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Biological characteristics, factors affecting catchability, and abundance indices of capelin in the southern and northern Gulf of St. Lawrence multi species bottom trawl surveys

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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

The main objective of this study was to investigate, based on new analyses and a conceptual model of capelin summer-feeding habitat use, if biologically sound capelin abundance indices could be derived from the southern and northern Gulf of St. Lawrence (GSL) multispecies bottom trawl surveys. A series of predictions generated by the conceptual model, which states that capelin is associated with the cold intermediate layer (CIL) and performs diel vertical migrations making it more available to bottom trawls during the day, were supported by analyses of survey data. Size frequency distributions of capelin caught in the multispecies bottom trawl surveys indicated regional differences in size structure. Compared to length frequencies from the commercial fishery targeting spawning fish, the surveys captured on average smaller sized (and younger) capelin. The hypothesized negative effect of predation risk on capelin catchability in bottom trawls was quantified while accounting for other habitat descriptors. Results showed that, for the southern GSL (sGSL), capelin catchability was negatively related with predation risk but with a small overall effect relative to other factors. Among the abundance indices presented, an index computed from hauls performed in capelin preferred thermal habitat is promising because of its consideration of capelin behaviour and lower associated variability. This index, however, assumes that capelin density is horizontally homogenous in the CIL and this assumption has yet to be validated. An estimate of the order of magnitude of fishing mortality is also presented based on newly developed abundance indices and is considered low when compared to conservative estimates of capelin natural mortality, although the risk of local depletion where the fishery is concentrated was not investigated. These new analyses bring useful information in support of the assessment of NAFO Divisions 4RST capelin stock assessment.

1. INTRODUCTION

Capelin is a cold-water species generally occupying temperatures between -1 °C and 3 °C (Crook et al. 2017, Ingvaldsen and Gjøsæter 2013, Olafsdottir and Rose 2012). This temperature preference appears strong as the species distribution has been shown to track changes in the distribution of its optimal thermal habitat (Rose 2005). Capelin performs diel vertical migration in order to feed during the day on dense aggregations of its main prey, copepods of the genus Calanus and krill (Dalpadado and Mowbray 2013, Aarflot et al. 2020). In the Barents Sea, higher capelin abundances are generally associated with regions shallower than 200 m typical of shallow banks and their slopes, and where temperature is optimal and feeding success is higher due to higher light levels and zooplankton prey density (Aarflot et al. 2020).

The assessment of the Northwest Atlantic Fisheries Organization (NAFO) Divisions 4RST capelin stock is considered as data-poor. Capelin has occurred commonly in the catches of the southern and northern Gulf of St. Lawrence (GSL) multispecies bottom trawl surveys since 1990 (respectively sGSL and nGSL bottom trawl surveys; Grégoire et al. 2012, Savoie 2014). O'Driscoll et al. (2002) proposed two major uncertainties associated with the use of bottom trawls to assess pelagic fish abundance. First, capture efficiency (qe) in the trawl zone is uncertain because it is difficult to know how catches are representative of the volume sampled. Second, the proportion of fish available to the survey (e.g., within the trawlable habitat; qa) is possibly low and variable from year to year because the volume sampled by the bottom trawl only represents a small proportion of capelin's habitat due to the vertical distribution and migratory behaviour of this pelagic fish. An increase in capelin and Atlantic herring occupation of the supra-benthic habitat observed in the early 1990s supported the potential for interannual variations in capelin daytime vertical distribution and availability to the bottom trawl, casting doubts on the value of long-term Department of Fisheries and Oceans (DFO) bottom trawl surveys for providing useful information for the capelin assessment (Mowbray 2002, McQuinn 2009). The increase of supra-benthic habitat occupation by capelin and herring was interpreted as a behavioural response to the collapse of Atlantic cod stocks in the GSL and Newfoundland, explicitly implying that local cod abundance would affect capelin catch in the bottom trawl. However, there has been no targeted empirical analyses aimed at testing this prediction to date.

Our study had five distinct yet complementary objectives aimed at developing and validating capelin abundance indices using sGSL and nGSL bottom trawl surveys to inform the 4RST capelin stock assessment. First, a conceptual model of capelin vertical distribution in the GSL was developed by describing capelin temperature preference and testing predictions related to diel variation and their expected effects on capelin occurrence and abundance in the supra-benthic habitat based on catches in the bottom trawl. Second, capelin size frequency distributions in the bottom trawl surveys were compared to those from the commercial fishery which takes place in spring-early summer. These were further interpreted in the context of historical length at age data from the GSL. Third, we explicitly tested the hypothesis that capelin avoid the supra-benthic layer sampled by bottom trawl when demersal predator abundance is high, thereby decreasing their catchability to surveys, and quantify its importance relative to physical habitat characteristics. Fourth, abundance indices accounting for results obtained from previous objectives were computed and evaluated with regard to their associated variability. Finally, abundance indices were combined with fishery data and catchability coefficients for pelagic fish sampled by bottom trawl surveys to provide a coarse estimate of the relative magnitude of capelin fishing mortality and natural mortality in the GSL. This ratio provides an indicator of the sustainability of fishing on the stock. These analyses were part of a multidisciplinary approach aimed at integrating ecosystem-based knowledge to improve the assessment of the data-poor 4RST capelin stock.

2. METHODS

2.1. STUDY AREA, SURVEY DESIGNS AND SAMPLING GEAR

The GSL is a large semi-enclosed ecosystem reaching depths greater than 500 m. The sGSL is a shallow shelf with relatively homogenous depths, mostly less than 100 m with a mean sampled depth in the survey around 80 m. The nGSL is a more heterogeneous environment than the sGSL and includes deep channels, slopes, and channel heads with a mean sampled bottom depth of 240 m in the survey. Summer water temperature in the GSL is characterized by three layers: a warm surface layer, the cold intermediate layer (CIL) mainly formed in winter, and covering depths from about 50 m to 120 m, and a deep and slightly warmer layer of Atlantic origin (Galbraith et al. 2019). The CIL covers a large proportion of the bottom area in the sGSL but not the nGSL. Therefore, capelin preferred summer thermal habitat would be mostly constrained vertically by warmer surface and deep layers in the nGSL, and by the warmer surface layer and the ocean floor in the sGSL.

Both sGSL and nGSL bottom trawl surveys rely on a random stratified design, where the study area is divided into strata of relatively homogenous depths. The number of stations sampled annually in each stratum (effort) has typically been proportional to stratum surface area (Figure 1). The surveys are conducted respectively in September and August. Catch data were standardized to adjust for changes in vessel and gear specifications and hence each of the two surveys is individually considered standardized (Benoît and Swain 2003a, 2003b; Bourdages et al. 2007). However, the two surveys have employed different bottom trawls since the mid-1980s and cannot be considered as intercalibrated. The sGSL bottom trawl survey data set used in this study extends from 1971 to 2020, while the nGSL data set involves the 1990–2020 period. A detailed history of the surveys and protocols are given in Chadwick et al. (2007), with additional details in Hurlbut and Clay (1990) for the sGSL.

2.2. CAPELIN VERTICAL DISTRIBUTION CONCEPTUAL MODEL IN GSL

Capelin thermal habitat preference was first investigated by identifying discontinuities in the empirical cumulative frequency distribution (ECD) of temperatures weighted by standardized capelin survey catch (Perry et Smith 1994) for both the sGSL and nGSL bottom trawl surveys.

