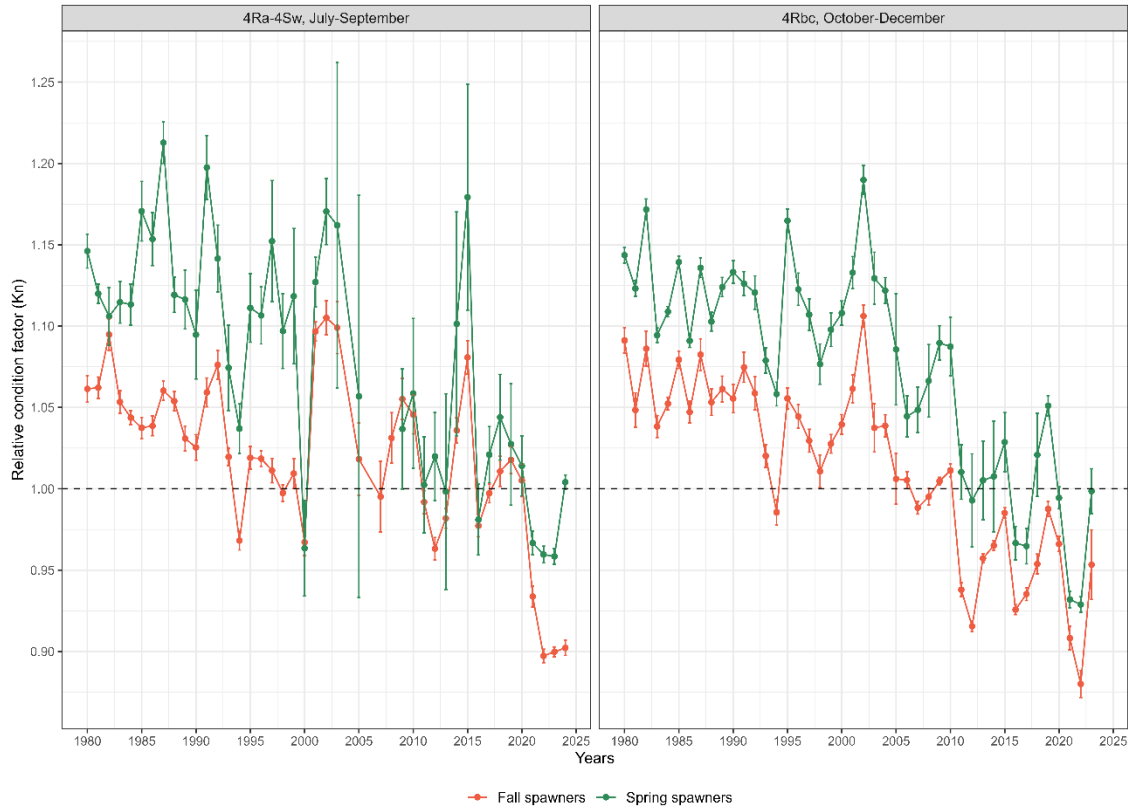


Figure 6. Le Cren's relative condition factor (mean $\pm$ 95% confidence intervals) for spring- and fall-spawning herring in subdivisions 4Ra and 4Sw from July to September, and in subdivisions 4Rbc from October–December, 1980–2024. The dotted black line represents the expected relative condition factor, where values above 1 indicate better-than-average condition and values below 1 indicate poorer condition.

Over the period 1985–2024, a negative relationship was observed between the central fall fishing period and spring- and fall-spawning herring body condition (Figure 7). This indicates that better physical condition might indeed be associated with earlier migration. The relationship was, however, weaker for body condition measured during the feeding period than for post-feeding condition (Figure 7). This difference could be expected, as post-feeding body condition integrates the cumulative effects of the entire feeding season and is less influenced by biological variability such as spawning-related energetic costs.

Overall, observed changes in body condition support the hypothesis that herring may be entering the survey area later in response to environmental conditions. These findings further suggest that the timing of landings could serve as a useful indicator of shifts in migration timing. In addition, the negative relationship between body condition and migration timing provides empirical support for the retention hypothesis, strengthening the link between physiological state and delayed arrival into the survey area.

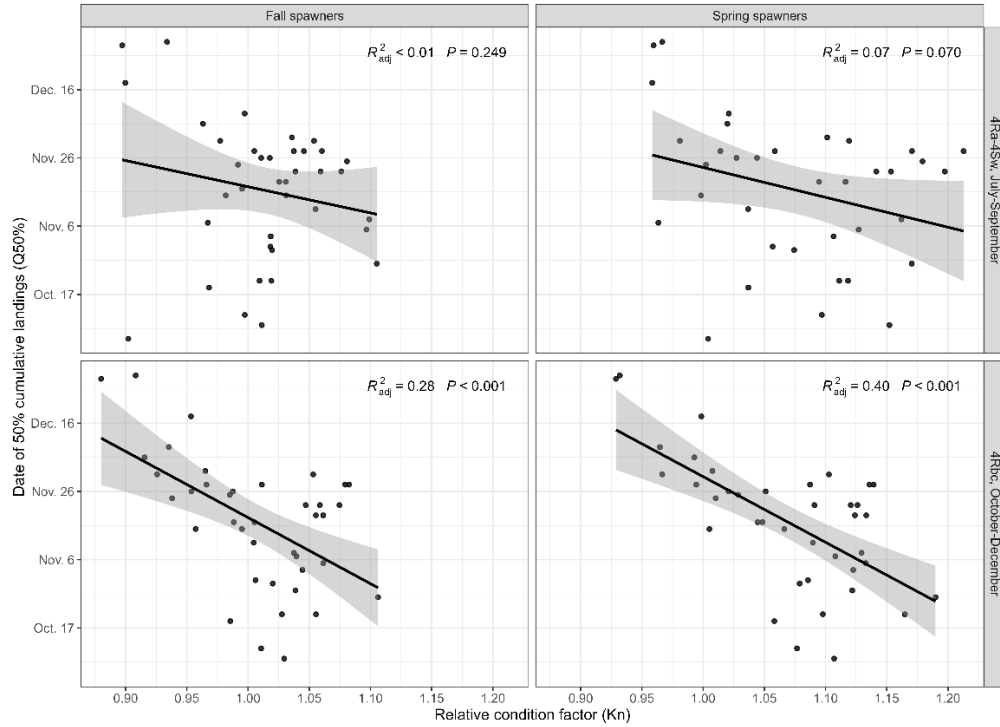


Figure 7. Relationship between the timing of the 50% cumulative landings in the fall and early winter commercial fishery and the mean Le Cren's relative condition factor (K_n) for spring- and fall-spawning herring. Each panel shows the relationship for a specific spawning component (spring or fall) and area/season. The mean K_n was calculated for 4Ra–4Sw (north) from July to September (summer) and for 4Rbc (south) from October to December (fall), for the period 1985–2024.

3.2.3. Avoidance hypothesis

3.2.3.1. Spatial modelling and validation of GAMs

The most parsimonious GAM, selected based on AIC, included the variables $T0_{50}$, log-transformed biomass of *Calanus* spp., T_{min} , and the spatiotemporal smoothers (Table C1). All predictors were highly significant ($p < 0.001$; Table C2). Model assumptions were met, and diagnostic checks revealed no significant residual patterns or spatial autocorrelation (Figure C3). The Gaussian GAM accounted for 25.3% of the deviance in data. Comparison between GAM-predicted herring densities and acoustic survey observations indicated a reasonably good fit ($R^2_{adj} = 0.25$, $p < 0.001$; Figure C3). The Gaussian GAM yielded an adjusted R^2 of 0.24 and a mean MAE of 1.80 based on cross-validation. Finally, validation using the forecast skill approach confirmed the model's predictive reliability, with relative errors indicating no apparent systematic bias (Figure C4).

3.2.3.2. Influence of environmental variables on herring spatial distribution

Herring density was strongly and positively associated with the biomass of *Calanus* spp., with an average concentration of 1,200 mg/m² leading to higher herring densities (Figure 8). Food availability is recognized as one of the key drivers of herring migration, with several studies highlighting its central role (Melle *et al.* 2020, Broms *et al.* 2012). Temperature also played a key role, as herring tended to favour warmer waters and actively avoided areas where minimum temperatures fell below 2°C (Figure 8). This observation aligns with documented herring thermal preferences, as previous studies have shown that herring generally avoid waters colder than 1–2 °C (Misund *et al.* 1997, Fernö *et al.* 1998, Broms *et al.* 2012).

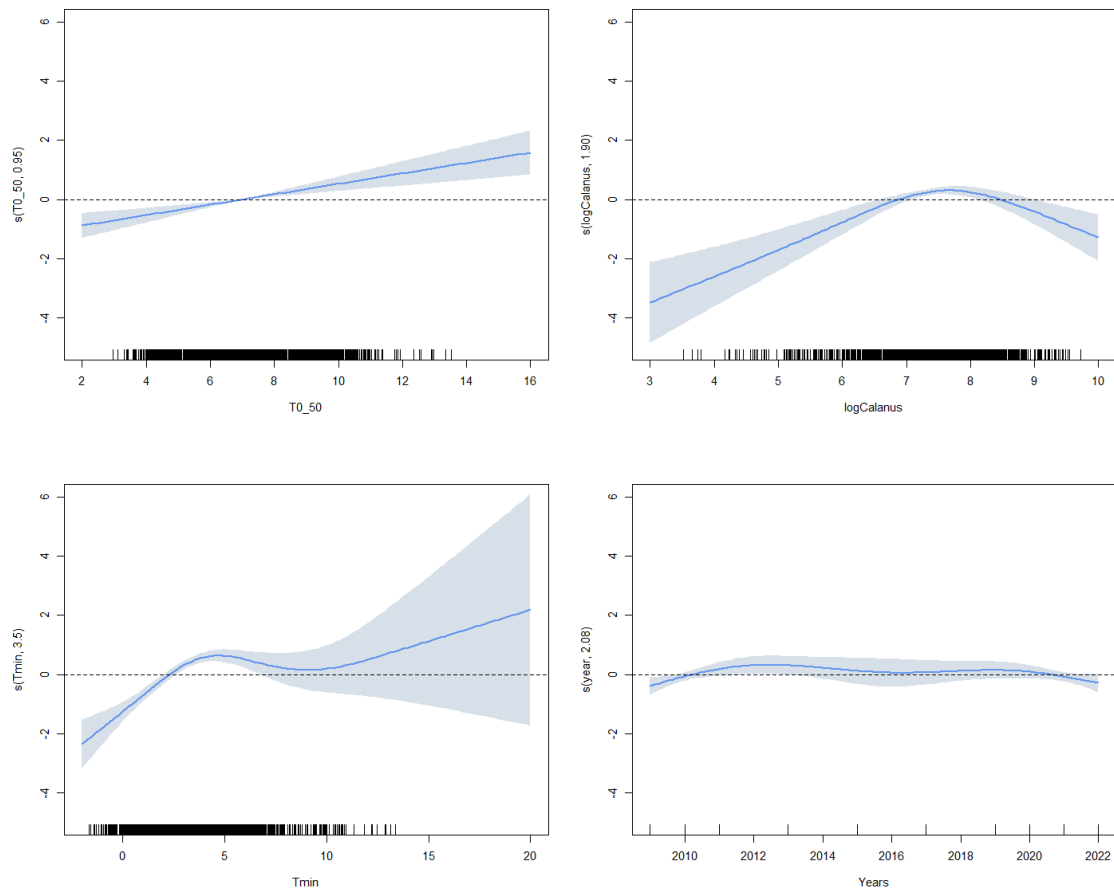


Figure 8. Partial response of GAM showing the influence of variables on the spatial distribution of herring density for the GAM model. The 95% confidence interval for response curves is shaded in colour. Inclusion of the zero on the y-axis (black dotted line) in the smoother confidence intervals means the variable has no effect.

3.2.3.3. Temporal changes in predicted habitat suitability during the second survey period (2009–2022)

Our models indicated that, during 2009–2022, herring habitat during the survey period (October–November) was generally more suitable around St. John Island, near Port au Choix (4Ra), Bonne Bay (4Rb), and Bay of Islands (4Rc). In the northern part of the study area, particularly the Strait of Belle Isle and the area near Blanc-Sablon (4Sw), habitat suitability has increased over time, with recent estimates generally higher than those from earlier years (Figure 9). Importantly, although the Strait of Belle Isle was surveyed only in 2021 and 2022, environmental conditions were already suitable for herring in some of the previous years. The unsurveyed Labrador Shelf likely experienced conditions that were mostly unsuitable for herring in the earlier years, although in the most recent years, some abundance could likewise not be excluded (Figure 9). Thus, it is plausible, based on the available environmental data and knowledge, that, especially after 2017, the habitat likely has been more suitable in northern regions (i.e., Strait of Belle Isle), suggesting that a portion of the stock may have been present outside the surveyed area.

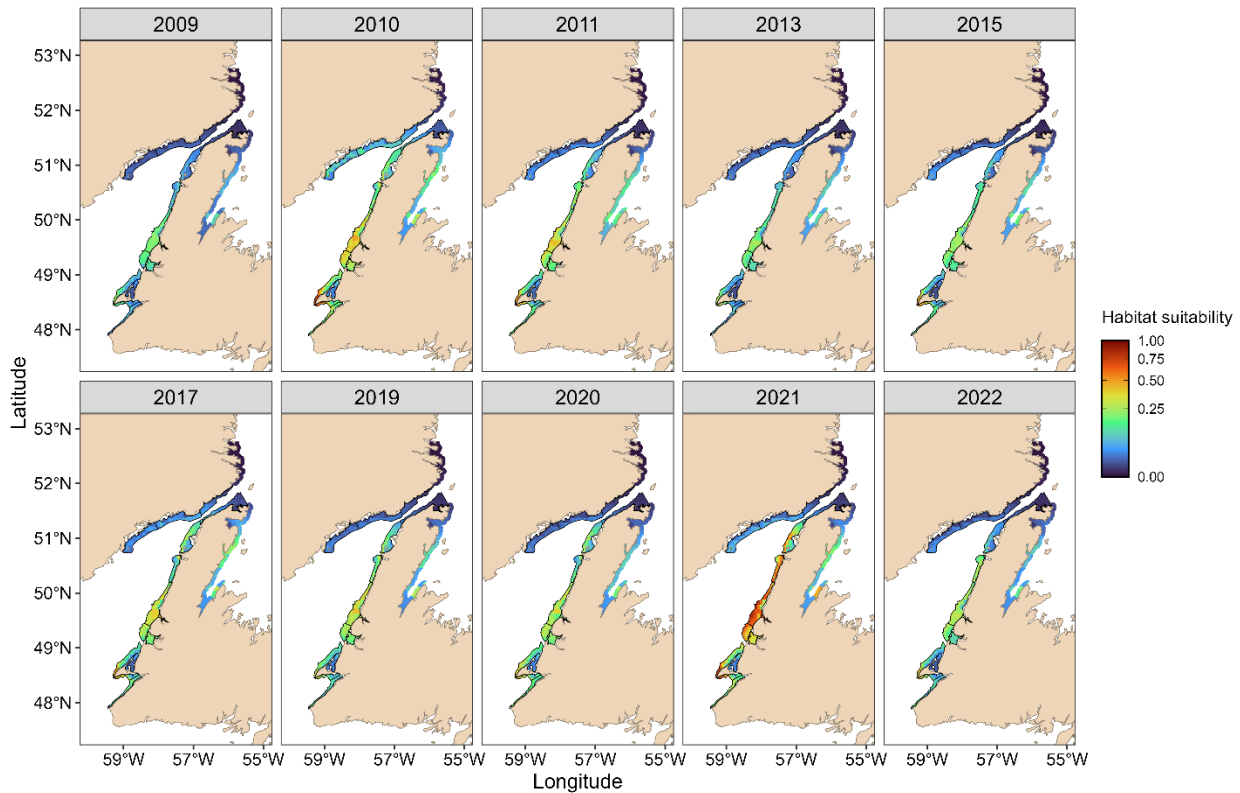


Figure 9. Habitat suitability in autumn based on predictions from the GAM model for 2009–2022, with survey strata outlined in black. Values of 1 indicate higher habitat suitability whereas values of zero indicate the most unsuitable habitat. Note: The Strait of Belle Isle was only surveyed in 2021 and 2022.

3.2.3.4. Changes in habitat suitability between survey periods

When comparing the first survey period (1991–2002) with the second period (2009–2022) across September–December, predicted HS along the west coast of Newfoundland was generally higher during the more recent period. This increase was consistent across months, being most pronounced in northern areas (Figure 10). Rising water temperatures also appear to have provided more favourable conditions for herring in northern regions (Figure E1, Figure E2). This is not unexpected, as herring stocks around Newfoundland represent the northernmost populations of the West Atlantic, and their distribution is influenced by thermal regimes. These patterns also coincided with increased *Calanus* biomass in more northern regions later in autumn, further enhancing feeding opportunities for herring (Figure E3). Indeed, acoustic fish detections of herring were also observed farther north, including at St. Anthony (3K) and Port Hope Simpson (2J; Émond and Nilo 2025).

The comparison between survey periods suggests that shifts in herring migration are unlikely to have been driven by deteriorating local conditions in the southern survey area or by avoidance of that region. Rather, because there is currently also no evidence for a cascading effect early on (see section 2.2.1 on spawning phenology), the most likely hypothesis might be that herring are spending the summer outside the surveyed area and are delaying their fall migration into the

surveyed waters. Indeed, environmental conditions outside the survey area have improved (Figure 10, Figure E1, Figure E2) and this hypothesis aligns with the observed changes in fish condition.

To further explore the retention hypothesis, in September, traditional northern feeding habitats (i.e., 4Ra–4Sw) appeared to have remained relatively stable in 2009–2022 compared to 1999–2002 (Figure 10). Other northern areas (i.e., Strait of Belle Isle and Labrador) exhibited a positive change in suitability (Figure 11). Despite these differences, conditions across all areas in September remained broadly suitable for herring, providing multiple potential habitats during this period.