The results of the thermal preference analyses, other exploratory analyses and previous works indicated that capelin prefer cold waters that fall in a temperature range consistent with the CIL in the GSL in the summer (-1 °C to 3 °C) (Galbraith et al. 2019). The strength of this preference suggested that capelin may in fact be largely restricted to the CIL in this ecosystem during the summer. Thus, although capelin have been captured over broad geographic areas in bottom trawl surveys in the GSL (e.g., Grégoire et al. 2012), catches in hauls conducted at depths deeper than the CIL may reflect capture during trawl haul back, and to a lesser extent when it is deployed (as the trawl is not fully opened), as it passes through the CIL, rather than capture during the standard haul on bottom. There have been no analyses of hydroacoustic data in the GSL that can confirm the hypothesis that capelin are restricted to the CIL in summer months. However, this hypothesis generates several predictions that can be evaluated using the trawl survey data. Specifically:

1. Catches in survey hauls conducted at depths above the CIL, in the warm mixed layer, should at most reflect straggling individuals.

    a. Catches will therefore be sporadic, with a low probability of occurrence, and comprise very low densities when they occur.

2. Catch in survey hauls conducted at depths occurring in the CIL should reflect capture of capelin available near the bottom.
    b. Densities of capelin in catches should be the highest, compared to hauls made above or below the CIL.
    c. Catches should vary over the diel cycle as capelin are known to undergo diel vertical migrations within their preferred habitat, and should be largest during the daytime when capelin depth distribution is deepest (O'Driscoll et al. 2002).
3. Catch in survey hauls conducted at depths lying below the CIL should reflect captures occurring only as the trawl traverses the CIL, principally during haul back. Thus,
    d. The probability of occurrence of capelin in these hauls should be similar to that for hauls undertaken in the CIL, but perhaps slightly lower owing to stochasticity associated with a much more limited duration of sampling.
    e. Densities of capelin in these hauls should be considerably lower than densities in hauls undertaken in the CIL.
    f. Standard trawl durations in sGSL surveys are longer (30 min) than those in nGSL surveys (20–24 min, 1990–2003, and some hauls in 2004–2005; 15 min since then), and therefore trawl recovery represents a smaller fraction of the time the trawl is in the water in the sGSL. In turn, this means that the difference in catch densities between hauls conducted in versus below the CIL should be greater in sGSL surveys compared to nGSL surveys.
    g. Diel vertical migrations by capelin should not affect catches from hauls at deeper depths if these vertical migrations are constrained within the boundaries of the CIL. In other words, there should be no diel variation in catches in the deeper hauls.

These predictions were evaluated by analyzing catches in the trawl surveys. The data from the sGSL and nGSL were analyzed separately because these surveys employ different trawls for which the relative catchability is not known. Furthermore, treating the surveys separately allows for an assessment of prediction 3c. Data for the sGSL survey were limited to 1990–2020 because capelin catches were small and infrequent (less than 12.5% of tows) prior to 1990. Analyses were conducted separately for positive catches (excluding zeros) and for presence-absence principally because different predictions were made for catch densities and the probability of occurrence, although the separate treatment of zero catches somewhat simplified the analyses.

The basic model in each case had the following form:

$$Response \sim \beta_0 + depth\ class + s(time) \times depth\ class + year\_strat + \varepsilon$$

where

- β_0 is the intercept*,*
- *depth class* is a factor representing 25 m or 50 m depth classes, depending on data availability,
- *time* is the time of day modelled using a cyclic cubic regression spline, denoted as s(),
- *year_strat* is a random effect to account coarsely for spatiotemporal variation in mean densities,

- *year_strat*~$N(0,\sigma^2)$ and
- ε is the error term.

Modelling of catch densities used the log(standard catch) as the response, where catches were restricted to positive catches and adjusted for swept area. Modelling of occurrence employed presence as a Bernouilli response in a binomial model, and an offset term was added to the basic model to account for swept area differences. Models were fitted using the gamm4 package (Wood and Scheipl 2020) in R (R Core Team 2020).

2.3. SIZE STRUCTURE

In the sGSL bottom trawl survey, total capelin catch in a tow was weighed, a length frequency (total length, cm) was obtained either for the total catch when it was small or from a random sample of up to around 100 individuals otherwise, and length-stratified subsampling was used to obtain an individual weight (g) for 1 fish per 1 cm bin. Annual percentage of fish in 1 cm length categories was computed, adjusting for any subsampling (capelin length frequencies were scaled to the number captured in the tow). In the nGSL bottom trawl survey, total capelin catch in a tow was weighed and random sample of about 30 fish was chosen to obtain individual lengths (total length, mm) and weights (g). Capelin length frequencies were also scaled to the capture in the tow before computing annual length distributions. Relative size frequency distributions were compared between surveys for tows located in sGSL strata 415, 425 and 439 (strata sampled by both surveys, Figure 1).

Size structure in both surveys were also compared with size frequency distributions from the commercial fisheries in the nGSL (NAFO Divisions 4R and 4S) and sGSL (NAFO Division 4T). They were also compared with length at age data collected from 1984 to 1993 in the nGSL, as described by Hurtubise (1994) and Grégoire et al. (1995). Age determination was done with the method described in Bailey et al. (1977; birth date was chosen as January 1).

2.4. INFLUENCE OF PREDATION INDICES AND ENVIRONMENTAL CONDITIONS ON CAPELIN CATCHABILITY

The increase of small pelagic presence in the eastern Scotian Shelf bottom trawl survey following the 1990s groundfish collapse was interpreted by some authors (Frank et al. 2005) as a trophic response to the reduction of predation. On the other hand, McQuinn (2009) and Jech and McQuinn (2016) advocated that the increase in bottom trawl indices for small pelagic fish was mainly caused by their greater availability in the demersal zone due to a change in their vertical distribution (Suprabenthic Habitat Occupation; SHO). According to the SHO hypothesis, capelin catchability in the GSL bottom trawl surveys should be negatively correlated to predation risk in the demersal zone. Furthermore, the relationship between observed capelin abundances and predation risk should not vary if habitat preferences are taken into account.

Analyses aimed to test these predictions were designed using the sGSL and nGSL bottom trawl survey data. The analyses were structured to account for differing capelin-predator habitat use that would produce negative relationships. The predators were selected due to the prevalence of capelin in their diet and a range of local abundance in the demersal zone that was large enough to expect an effect of predation risk on capelin catchability: Atlantic cod (*Gadus morhua*) and Greenland halibut (*Reinhardtius hippoglossoides*, hereafter referred as turbot).

2.4.1. Predation indices

The sGSL and nGSL bottom trawl survey data were processed following the same approach (except when specified), but were analyzed separately.

Predation indices were calculated by tow based on the abundance of predators and their presumed prey consumption rate. Consumption was estimated based on scaling laws and metabolic theory (Kleiber 1932, 1947), which states that metabolic rate in fish is proportional to individual body mass (*Mj*) and temperature (*t*):

$$metabolic\ rate \sim M_j^{0.75} e^{0.036\,t}$$

Prey consumption should be proportional to metabolism, and hence our predation index was calculated as follows:

$$predation.index_i \propto \sum_{j=1}^{Max\ length} N_{ij} M_j^{0.75}\ e^{0.036\,t_i}$$

Where

- N_{ij} is the standardized number of fish in tow *i* of size class *j*,
- M_j is the mean mass of a fish of this size class according to the length-weight relationship of the corresponding year and
- t_i is the bottom water temperature recorded during tow *i*.