During 2009–2022, in the northern part of the study area—particularly near Blanc-Sablon (4Sw), Pistolet Bay, Strait of Belle Isle, and east of Newfoundland—habitat suitability was generally still high in October, indicating the ecological importance of this region during the second survey period (Figure 10). Greater differences were evident among the northern regions, while conditions in 4Ra–4Sw were generally more suitable in 4Ra than in 4Sw in the first survey period. Although habitat suitability reflects the environmental tolerances of the species, changes in HS do not necessarily translate directly into shift in spatial distribution, particularly for a species with broad environmental tolerances. Nonetheless, the available evidence is consistent with a potential expansion or shift of the population toward the unsurveyed areas during late summer/early fall.

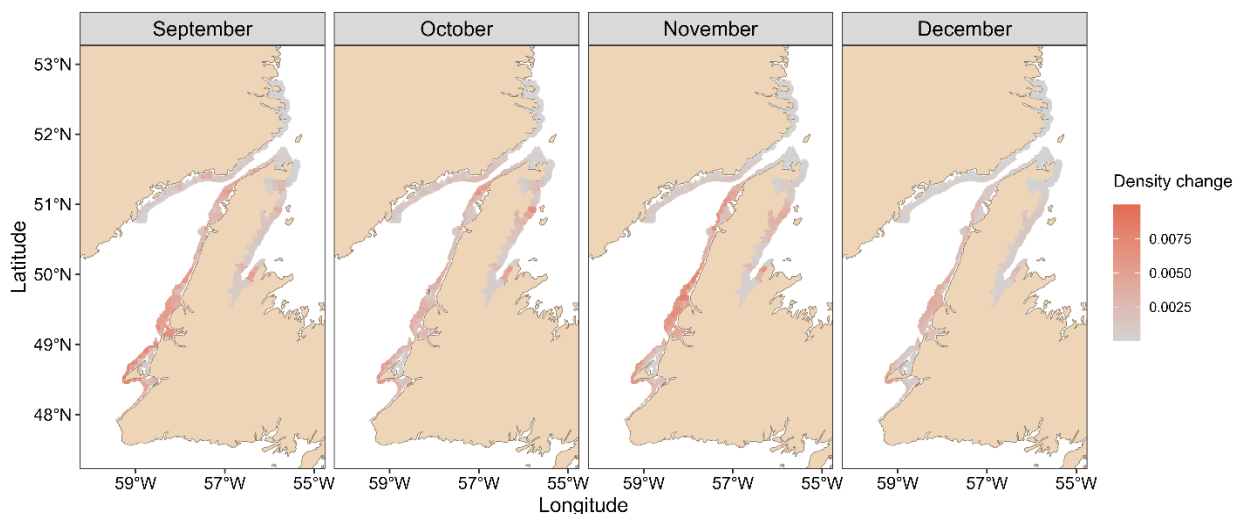


Figure 10. Temporal change in predicted total herring density between 2009–2022 and 1999–2002 from September to December.

3.2.3.5. Changes in habitat suitability across the fall season

Environmental habitat suitability for herring over the entire area of interest shifted markedly from September to December (Figure 11). In November, suitability declined across northern regions; however, this decrease was particularly pronounced in the unsurveyed areas, where the Strait of Belle Isle became characterized by less suitable habitat. Notably, the relative importance of 4Ra–4Sw area varied among years, with some recent years standing out as years in which herring presence in the area later in the year appeared plausible. Over the full-time series (1999–2023), habitat suitability significantly improved in both the traditional summer feeding

region (4Ra–4Sw) and the fall fishing grounds (4Rbc), both covered by the second survey series, with the fall fishing grounds generally offering the most optimal habitat. Note that these values represent an average monthly condition and therefore provide an approximation of the situation near the end of, or shortly after, the survey period. Before roughly 2010, the estimated seasonal shift in environmental conditions would have provided a strong incentive for herring to move toward the key fishing grounds prior to or during November. By December, suitable habitat dropped further across all regions, and 4Rbc remained an optimal area, albeit with substantial interannual variability.

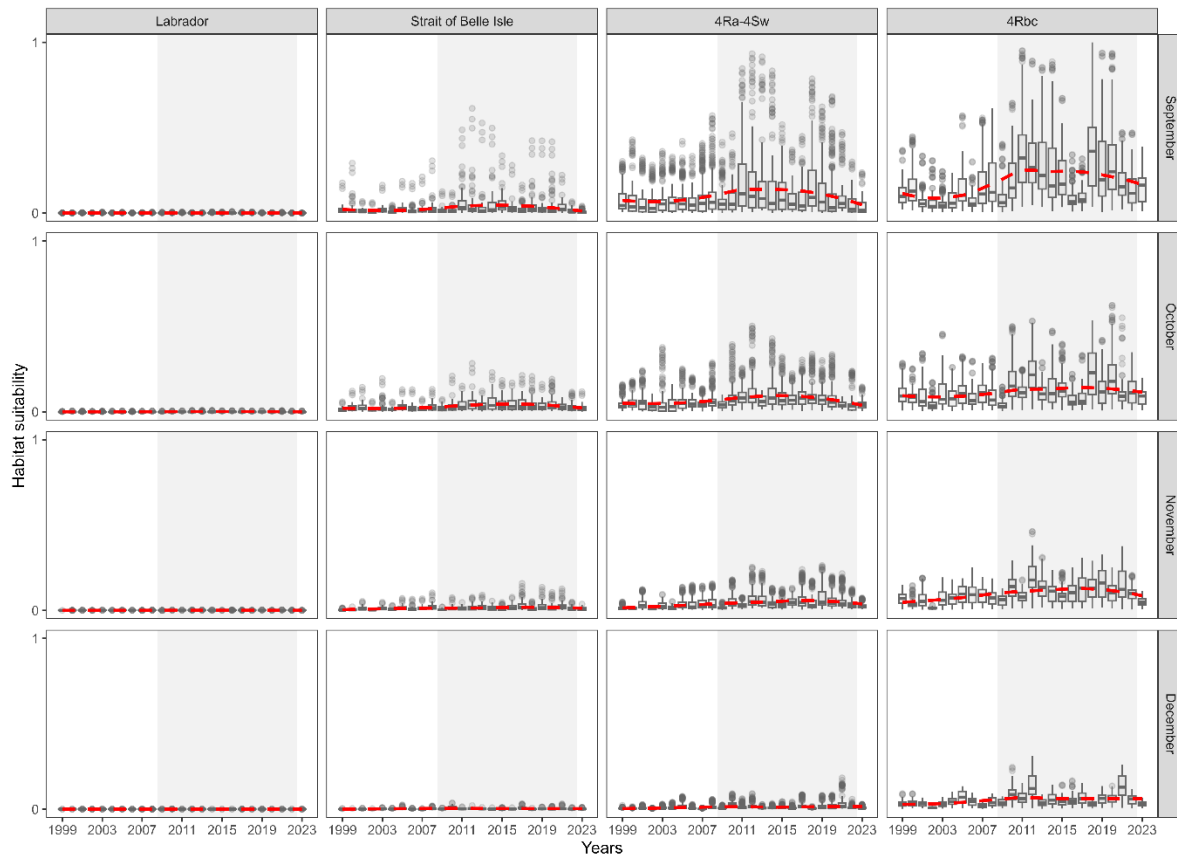


Figure 11. Boxplots showing habitat suitability for herring from the GAM for 1999–2023 from September to December and four regions of interest (i.e., Labrador, Strait of Belle-Isle, subdivisions 4Ra–4Sw, and 4Rbc). Values of 1 indicate maximal historical habitat suitability. The red dashed line shows the smoothed trend and the grey window represents the second survey period (2009–2022) on which the model was calibrated.

The effect of changes in habitat suitability could not be confidently linked to shifts in the timing of migration (proxied by fish landings). Migratory patterns may vary across different regions and temporal scales. For instance, migratory shifts could be influenced by environmental conditions prior to (e.g., September–October) or during (e.g., October–November) the survey period, driven by environmental variability in multiple northern regions such as 4Ra–4Sw, the Strait of Belle Isle, or Labrador. Although we tested for correlations between habitat suitability and the timing of landings across several spatial and temporal scales, no conspicuous relationship emerged. A link between habitat suitability and fish condition should be more direct and therefore perhaps stronger. However, again no consistent relationship was found.

4. CONCLUSION

Changes in catchability of the acoustic survey represent a major source of uncertainty for the assessment of the spring- and fall-spawning herring of the northeastern Gulf of St. Lawrence stock (NAFO Divisions 4RSw). Not accounting for these changes poses a substantial risk of biasing population trend estimates, whereas estimating catchability freely without external constraints risks producing spurious or unstable results. This document examined the observed shift in migration timing, outlined the hypotheses that could explain this temporal change, and evaluated these hypotheses using the available data.