Predator of size classes known to consume no or insignificant amounts of capelin were excluded from the computation of predation indices. Atlantic cod predation indices were computed respectively based on individuals greater than 25 cm (Hanson 2011). The turbot predation index used individual of all sizes (Bernier and Chabot 2013).

Time series of cod and turbot abundances in the bottom trawl surveys are available for reference in APPENDIX 1.

2.4.2. Predation and environmental correlates of capelin catchability

To quantify the impact of predation and environmental indices on capelin relative catchability in the bottom trawl surveys, three sets of Negative binomial generalized additive mixed-effects models were fitted and compared: one based on predation indices, one based on both predation indices and habitat covariates, and one for habitat covariates only. Models were formulated as

$$g(\mu) = \beta_0 + s(x1) + s(x2) + s(x3) + \cdots + offset\big(log.area_{ij}\big) + year\_strat_i + \varepsilon_i$$

where

- μ is the capelin catch (in numbers),
- *g()* is the log link function,
- β_0 is the intercept,
- *s()* are smooth functions of the covariates (*x1*, *x2*, *x3*, …) and
- ε_i is the error term.

Models included a cyclic cubic regression spline for the time of the day (hour) with a maximum of 4 knots to model the diel availability of capelin in the demersal zone (Benoît et Swain 2003b). Thin plate regression splines were used for predation and environmental indices allowing shrinkage, with a maximum of 5 estimated degrees of freedom (edf) to avoid overcomplex multimodal effects. An offset term (offset[log.area$_{ij}$]) was included to account for swept area and standardization changes in the vessel and gear used for the survey in the sGSL survey. All models included the combination of year and stratum (year_strat$_i$) as random intercepts in order to account for spatial and temporal autocorrelation in catches (model G in Pedersen et al. 2019). In our models, this random effect also accounted for average capelin density in stratum-year cells. Because strata were assumed to have homogenous capelin densities, we effectively model the relative effects of covariates on deviations from these average catches, hence representing their effects on capelin catchability. The negative binomial was used as a reference distribution because it is considered appropriate for modelling count data from trawl surveys (Cadigan 2011). The gam function of the mgcv package (Wood 2019) was used. For each modelled species, predictor effects, Akaike Information Criteria (AIC) and deviance explained were compared.

The datasets used in this section included survey years from 1971–2016 in the sGSL and 1990–2018 in the nGSL bottom trawl surveys. Prior to the analyses, we removed observations in each combination of year and stratum where capelin was absent in order to meet model assumptions of normally distributed random intercept. All the covariates were scaled to a mean of 0 and a standard deviation of 1.

In preliminary model fitting for nGSL data, the estimated effect of hour did not conform with the expected diel vertical migrations of capelin, predicting maximum capelin abundances at around 3 AM. Many studies have shown that capelin undergo diel vertical migrations where they are found deeper during the day and closer to the surface during nighttime (Bailey et al. 1977, O'Driscoll and Rose 1999, Mowbray 2002, Davoren et al. 2006, Regular et al. 2010). Greater abundances in the bottom trawl surveys should be observed during the day when capelin depth distribution is deepest. Based on this information we have interpreted the effect of hour in the nGSL catches as spurious. Because a greater proportion of the trawls are performed at depths greater than capelin preferred thermal habitat in the nGSL than in the sGSL (see section 3.1), capelin were probably sampled as the trawl passed through the water column rather than when it was fishing on bottom. There should be no effect of predation risk by demersal fish on the catchability of capelin sampled in the water column rather than on bottom. We therefore subsequently refitted the same models using the subset of trawls restricted to the formerly identified thermal habitat and compared the hour effect with the preceding results.

Model assumptions were validated by inspecting scaled (quantile) residuals with DHARMa diagnostic tools (Hartig 2020): quantile-quantile plot, Kolmogorov-Smirnov, dispersion and outlier tests as well as residuals against predicted values. Simulated residuals were conditioned on fitted random effects (random effects were not re-simulated). All statistical analyses and figures were made in R (R Core Team 2020).

2.5. CAPELIN ABUNDANCE INDICES

Catches of small pelagic fish in trawl surveys are often quite variable. Models assuming negative binomial error and a log-linear mean have been found to be appropriate for modelling catch numbers in such cases, and for modelling bottom trawl survey data in general (Cadigan 2011, Surette 2016).

The survey in the nGSL regularly fails to sample one or more strata in a year due to constraints on survey timing and duration. This has also occurred in the sGSL survey, although to a lesser extent. To avoid introducing biases to estimated survey indices, mean catch densities in missing stratum-year cells were imputed via an ad hoc estimation using general linear models based on survey catches in neighbouring years.

Here we employ a model assuming negative binomial (NB) error and a log-linear mean that is a function of a fixed overall stratum effect and an annual stratum effect that follows a first-order autoregressive (AR[1]) process. The use of an AR(1) stratum term permits the estimation of annual stratum means even in the absence of survey sampling, and will contribute to attenuating strong interannual fluctuations in stratum means resulting from highly variable survey catches. Specifically the model was defined as follows:

$$Y_{i,s,t} \sim \mathrm{NB}(\mu_{s,t}\ , k)$$

$$E[y_{i,s,t}] = \mu_{s,t} = \exp(\ \lambda_S + \delta_{s,t} + offset), \text{where } \delta_{s,t} = \ \phi\ \delta_{S,t-1} + \ \varepsilon_{S,t}$$

$$Var[y_{i,s,t}] = \mu_{s,t} + \mu^{2}{}_{s,t}/k$$

$$\overline{x_t} = \frac{\sum_{s=1}^{L} N_s \mu_{s,t}}{N} \text{ where } N = \sum_{s=1}^{L} N_s$$

where

- $Y_{i,s,t}$ is the catch in numbers in tow *i*, stratum *s* and year *t*,
- $\mu_{s,t}$ is the mean density in *s* and *t*,
- *k* is the negative binomial dispersion parameter,
- λ_s is the overall stratum effect,
- $\delta_{s,t}$ is the stratum-year effect that follows an AR(1) process with autocorrelation parameter ϕ,
- $\overline{x_t}$ is the mean number per tow for year *t*, and
- N_s is the weight for stratum *s* (proportion of study area in stratum s).

Confidence intervals on $\overline{x_t}$ were derived using the delta method. The offset term was equal to the log(swept area/standard swept area), and for survey catches prior to 1992 in the sGSL also accounted for differences in catchability associated with the vessels and trawls used, relative to those employed as of 1992 (Benoît and Swain, 2003a; Benoît, 2006). In 2003, the sGSL survey employed the Canadian Coast Guard Ship (CCGS) Wilfred Templemen. Although this vessel was not specifically calibrated for the survey, it was the sister ship of the regular survey vessel, CCGS Alfred Needler, and assumed to fish comparably to that vessel. No conversions for changes in vessel or gear are required for capelin in nGSL surveys (Bourdages et al. 2007). Capelin catches from the nGSL survey occurring in the portion of NAFO Division 4T spatially overlapping the sGSL survey (Figure 1) were removed to keep the abundance indices for the two areas independent.