Both Chamberland *et al.* (2022) and Émond *et al.* (2024) previously documented a shift in the timing of the fishery, and the fish tagging data included here confirms that this delay likely reflects a biologically driven shift in migration. Temporal shifts in landings of small pelagic species are also generally recognized to track changes in stock dynamics (e.g., Kindong *et al.* 2020), and thus the timing of the fishery relative to the survey may serve as a reasonable proxy for changes in survey catchability. Under this interpretation, a temporal delay in landings would be linearly related to biomass availability during the survey. The evidence presented here supports the hypothesis that this delay reflects a northward shift or expansion of the stock, and a postponement of its arrival into surveyed waters (retention hypothesis). An expansion in area occupied does not necessarily imply an increase in total biomass detectable by the survey, particularly if a substantial fraction of the stock moves into unsurveyed regions as has been documented for other herring stocks (e.g., Georges Bank, Overholtz 2002). We currently have no strong indications of a cascading delay earlier in the year (for example, through altered spawning phenology), although spring data remain limited. Fall environmental conditions also did not appear unfavourable enough to prevent herring from following their historical migration route (avoidance hypothesis). Taking together, the retention hypothesis appears most consistent with the observed physiological and environmental changes, and we suggest focusing on this process and period to improve our understanding of the shift in migration.

The moderate negative correlation between the timing of landings and post-feeding body condition in both spring- and fall-spawning components suggests that the temporal shift in landings reflects a biologically meaningful signal. Environmental analyses further show that northern regions outside the survey area may have become increasingly suitable for herring during summer and fall, making the presence of a substantial biomass in unsurveyed areas plausible. Indeed, in 2021 and 2022, when the Strait of Belle Isle was included in the survey, considerable herring biomass was detected (between 43–70% of the total estimated biomass; Émond *et al.* 2024). Establishing a direct relationship between the timing of the fall/winter fishery and environmental drivers remains however challenging due to the complexity of underlying processes and the inherent noise in both datasets. Consequently, we recommend that the mismatch between survey dates and the timing of landings be explored as a potential proxy for changes in catchability, given its consistency with independent biological indicators (e.g., body condition) and its more direct connection to migration timing than other available metrics.

This document summarizes the available information relevant to evaluating changes in survey catchability, while acknowledging that substantial uncertainties remain. First, the relationship between survey catchability and the timing of the fishery is expected to be noisy (e.g., the timing of landings is an imprecise proxy) and might not be linear. Second, although key evidence has been presented, refining them or developing new evidence should remain a priority. For instance, spring-spawning phenology could not be characterized due to the mismatch between spawning timing and sample availability. Third, interpretations of environmental shifts should also be restricted to broad, large-scale, and low-frequency patterns, which are the types of signals most consistent with a substantive shift in the timing of herring migration. This is partly because zooplankton and temperature estimates, although available at a useful spatiotemporal

resolution, are model-derived. The zooplankton SDM relies on low-frequency zooplankton samples collected at a limited number of locations during October–November along the west and east coasts of Newfoundland, making estimates less precise for data-poor months such as September and December. Temperature estimates were derived from a data-assimilation oceanographic model (GLORYS12v1) whose calibration relies on CTD and satellite data. CTD measurements are likewise scarce in September and December. Consequently, confidence in, for example, surface temperature indices (T0_50) is higher than for minimum temperature within the water column (Tmin) indices (Lellouche *et al.* 2021). Uncertainty in environmental variables, combined with the highly dynamic behaviour of herring, may partly explain the relatively low explanatory power of the spatiotemporal models. Although we verified that extrapolation beyond the survey window does not introduce systematic bias, it inevitably increases the signal to noise ratio of the results. Despite these limitations, the analyses conducted offer the most comprehensive interpretation of the shift in the timing of herring migration currently available for 4RSw, and support more informed modelling than would be possible otherwise.

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APPENDIX A: HYDROACOUSTIC SURVEYS

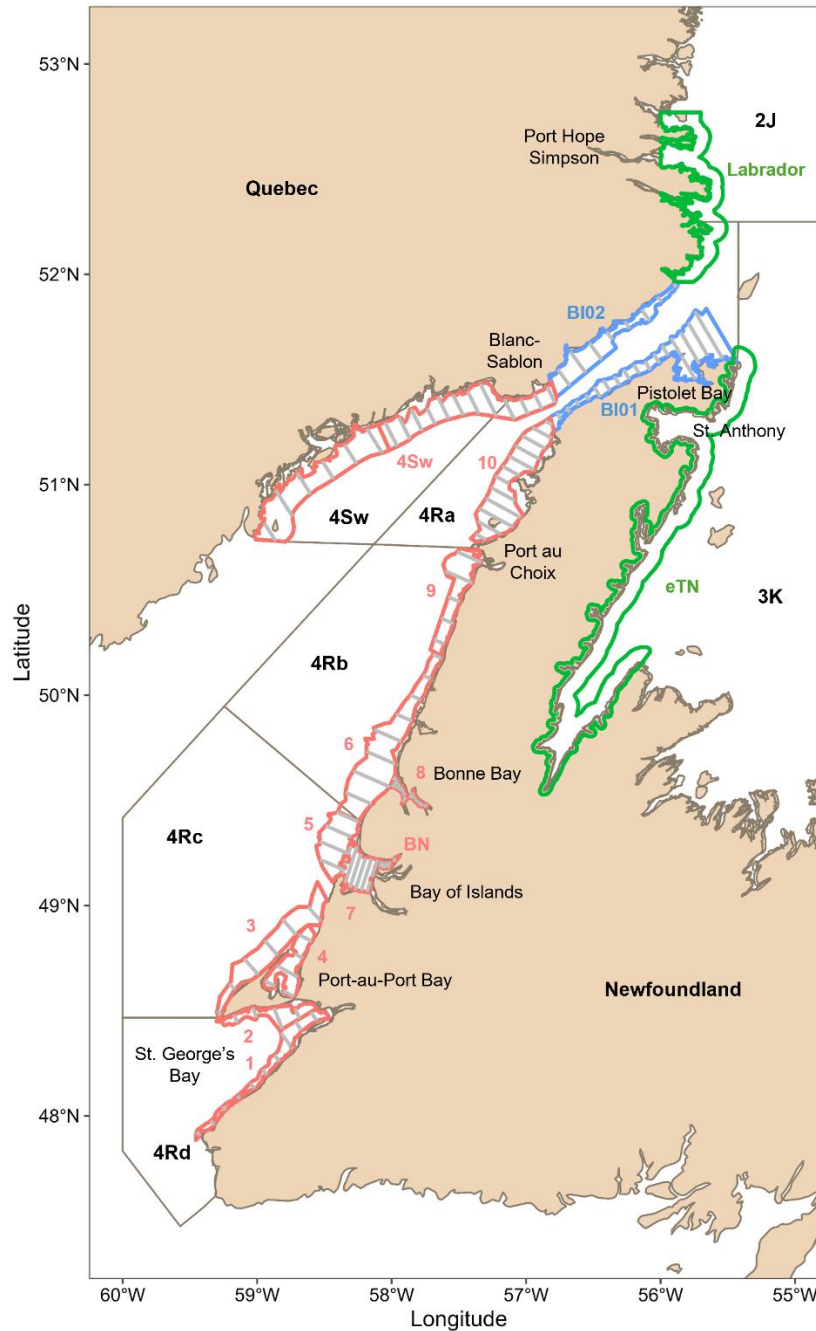


Figure A1. Map showing the 14 fall 4RSw herring hydroacoustic survey strata (red) for 2009–2022, including those added in 2021–2022 (Strait of Belle Isle; blue). Green polygons (Labrador region; east coast of Newfoundland, eTN) indicate unsurveyed regions that were used for herring suitable habitat predictions. Example transects are shown in grey. NAFO (Northwest Atlantic Fisheries Organization) subdivisions (4Sw, 4Ra, 4Rb, 4Rc, 4Rd) and Divisions (2J and 3K) are indicated in bold, along with the point of interest identified within the study area. The Strait of Belle Isle (blue) is part of subdivision 4Ra, but it was considered separately for the purposes of this study, as it was only surveyed in 2021–2022.