Capelin catches have been shown to vary over the diel cycle in the sGSL survey (Benoît and Swain, 2003b). Accounting for this effect is normally necessary for the production of abundance indices from sGSL survey data because the survey only operated during daylight hours (7:00-19:00) from 1971 to 1984, and failure to account for the diel effect will introduce a bias for these earlier years compared to the post 1984 period during which the survey operated 24 hours per day. However, analyses presented below revealed that diel variation in catch does not occur in all strata and it is therefore inappropriate to apply an overall correction as suggested by Benoît and Swain (2003b). It was not possible to implement stratum-specific diel effects in the above model in time for the present document. Although this will result in some bias in the sGSL series, this bias is expected to be small and inconsequential because capelin catches in the survey prior to the 1990s were infrequent and of small magnitude.

Two series of abundance indices were estimated for both the sGSL and nGSL surveys. The first employed all strata that were consistently part of the sampling plan over the survey series, 1971–2020 for the sGSL (strata 415 to 439), and 1990–2020 for the nGSL (strata 401 to 841). The second estimated the average density of capelin in strata occurring in their preferred habitat (roughly the CIL) and assumed that those densities were also relevant at survey locations that were deeper than that habitat. In survey strata that occurred above the preferred habitat (sGSL only), densities were estimated using survey catches. In other words, annual stratum means were estimated as usual for strata occurring above or in capelin preferred habitat, while the stratum means for strata occurring below that habitat were set equal to the mean from the preferred habitat, based on the assumption that capelin are roughly homogeneously distributed in that habitat. Based on the analysis of habitat preference (section 3.1), strata for which depths were mostly contained in the 50–120 m range were considered to reflect preferred habitat in the sGSL survey, while the 50–175 m range was used for the nGSL survey (Figure 2).

2.6. ESTIMATED ORDER OF MAGNITUDE OF FISHING MORTALITY

The order of magnitude of fishing mortality for the whole capelin stock (4RST) was estimated using data from bottom trawl surveys, catchability coefficients (q) from the literature for small pelagic in this type of survey and average landings over the last three years (8 946 t/year; 2018–2020). Specifically, for each survey and abundance index (core and CIL strata), mean number per tow (MNPT) for the 2017–2020 period was multiplied by mean individual weight and number of survey trawlable units to obtain mean trawlable biomass. Estimated order of magnitude of biomass and exploitation rates were respectively obtained by dividing trawlable biomass by catchability coefficients, and by dividing average landings by estimated order of magnitude of biomass. Decisions on the choice of the period for average landings (excluding the 2017 low landings), MNPT (excluding the high 2017 value for both surveys) and value of q (maximal value from the literature) were made in order to obtain a conservative estimate of the order of magnitude of fishing mortality. Results were then compared with estimates of natural mortality (M) using three different methods:

- Hoenig (1983) equation for all species groups,
- Equation 8 from Hamel (2015) combining estimates of M from three methods using maximum age (one-parameter t_{max}, $Hoenig_{lm}$ and $Hoenig_{nls}$ methods; see Table 3 in Then et al. 2015), and
- The updated Hoenig method (Then et al. 2015).

Maximum age was set to 7 years old and hence estimates of M are considered conservative. All computations and statistical analyses were performed in R (R Core Team 2020).

3. RESULTS

3.1. CAPELIN HABITAT PREFERENCE

Capelin thermal habitat association in the sGSL shows that 94% of fish were caught at bottom temperatures lower than 2.2 °C, while this range of temperature only accounted for 61% of all survey tows, clearly indicating a preference for these temperatures (Figure 3). On average, bottom temperatures below 2.0 °C occurred at depths between 50 m and 125 m in the sGSL. In the nGSL, 87% of capelin were caught at bottom temperatures lower than 3.3 °C, while this range of temperatures only accounted for 28% of all survey tows (Figure 4). On average, bottom temperatures below 3.3 °C occurred at a depth below 170 m in the nGSL.

Tows performed in capelin preferred thermal habitat represented on average 55.3% of the sGSL tows, but only 28.4% in the nGSL (Figure 5). In the nGSL, tows performed in capelin preferred thermal habitat were restricted to the more coastal strata along the Québec North Shore, the Anticosti Island and the West coast of Newfoundland (Figure 5).

Based on the results of thermal preferences in each survey, preferred capelin habitat is expected to occur between 50 m and 120 m in the sGSL and 50 m and 175 m in the nGSL, roughly the CIL. Results of analyses aimed at evaluating whether capelin are largely restricted to this layer generally support the predictions made for the conceptual model in section 2.2.

Both mean densities and the probability of occurrence were very low in strata shallower than the preferred habitat in the sGSL (Figure 6; note that there are essentially no such depths in the nGSL). Furthermore, there was no evidence of diel variability in catches. This is consistent with prediction 1a, that capelin caught in trawl hauls at these depths are likely stragglers.

Catches in the preferred habitat were larger on average at preferred depths, particularly on the lower end of the range of these depths in both surveys, consistent with predictions 2a and 3b (Figure 6, Figure 7). Furthermore, diel variation in positive catches resulting in peak catch around noon was only found for these depth classes in the sGSL and nGSL (Table A4,Table A6). While a significant effect of hour was also estimated for some deeper depth classes in the nGSL (Table A6), the amplitude of the variation was considerably smaller and out of phase compared with diel patterns for preferred depths (Figure 7). These results are consistent with prediction 2b, and somewhat inconsistent with prediction 3d.

Generally speaking, the probability of occurrence was of similar magnitude in depth classes occurring in preferred habitat and those below it in both surveys (Figure 6, Figure 7, Table A5, Table A7). A notable exception was for the nGSL survey where the mean probability decreased for stations fishing deeper depths (>400 m). This might reflect decreased trawl opening while passing through the CIL as a result of the longer retrieval period, but could also indicate reduced capelin presence (and density) in areas where the CIL is well above bottom. These results are partly consistent with prediction 3a.

Finally, the difference in peak densities (mean positive catch) in depth classes covering preferred habitat versus those below it were greater in the sGSL compared to the nGSL for the depths sampled by both surveys (<375 m; Figure 6, Figure 7). This is consistent with prediction 3c which states that the incidental catch of capelin as the trawl passes through the CIL should be relatively smaller in the sGSL survey given that trawl retrieval and deployment represent a smaller fraction of the total time the trawl is in the water in that survey.

Jointly these results indicate that capelin are principally distributed and perhaps largely restricted to cool waters characteristic of the CIL. There is evidence to suggest that survey catches from hauls fishing below the CIL may occur largely or exclusively as the trawl passes through that layer. It is not possible to conclude, however, whether densities in the CIL are spatially homogenous. The analyses indicate that both mean positive catch and occurrence decrease particularly for hauls performed at the deeper depths of the nGSL. While this could indicate that capelin density in the CIL at these locations is lower, it may be possible that the longer retrieval time and distance for the trawl results in a smaller trawl opening as it passes through the CIL, which in turn would reduce both catch numbers and occurrence. An evaluation of trawl mensuration data would allow an evaluation of this hypothesis.