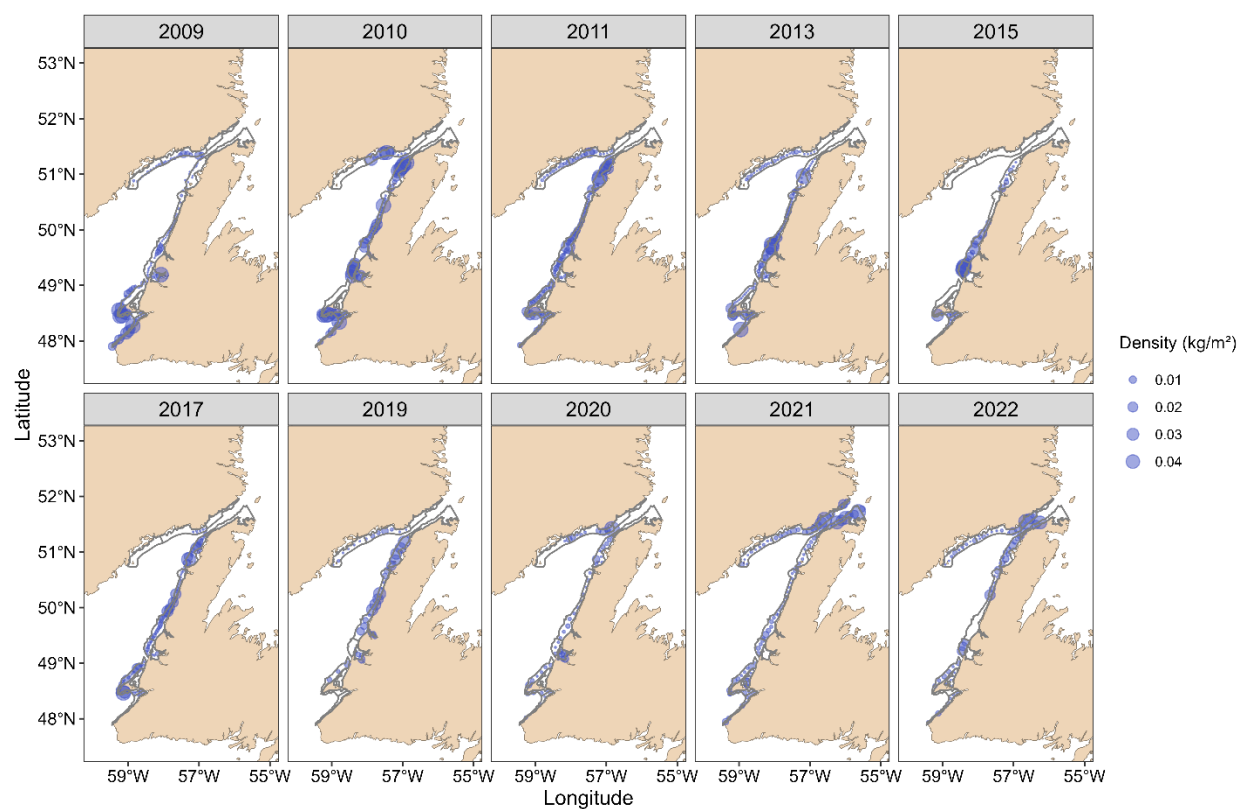


Figure A2. Mean herring density (kg/m^2) per transect from fall hydroacoustic surveys (2009–2022), with each bubble representing one transect across the fourteen strata (black polygons).

APPENDIX B: CORRELATION MATRIX BETWEEN LE CREN'S RELATIVE CONDITION INDEX (KN) OF AGES 2–11+

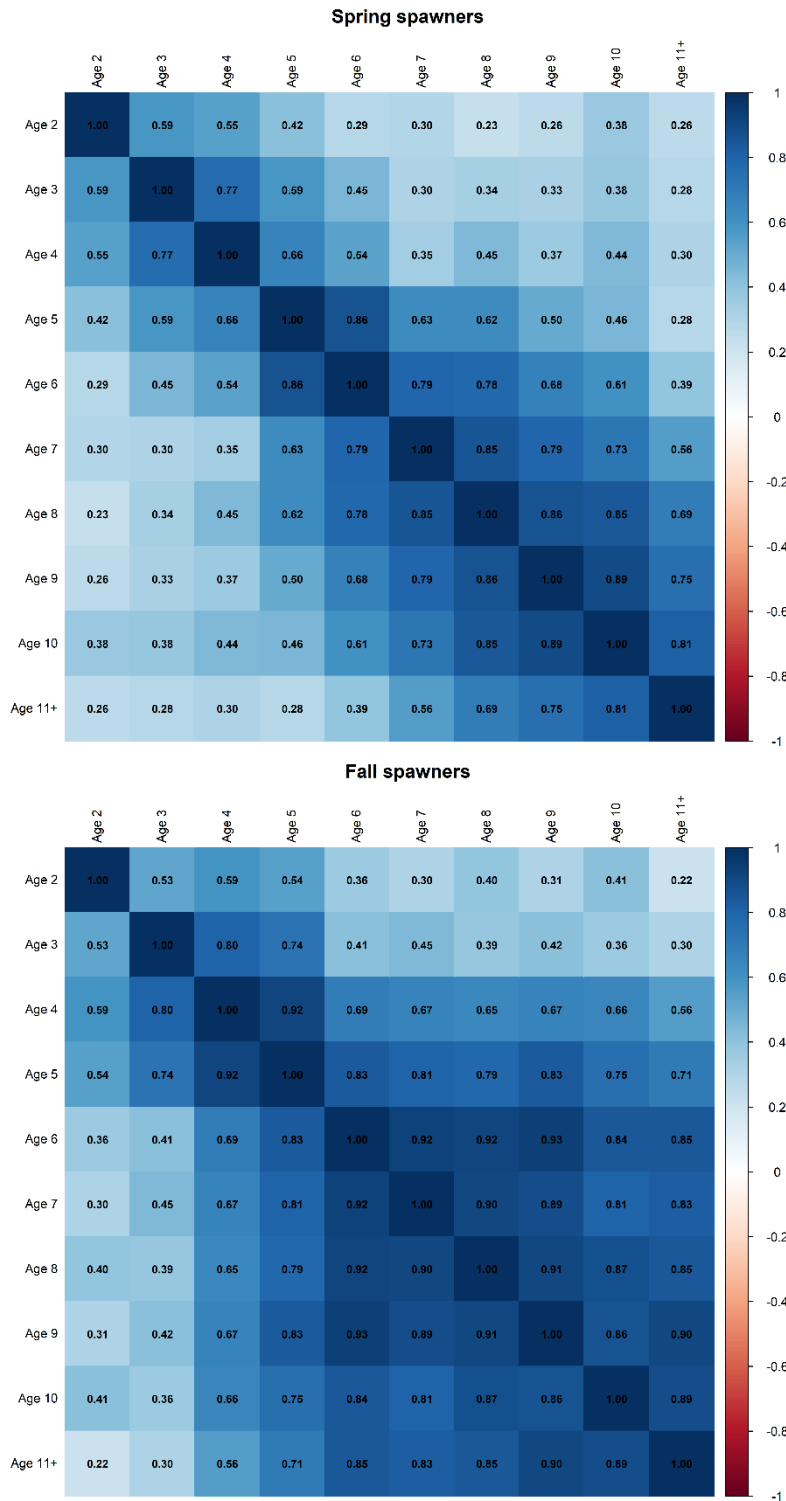


Figure B1. Correlation matrix of Le Cren's relative condition index (K_n) for ages 2–11+ of spring- and fall-spawning herring. Each cell reports the corresponding Pearson correlation coefficient, with colour intensity proportional to the magnitude of the correlation.

APPENDIX C: VARIABLE EXPLORATION AND MODEL VALIDATION

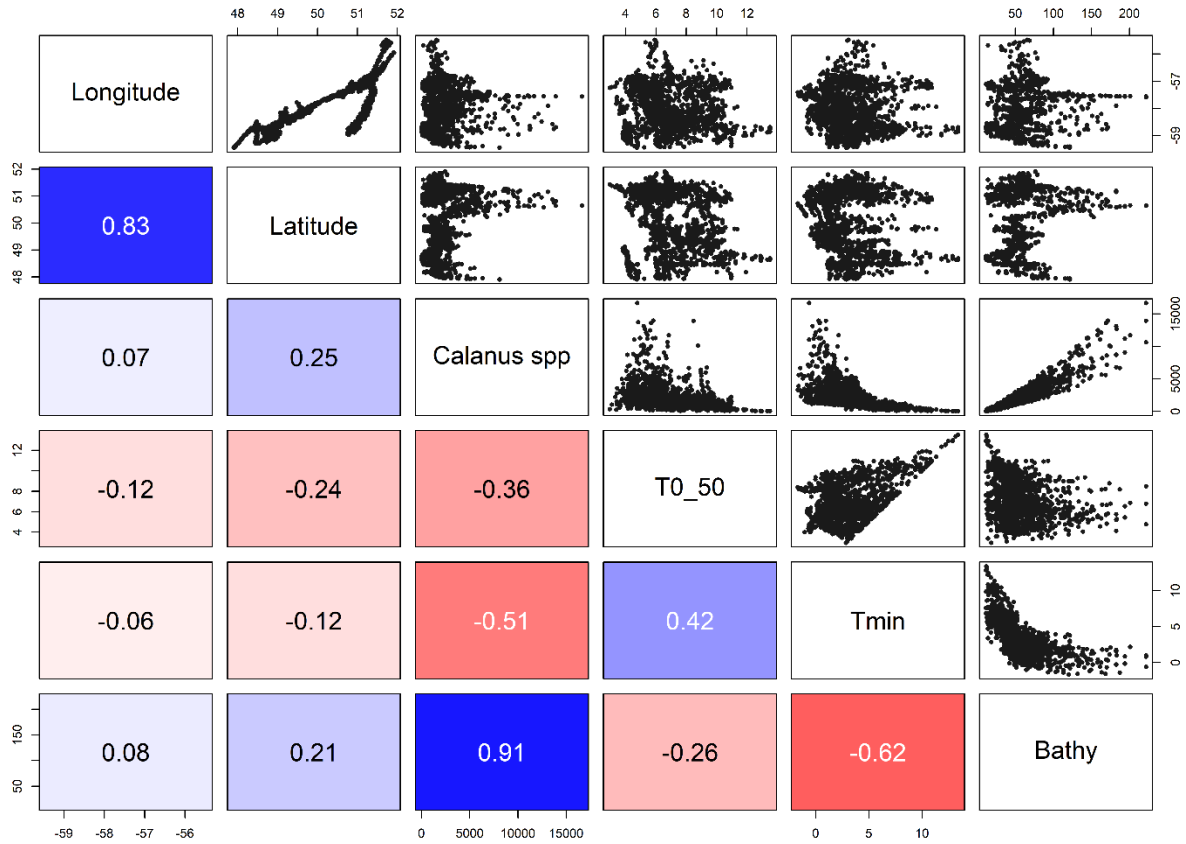


Figure C1. Multi-panel scatterplot of environmental variables. The upper-right panels display pairwise scatterplots for each variable combination, while the lower-left panels show Pearson correlation coefficients, with colour intensity proportional to the magnitude of the correlation. Abb.: Calanus (average Calanus spp. abundance in the water column), T_0_50 (average temperature in the 0–50 m layer), Tmin (the minimum temperature within the water column), and bathy (Bathymetry).

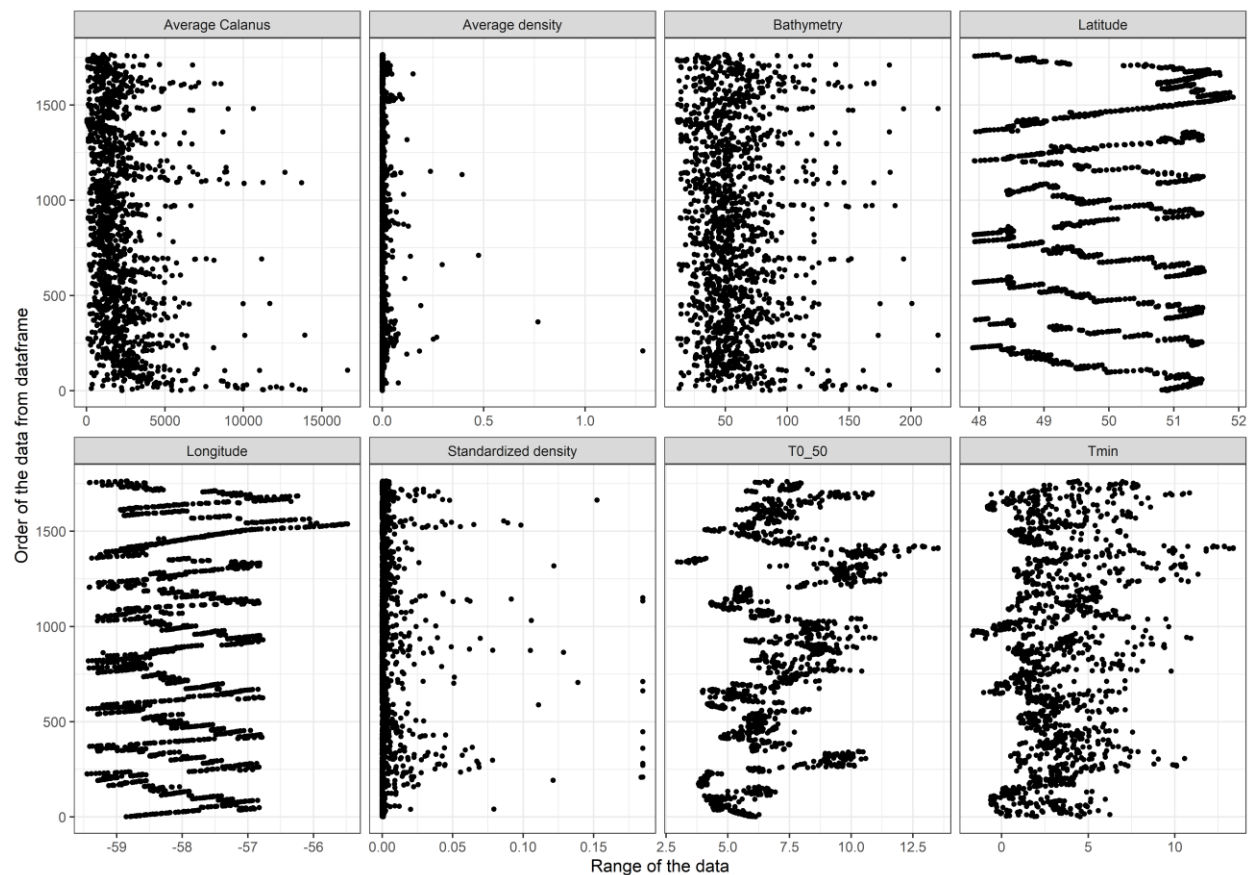


Figure C2. Multi-panel Cleveland dotplot for environmental variables and herring density data. The y-axis shows the row number of each observation, and the points are plotted according to their values. Points that extend far to the right or left indicate observations that are much larger or smaller than the rest and may warrant further investigation as potential outliers. Abb.: Average Calanus (average Calanus spp. abundance in the water column), T_0_50 (average temperature in the 0–50 m layer), Tmin (the minimum temperature within the water column), Average density (average herring density in the 8 x 8 km grid), and Standardized density (herring density values after the winsorization).

Table C1. Candidate models to evaluate the relationship between spatial herring density and explanatory variables using a Gaussian distribution. The most parsimonious model selected according to Akaike's information criterion (AIC) and AIC weights (ω_i) is indicated in bold. *df* is the degree of freedom.

Model no	Model formula	Presence-only (Gaussian)			
		df	AIC	Δ AIC	ω_i
M1	s(T0_50) + s(logCalanus) + s(year) + te(latitude, longitude) + ti(latitude, longitude, year)	38.2	7,705.3	69.8	< 0.001
M2	s(T0_50) + s(logCalanus) + s(Tmin) + s(year) + te(latitude, longitude) + ti(latitude, longitude, year)	53.8	7,635.5	0.0	1.000
M3	s(logCalanus) + s(year) + te(latitude, longitude) + ti(latitude, longitude, year)	37.1	7,726.4	90.9	< 0.001
M4	s(T0_50) + s(logBathymetry) + s(year) + te(latitude, longitude) + ti(latitude, longitude, year)	42.5	7,703.0	67.5	< 0.001
M5	s(logBathymetry) + s(year) + te(latitude, longitude) + ti(latitude, longitude, year)	39.6	7,723.4	87.9	< 0.001

Table C2. Parameter estimates from GAM fitted with Gaussian distribution including smooth term significance and model fit metrics. *edf* is the effective degrees of freedom.

Presence-only (Gaussian)			
Parametric coefficients	Estimate	t-value	p-value
intercept	-7.87	-133.9	< 0.001*
Smooth terms	edf	F-value	p-value
s(T0_50)	0.95	4.55	< 0.001*
s(logCalanus)	1.90	8.89	< 0.001*
s(Tmin)	3.50	17.67	< 0.001*
s(year)	2.08	2.06	0.00437*
te(latitude, longitude)	12.16	0.66	< 0.001*
ti(latitude, longitude, year)	21.17	2.78	< 0.001*
Deviance explained (%)			25.3