3.2. SIZE STRUCTURE

Annual capelin relative length frequency distributions in the sGSL bottom trawl survey generally showed a mode around 110 mm sometimes accompanied by a second smaller mode around 60 mm, whereas a single mode around 140 mm was usually observed in the nGSL bottom trawl survey (Figure 8). Note that the size mode from the sGSL bottom trawl survey in 1991 and 2013 was greater than usual.

Length distributions from both bottom trawl surveys restricted to sGSL strata 415, 425 and 439 (covered by both surveys) were more similar to each other than the overall pattern (Figure 9, Figure 10). The capelin from the sGSL survey sampled in these strata in September showed a mode at 110–120 mm whereas capelin sampled in these strata during the nGSL survey in August showed a wider mode between 120–140 mm (Figure 9), which slightly differs from the overall pattern for this survey (Figure 10). These results indicate that the two surveys have a similar size-selectivity for capelin. Consequently differences in length frequencies at the scale of whole survey areas likely reflect differences in the size of capelin present in those areas.

Length at age data collected from the commercial fishery between April and July from 1984 to 1993 (Hurtubise 1994) suggested that capelin from the sGSL bottom trawl survey would be mostly 1 and 2 year old individuals, nGSL bottom trawl survey would catch mostly 2 and 3 year old individuals, while the commercial fishery in the sGSL and nGSL targets individuals corresponding mostly to mature 3 years old and older individuals (Figure 10).

3.3. INFLUENCE OF PREDATION INDICES AND ENVIRONMENTAL CONDITIONS ON CAPELIN ABUNDANCES

After excluding year-stratum combinations with no capelin (and excluding tows outside capelin preferred habitat in the nGSL), 3634 and 969 tows were conserved for the sGSL and nGSL analyses respectively. The absence of capelin could reflect complete avoidance of the bottom when predators are present and consequently this data selection step could bias the estimation of the predation risk effect. To verify whether this could be the case, the frequency distribution of values of the predation indices were compared for datasets including or excluding strata with no capelin catches to determine whether the exclusion coincided with the exclusion of high predation risk values. For the sGSL (cod, turbot) and nGSL (cod) data, there were no striking differences between datasets including or excluding strata with no capelin catches (APPENDIX 2, Figure A22, Figure A23). In nGSL data, larger values of predation risk by turbot were associated with capelin absence from some year-strata and were therefore excluded. However, based on the preceding analyses we interpret this result as a coincidence given that this predators occurs principally in deeper warmer waters (Figures 11 and 32 of Bourdages et al. 2020) that are not preferred by capelin for physiological reasons and not because of the presence of predators.

Diagnostic plots for the best sGSL model (3.1) showed residuals with a minor departure from the uniform distribution (Kolmogorov-Smirnov test significant), as shown by the quantile-quantile and residuals vs. fitted plots. Observed frequency of catches with no capelin (zero catch) was within the 95% confidence intervals of simulated values from the fitted model. Standard deviation of residuals (dispersion) was also within 95% of simulated values (Figure 11). All other sGSL model residuals had the same minor departure from the uniform distribution and no other apparent problem (results not shown). Overall we conclude from these diagnostics that the assumptions for the models employed were met.

Quantile residuals of the best nGSL model (2.1) had a more severe departure from the uniform distribution: for medium to large predicted values, simulated values were smaller than the observed value. There were also fewer observed zeros than predicted by the fitted model, but no over or under-dispersion was apparent (Figure 12). All other nGSL models had the same problems, including models fitted with data from all core strata. Since diagnostic plots showed the nGSL models did not fit adequately to the data, the interpretation of the covariate effects could be misleading and results were not presented. It is worth mentioning that the nGSL model considering only the tows in the preferred thermal habitat of capelin showed an “hour” effect consistent with the expected behaviour of fish (greater abundances observed in the day).

The best capelin sGSL model in terms of AIC included time of day, the cod predation indices and habitat descriptors. This model resulted in a 7.9% increase in the deviance explained compared to a model including only the random intercept and time of day (Table 1). A small negative effect of cod predation indices on capelin catches was estimated, while there was a weak positive relationship with the turbot predation index (Figure 13). Negative and bimodal relationships were observed respectively for the effects of bottom temperature and depth (Figure 13). The addition or removal of covariates in the models had very small or no impact on other descriptor effects or their probability of type 1 error (p values).

The inclusion of predation indices and habitat descriptors to models including only the random intercept or random intercept and time of the day covariate(s) increased the deviance explained by a maximum of 9.9% for sGSL models (Table 1). The inclusion of predation indices alone increased the deviance explained by no more than 1.5% (Table 2). Consequently, the predation effect on capelin catchability was small and ignoring it will at most result in a minor bias in the computation of abundance indices.

3.4. CAPELIN ABUNDANCE INDICES

Compared to the traditional design-based estimator used to estimate trawl survey abundance indices, the NB AR(1) model produced estimates that were generally of higher precision and less temporally variable (see Figure 14 for the sGSL; results for the nGSL are not shown). All of the results that follow are from the latter model. Fits to the NB AR(1) model appeared to be decent (Figure A21, for the sGSL survey shown as an example).

Capelin were captured very infrequently and only in small numbers in the sGSL survey prior to 1990 (Figure 14). The abundance index for core strata increased from the mid-1990s to a peak around 2000, before declining to the mid-2000s and increasing again to a series high in 2010–2011. The index has subsequently declined. The index based on the assumption of homogenous density in the CIL followed similar trends, although the peak around 2010 was more pronounced, while the subsequent period was more variable and suggested a less pronounced decline (Figure 15).

The abundance index for all strata in the nGSL was elevated and somewhat increasing over the 1990s, declining to lows during the first half of the 2000s, before increasing gradually to a peak in 2011 (Figure 16). The index subsequently declined and, with the exception of 2017, has fluctuated around a relatively low level. When strata from the St. Lawrence Estuary added to the survey in 2008 are included in the index, the general trends remain, although the difference in the MNPT during the late 2000s peak and the subsequent period is more pronounced. The index based on the assumption of homogenous density in the CIL followed a similar trend to those described for all strata (Figure 17).

3.5. ESTIMATED ORDER OF MAGNITUDE OF FISHING MORTALITY

Considering only the trawlable biomass (Table 2), the exploitation rate estimates varied between 16 and 36% (respectively $F = 0.17$ and $F = 0.44$) depending on the choice of the abundance index and their interannual variation. By considering an estimate of the order of magnitude of the total biomass calculated from the trawlable biomass and a maximum value of q identified in the literature ($q = 0.0045$, herring in the sGSL survey, Benoît and Swain 2008), the estimated exploitation rates varied between 0.07 and 0.16% (respectively $F = 0.0007$ and $F = 0.0016$). In comparison, conservative estimates of natural mortality obtained from empirical equations ranged between 46 and 56% (respectively $M = 0.62$ and $M = 0.82$; Table 3).

4. DISCUSSION

The results presented in section 3.1 showed the association of capelin with waters ≤ 3 °C in the nGSL and ≤ 2° C in the sGSL is consistent with Ingvaldsen et Gjøsæter (2013) and Rose's

(2005) review of capelin temperature preference (mainly <2° C). Moreover, diel variation in positive catches resulting in peak catch around noon was only found in capelin preferred thermal habitat, in line with the well-documented diel vertical migration behaviour of capelin (e.g., O'Driscoll and Rose 1999, Mowbray 2002, Regular et al. 2010). Hence, data from the GSL multi species bottom trawl surveys support the idea that capelin is associated with cold conditions, and performs diel vertical migrations making it more available to the bottom trawl surveys during the day, when fishing on the bottom takes place within capelin preferred thermal habitat.