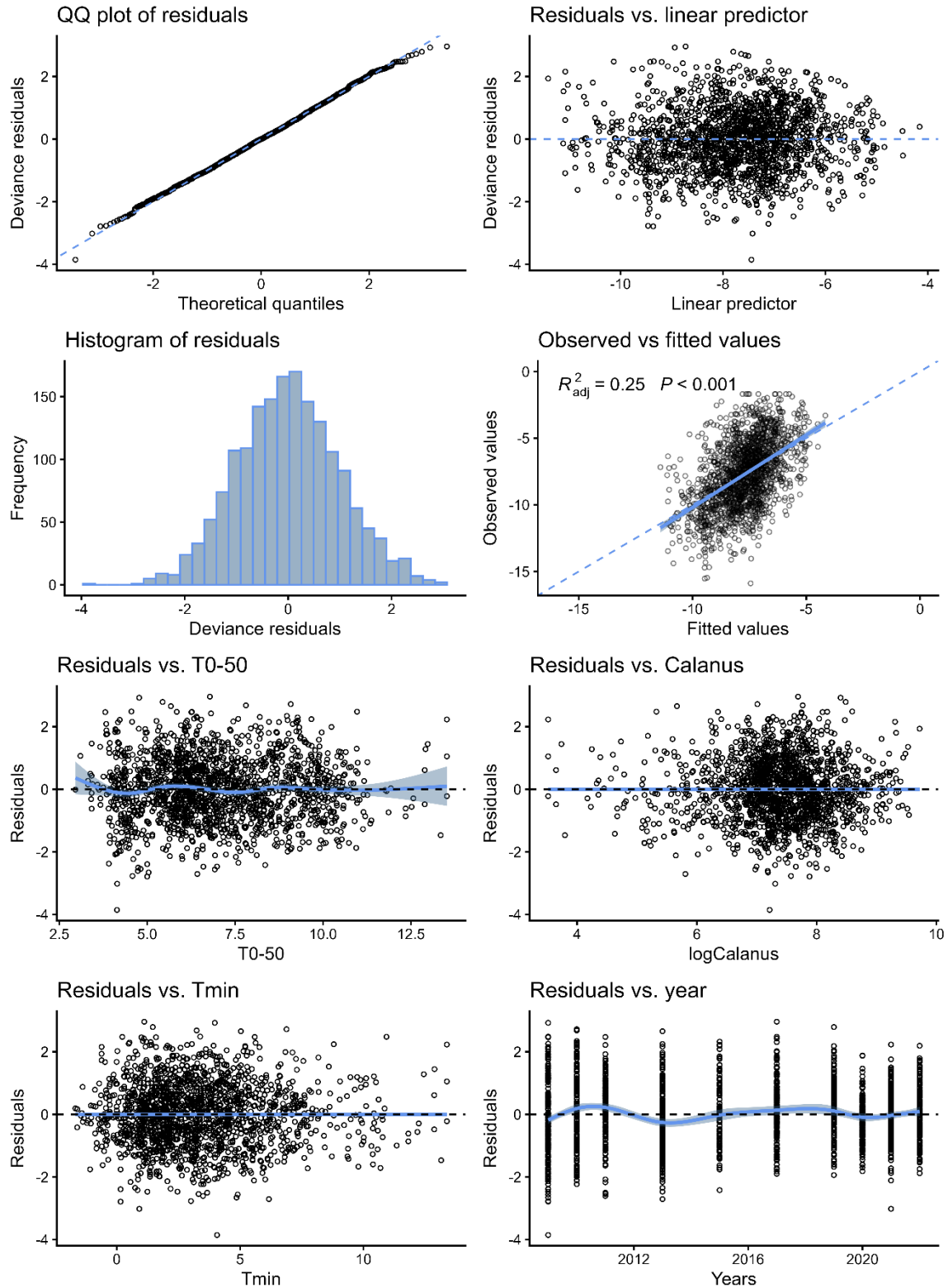


Figure C3. Residual diagnostic checks and spatial autocorrelation for the presence-only model.

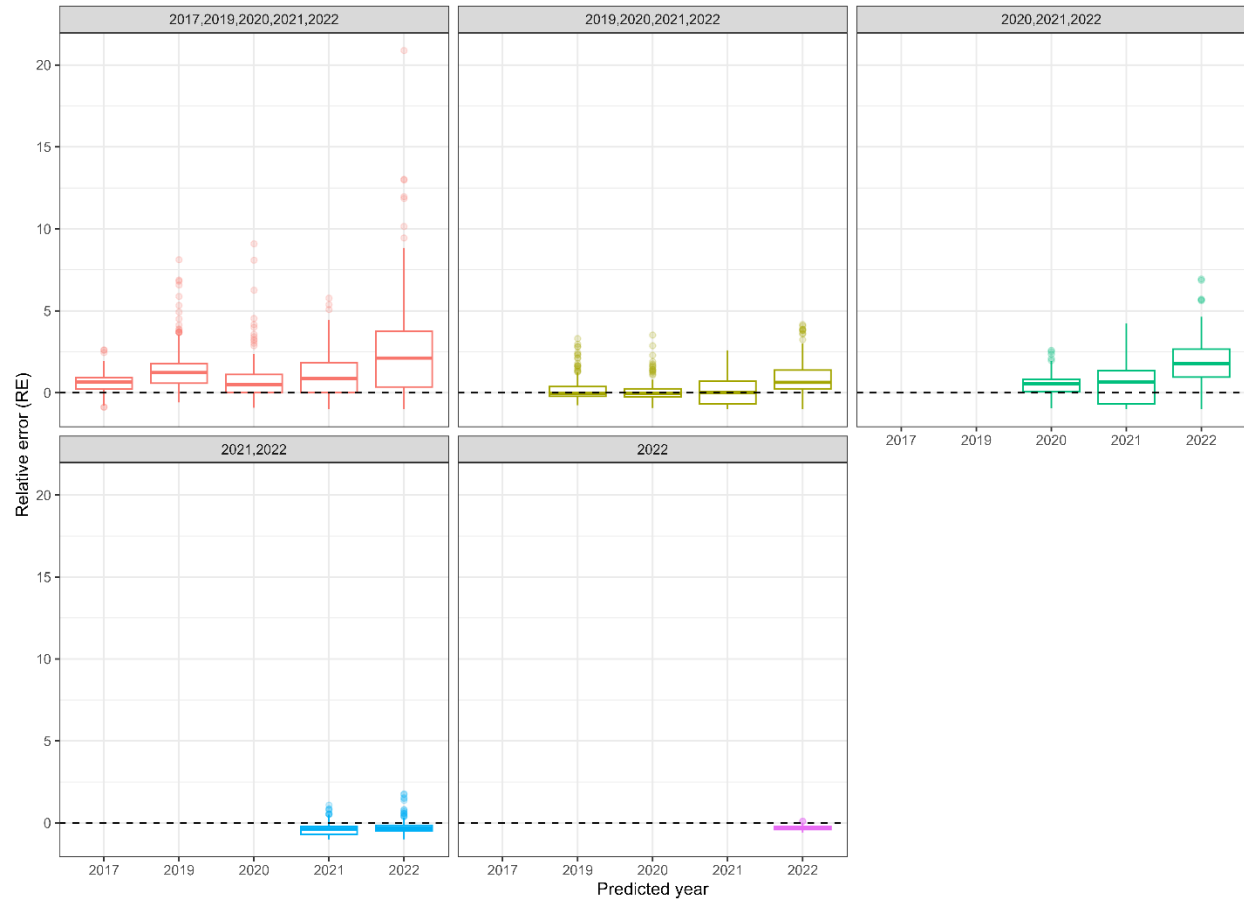


Figure C4. Forecast skill evaluation of the species distribution model. Predicted herring densities were generated by sequentially excluding the last year(s) of the time series (up to five years) and compared to observations using the relative error (RE).

APPENDIX D: HERRING VERTICAL DISTRIBUTION

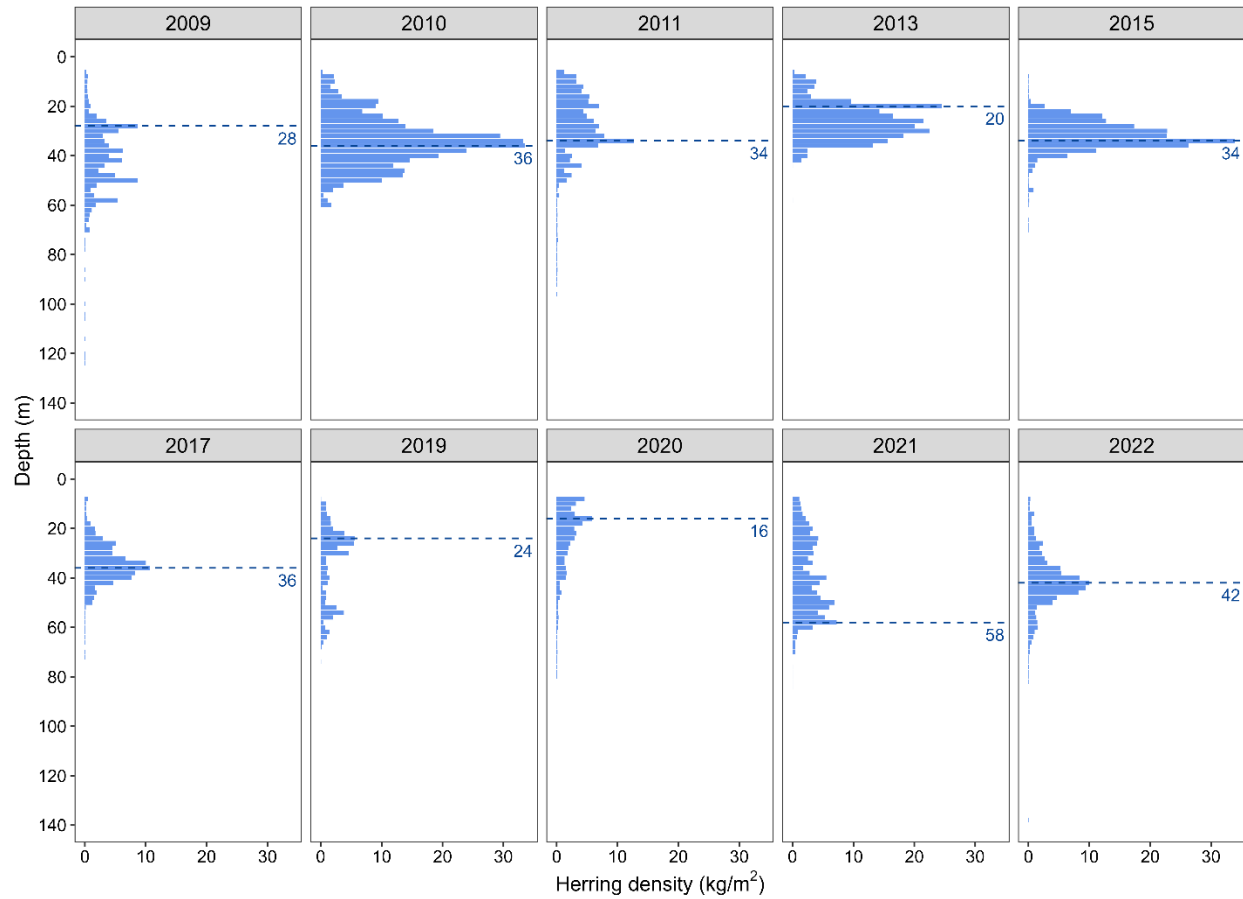


Figure D1. Vertical distribution of herring density (kg/m²) using the acoustic survey for the period 2009–2022. The blue horizontal bars represent the total density by depth and by year and the dotted blue lines represent the depth (m) at which herring density is highest.