In addition to reflecting species-specific temperature preferences, the association of capelin with the CIL would likely result in favourable foraging opportunities near the bottom along the slopes of the nGSL deep channels and over large areas in the sGSL (Plourde et al. 2019). In the Barents Sea, capelin feeding success in late summer is associated with bottom depth above 200 m where both light level and high densities of their main prey, Calanus species and krill, promote high prey encounter rate (Dalpanado and Mowbray 2013, Aarflot et al. 2020). In the GSL, vertical distribution of Calanus species overwintering stages is constrained by bottom depths above 200 m, resulting in high near bottom densities potentially greater than in deeper areas (Plourde et al. 2019). Moreover, dense daytime aggregations of krill in the nGSL are generally located over the slopes of deep channels at depths and temperatures typical of the CIL and capelin preferred thermal habitat (Plourde et al. 2014, Maps et al. 2014, McQuinn et al. 2015). These optimal foraging conditions could constrain capelin distribution horizontally in the nGSL and make it more "available" to trawling in slope area than in the deep channels.

There is some uncertainty as to whether capelin density is roughly homogenous horizontally in the preferred thermal habitat, or whether densities in that habitat are lower when it occurs over deeper depths. Resolving this would inform assumptions made when devising an abundance index such as the negative binomial AR(1) model that assumed densities for deeper water sites. An examination of trawl mensuration data from the surveys to determine how trawl opening is reduced as the trawl moves through the water column during retrieval could reduce this uncertainty. The in-depth analysis of the acoustic data collected during the bottom trawl surveys could also be useful to validate the hypothesis of homogenous horizontal density in the CIL and possibly lead to the development of an acoustic abundance index.

Capelin caught in the sGSL September bottom trawl survey are on average smaller than the ones caught in the commercial fishery and, to a lesser extent, smaller than capelin observed in the nGSL bottom trawl survey. Comparison of the length frequencies of capelin in the surveys with historical length-at-age data from the commercial fishery in the GSL suggests that the capelin captured in the sGSL survey would be predominantly composed of 1 and 2 year old individuals while those caught in the nGSL survey would be mostly 2 years old with a low proportion of 1 and 3 year olds. These observations reinforce the hypothesis already proposed that the sGSL would act as a nursery ground for the GSL (O'Boyle and Lett, 1977, Hodder and Winters 1972).

It is unlikely that the observed differences in capelin length frequency distributions between the sGSL and nGSL bottom trawl surveys are caused by differences in gear selectivity. The western IIA trawl used in the sGSL is a groundfish trawl with fine liner in the codend (19 mm) whereas in the nGSL the bottom trawl survey used a URI trawl (1990–2005, 19 mm codend liner) and then a Campelen shrimp trawl (2004-present, 12.7 mm codend liner). Any differences in selectivity should result in lower retention of small fish in the western IIA (sGSL) compared to the Campelen (nGSL) trawl. Observed differences in capelin length frequencies between surveys are in the opposite direction, suggesting that these are not caused by differences in the gear used. More importantly, a comparison of length frequencies between surveys in the area where they spatially overlap indicated very little difference between the surveys. The differences in size structure observed in the nGSL and sGSL surveys therefore suggest regional differences in the demographic structure.

Based on known life history characteristics (high natural mortality) and inferred low fishing mortality in the GSL, capelin caught in the commercial fishery are likely not available to the bottom trawl surveys because of post-spawning senescence. Senescence is an age-related decline in adult fitness related to an increase in mortality rate and decline in fecundity. Capelin are known to have high post-spawning mortality where nearly all males die after the first reproduction, while varying proportions of female die in the post-spawning period (20 to 60%, Burton and Flynn 1998, Flynn et al. 2001). A more recent study showed that a population of ocean spawning Norwegian capelin was semelparous (death of both genders after reproduction), while both sexes of a beach spawning population were iteroparous (Christiansen et al. 2008). In the same study, post spawning mortality was also apparent in the iteroparous population since male and female mortality rates were respectively about 80 and 25% within 3 months of reproduction.

Our analyses represent the first empirical approach designed to test the hypothesis of predator-mediated changes in catches of a pelagic fish in bottom trawl surveys. The effect of Atlantic cod predation on capelin catches was representative of the whole period (Figure A22, Figure A23), but we cannot definitively reject this hypothesis for the period prior to the 1990s groundfish collapse since more than 90% of the data used in the analyses was collected after 1990. Although our analyses showed that demersal predators significantly reduced capelin catchability in the sGSL bottom trawl survey, this effect only accounted for <1.5% of explained variation in capelin's catches. McQuinn (2009) showed that Atlantic herring vertical distribution in 1989 differed strikingly from that of six surveys conducted in the fall off the western Newfoundland shelf over the 1991–2002 period. He interpreted this change as herring increasingly occupying the supra-benthic habitat vacated by its decreasing groundfish predators and therefore argued that the increase in herring abundance in bottom trawl surveys would be mainly caused by behavioural changes associated to changes in predation pressure. Whether or not this interpretation is transferable to capelin in the GSL is however debatable. Hanson and Chouinard (2002) concluded that the low capelin occurrence in sGSL Atlantic cod stomach content reflected their low availability compared to herring between 1959 and 2002. Moreover, we would expect that some capelin would be caught during the ascent and descent of the bottom trawl should capelin be abundant in the pelagic habitat, resulting in a relatively high occurrence in the survey. Finally, the fact that capelin abundance in the survey remained low until the late 1990s (Figure 14), i.e., several years after the cod stock collapsed, suggests that the increase in capelin abundance indices in the sGSL in the 2000s would not be solely associated with changes in capelin behaviour driven by changes in predation pressure. The effect of predators on capelin catchability in the demersal zone cannot be excluded, but our analyses of sGSL survey data, covering mostly the post-1990 period, suggest that it is not strong nor dominant.

The inclusion of habitat descriptors contributed more to explained deviance than predations indices and time of the day in the sGSL capelin catchability models. However, changes in the characteristics of the CIL such as CIL depth and thickness have not been linked to the catchability of capelin in the surveys and could bias the abundance indices. Additional analyzes would be needed to examine the effects of these changes and reduce the uncertainties associated with possible variations in capelin catchability in the surveys.

The choice of whether to estimate annual survey stratum means for deeper strata directly from catches in those strata or to assume that those means are equal to the means from strata in the preferred habitat does not affect the perception of long-term trends in capelin abundance. However, trends at a finer scale (e.g., semi-decadal) may be affected to some degree by the choice. Overall, capelin abundance in the sGSL, comprising mainly individuals aged 1 and 2 years, increased through the 1990s and again in the late 2000s, to reach a series high. In the past decade, abundance appears to have declined to levels comparable or slightly above those of the first half of the 2000s.

Capelin were captured very infrequently and only in small numbers in the sGSL survey prior to 1990 (Figure 14). This likely reflects very low abundance in this ecosystem during this period because evidence was shown that capelin can be caught while the trawl passes through the water column (Figures 6 and 7). Hence, small catches would have been observed even in the presence of strong capelin avoidance of demersal habitats. The decrease in catchability caused by large predators for this period cannot be excluded, but the evidence presented suggests it would not be enough to match the observed MNPT.

In contrast to the sGSL, abundance of capelin in the nGSL, mostly comprising individuals aged 2 years old, was relatively elevated through the 1990s. The subsequent trends have been very similar to those for the sGSL. As with the sGSL survey, recent abundances have been relatively low and comparable to levels observed in the first half of the 2000s. Survey index values for 2017 are an exception, as both surveys caught capelin at densities more comparable to the late 2000s.

The plausible levels of the inferred fishery exploitation rate (F <0.002) are considered low when compared to those of other cautiously managed small pelagic stocks. Patterson (1992) compiled data for 28 stocks of 11 species of small pelagics and concluded that F smaller or equal to 2/3 M should prevent a decline in biomass. The estimated capelin fishing mortality for the years 2018–2020, although coarse, was at least an order of magnitude lower than assumed natural mortality rates. However, these exploitations rates were computed based on estimates of the order of magnitude of capelin abundance at the GSL scale, while the fishery is concentrated on the west coast of Newfoundland. The potential for local depletion cannot be ruled out as this uncertainty has not been addressed for the moment.

5. CONCLUSION

Deriving abundance indices with bottom trawl surveys for a small pelagic species such as capelin is subject to bias if there are changes in catchability throughout the time series. However, the putative bias caused by a change in capelin occupation of the demersal habitat resulting from changes in predation and environmental characteristics was shown to be of minor importance in the sGSL survey. Also, capelin probability of occurrence and abundances observed in sGSL and nGSL bottom trawl surveys concurred with the predictions of the conceptual model of capelin summer-feeding habitat use. Moreover, variations in capelin abundance indices in the nGSL and sGSL were found to correspond with variations in environmental conditions known to regulate capelin survival and cohort strength on the adjacent eastern Newfoundland shelf (Lewis et al. 2019, Lehoux et al. 2022). Overall, these results provide evidence that capelin abundance indices derived from bottom trawl surveys in the GSL do track some of the variation in capelin population abundance and therefore support the use of data from the GSL bottom trawl surveys to derive biologically sound capelin abundance indices. However, these indices need to be interpreted cautiously because, the confidence intervals remain relatively large and several sources of uncertainty will need to be addressed in the future. In particular, there is uncertainty as to whether the density of capelin is horizontally homogenous in the CIL, or if the densities in this habitat are lower when the CIL is found above deeper depths. Resolving this would inform assumptions made when devising an abundance index. The in-depth analysis of the acoustic data collected during the bottom trawl surveys could be useful to validate the hypothesis of homogenous horizontal density in the CIL, and possibly lead to the development of an acoustic abundance index.

In conclusion, because capelin have a short lifespan and populations consist of only a few age groups, their abundance is subject to large fluctuations. As these variations are believed to be mostly regulated by environmental factors, it is currently difficult to accurately estimate the impact of fishing on GSL capelin. Nonetheless, plausible levels of the inferred exploitation rate from the fishery were at least an order of magnitude lower than natural mortality (M) calculated based on life history traits. It is therefore unlikely that the current fishing mortality is adversely affecting the capelin stock in NAFO Divisions 4RST.

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TABLES

*Table 1: Summary of sGSL capelin GAMM models. Each model has a random intercept by year strata and an offset accounting for swept area and inter vessel calibration. (n = number of tows after removal of year*strata with no capelin, EDF = estimated degrees of freedom, Dev % = percent deviance explained)*

Model	n	n tows removed	Number of year*strata	covariates	edf	ΔAIC	Dev %
sGSL Capelin 0	-	-	-	-	414.7	664.3	49.7
sGSL Capelin 1	-	-	-	Hour	418.0	583.6	51.0
sGSL Capelin 2.1	-	-	-	Hour + Cod25	418.6	505.5	52.2
sGSL Capelin 2.2	3634	2735	508	Hour + Turbot	418.3	575.7	51.2
sGSL Capelin 3.1	-	-	-	Hour + Cod25 + Temp. + depth	426.4	0.0	59.6
sGSL Capelin 3.2	-	-	-	Hour + Turbot + Temp. + depth	428.8	59.3	58.9
sGSL Capelin 4	-	-	-	Hour + Temp. + depth	428.6	58.9	58.9

Table 2: Estimated order of magnitude of capelin biomass in the southern (sGSL) and northern Gulf of St. Lawrence (nGSL) based on mean individual weight (wt), number of trawlable units in the sGSL and nGSL bottom trawl surveys, mean number per tow (MNPT) and catchability coefficients (q) for small pelagics in this type of survey.

Survey index	Mean wt (kg)	Trawlable units in survey	MNPT (2017–2020)	Trawlable biomass (t)	q	~Biomass(t)
sGSL core strata	0.0085	1 806 408	330.4	5 073	0.00450	1 127 359
					0.00087	5 831 168
sGSL CIL strata	0.0085	1 806 408	535.5	8 222	0.00450	1 827 181
					0.00087	9 450 939
nGSL core strata	0.015	7 933 617	167.6	19 945	0.00450	4 432 222
					0.00087	22 925 287
nGSL CIL strata	0.015	7 933 617	402.1	47 851	0.00450	10 633 691
					0.00087	55 001 149

q=0.00450 based on herring in sGSL (Benoît and Swain 2008)
q=0.00087 based on sandlance in the English groundfish survey (Harley et al. 2001)

Table 3: Estimates of capelin natural mortality using different methods based on a maximum age of 7 years old (conservative estimates). M: instantaneous natural mortality rate.

M	Method
0.62	Hoenig (1983)
0.77	Hamel (2015)
0.82	Then et al. (2015)

FIGURES

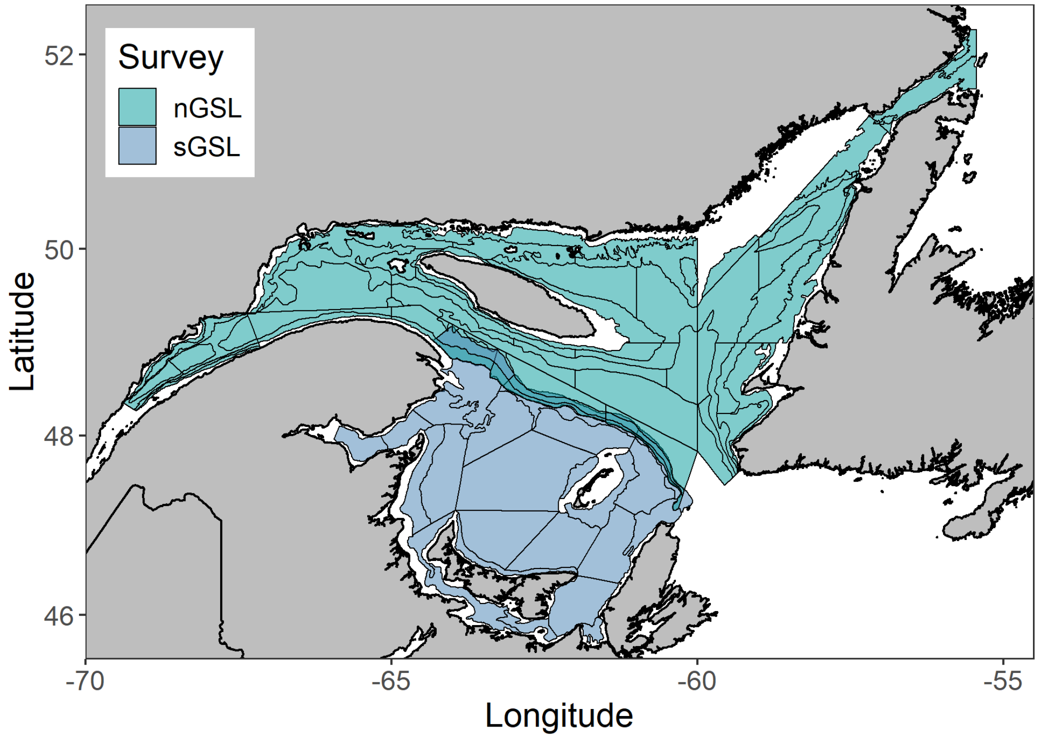

Figure 1: Map of the study area showing the different strata for the sGSL survey (blue) and the nGSL survey (green).