APPENDIX E: TEMPORAL TREND OF ENVIRONMENTAL DATA

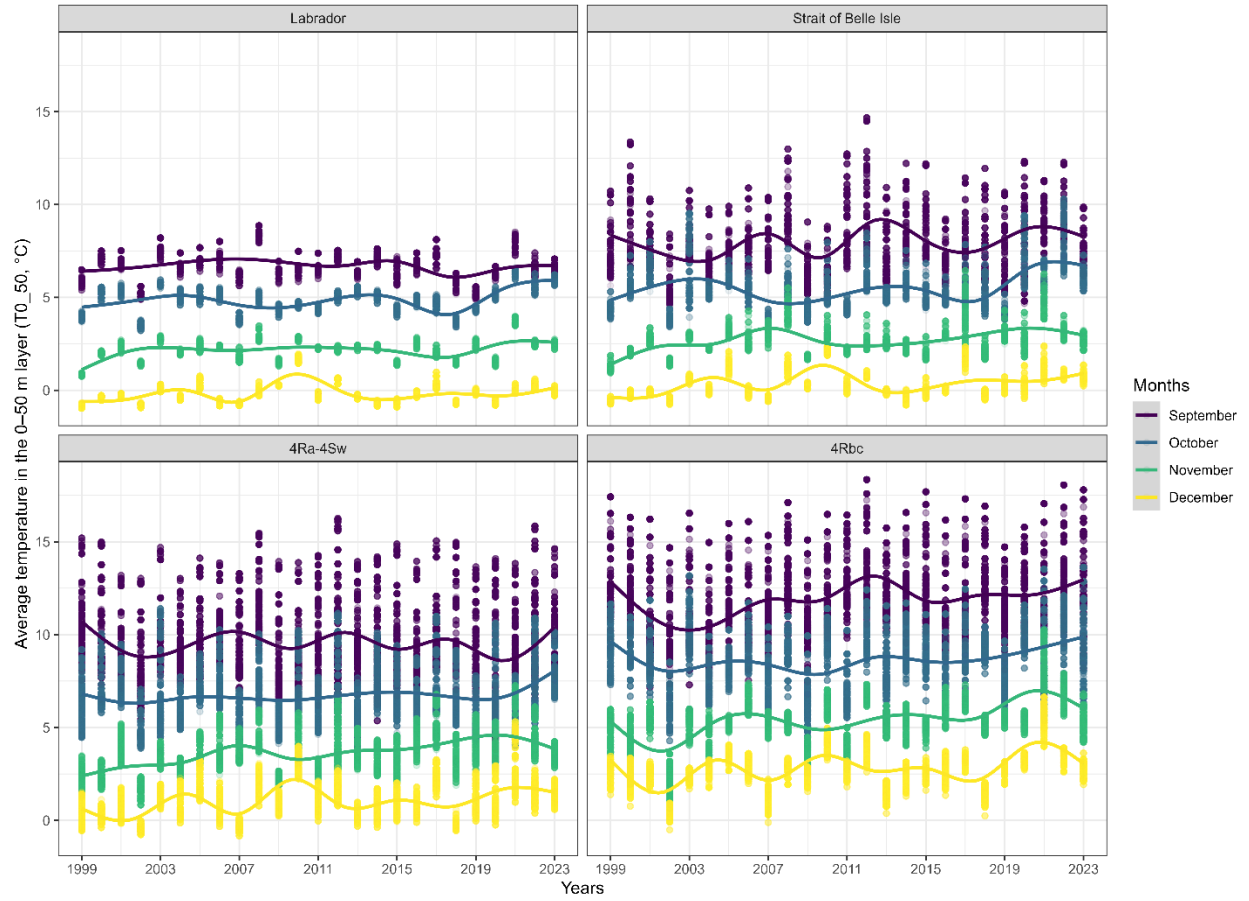


Figure E1. Temporal trend in the average temperature in the 0–50 m layer (T_{0_50} , °C) across four regions (4Ra–4Sw, 4Rbc, Labrador, Strait of Belle Isle) from September to December from the estimates of GLORYS12v1 product.

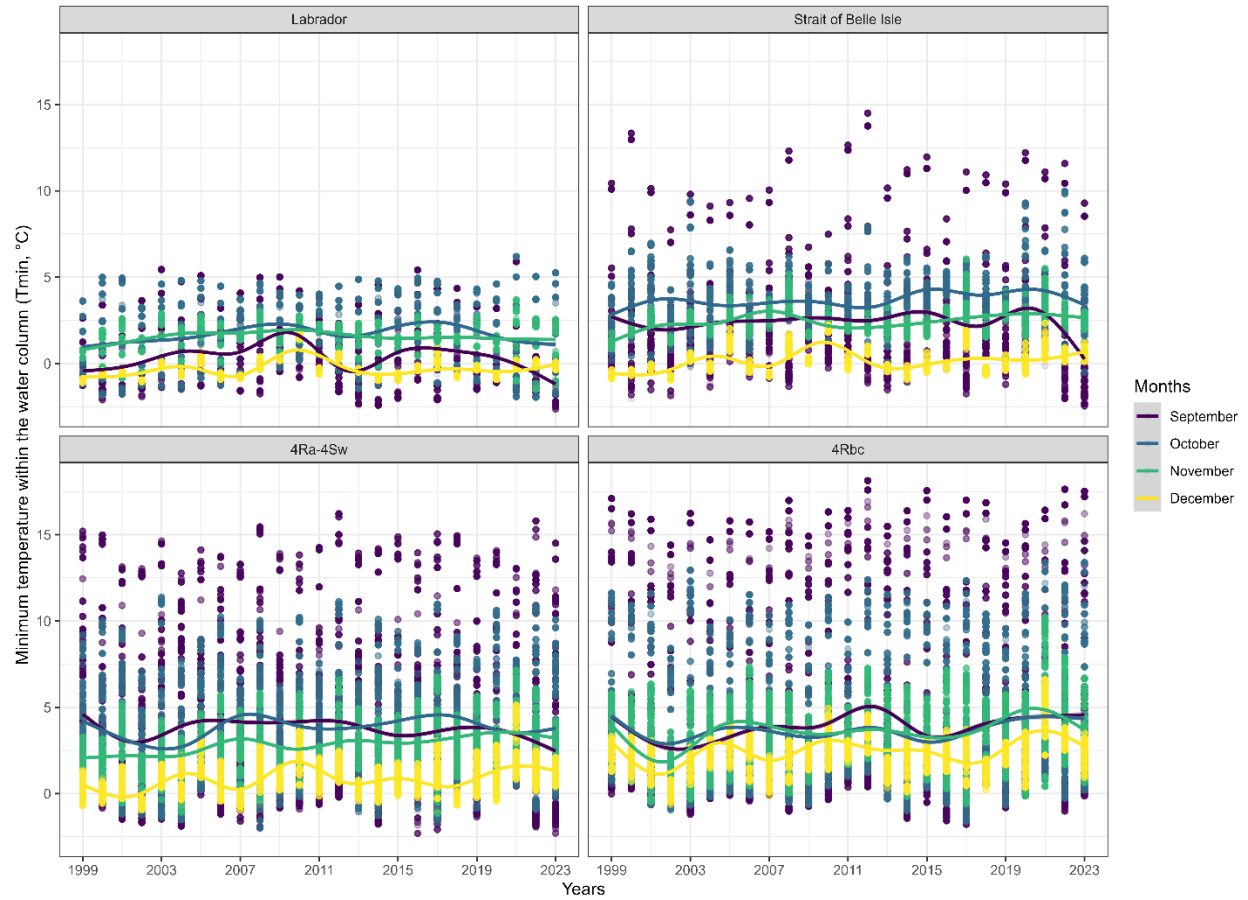


Figure E2. Temporal trends in the minimum temperature within the water column (T_{min} , °C) across four regions (4Ra–4Sw, 4Rbc, Labrador, Strait of Belle Isle) from September to December from the estimates of GLORYS12v1 product.



Figure E3. Temporal trends in log-transformed *Calanus* biomass (mg/m^2) across four regions (4Ra–4Sw, 4Rbc, Labrador, Strait of Belle Isle) from September to December from the estimates of the species distribution models of Plourde et al. (2024).