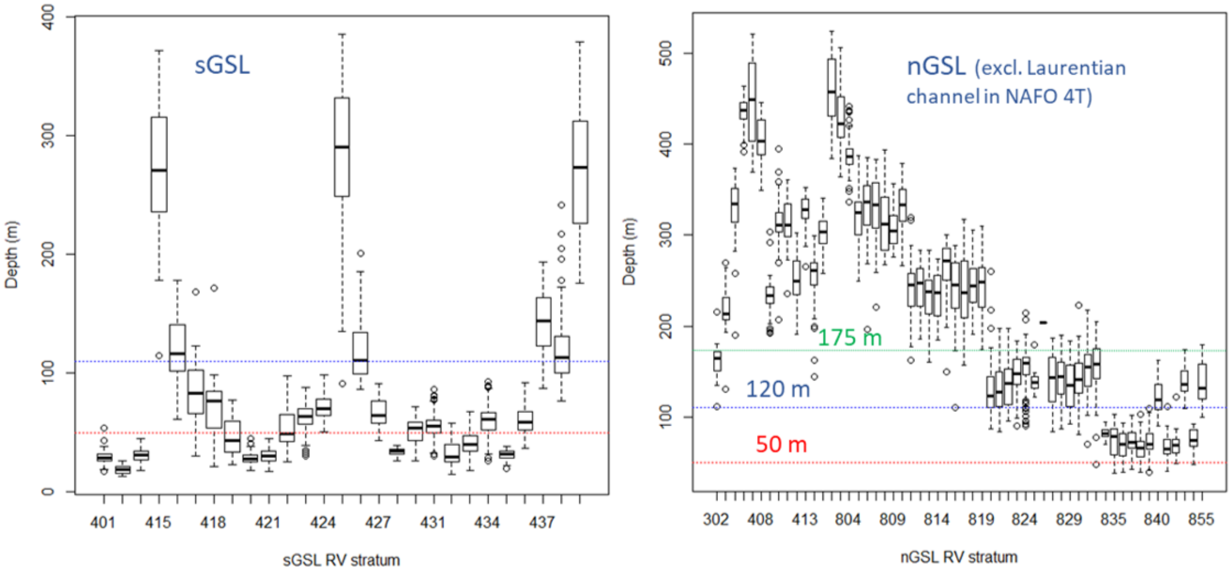

Figure 2: Boxplots of depths sampled in each stratum of the southern Gulf of St. Lawrence (sGSL, left panel) and northern Gulf of St. Lawrence (nGSL, right panel) bottom trawl surveys. The dashed lines indicate the bounds of the assumed preferred habitat for capelin, 50–120 m in the sGSL and 50–175 m in the nGSL.

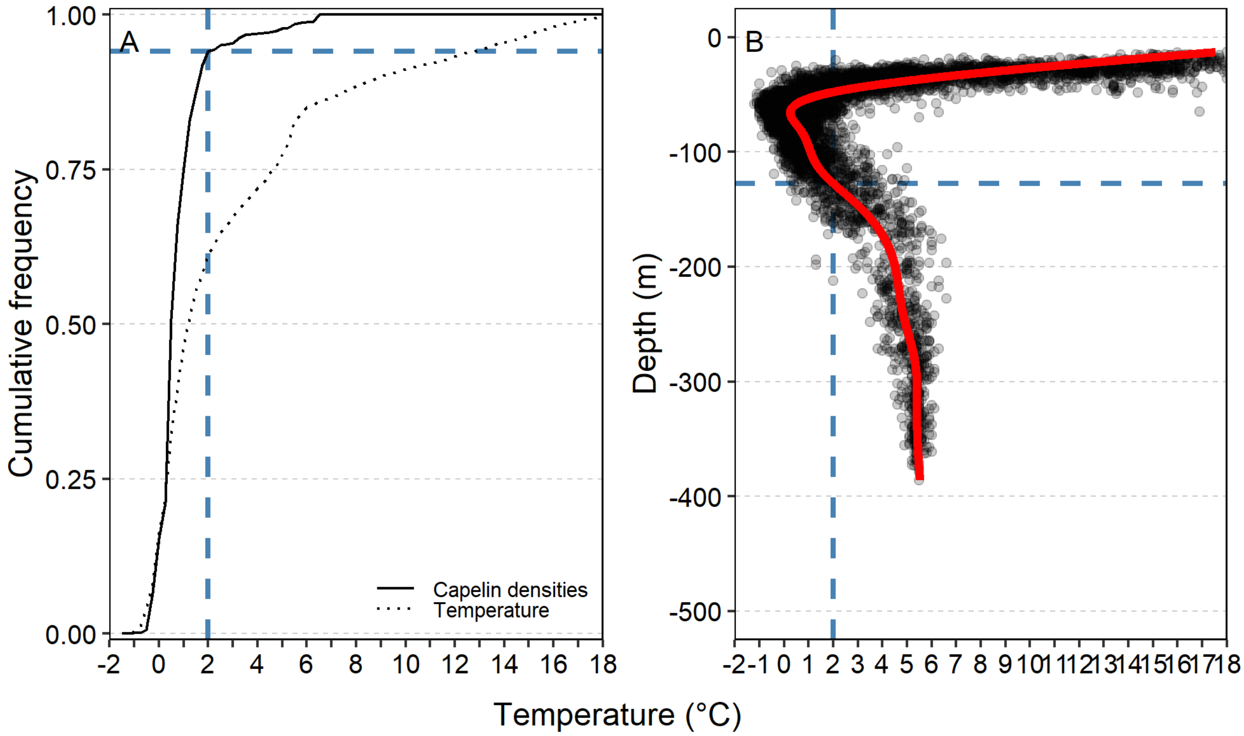

Figure 3: A) Empirical cumulative frequency distribution of observed temperatures and temperatures weighted by capelin densities from the sGSL bottom trawl survey. Dashed blue lines indicate where the cumulative frequency distribution changes sharply (2.2 °C, 94.0%). B) Depths and associated temperature observed in the sGSL bottom trawl survey. The grey dots represent temperature and depth of all tows for the 1971–2016 period. The red line indicates the predicted temperature by a cubic regression spline using depth as covariate. The dashed blue lines indicate 2.0 °C and mean associated depth (128 m).

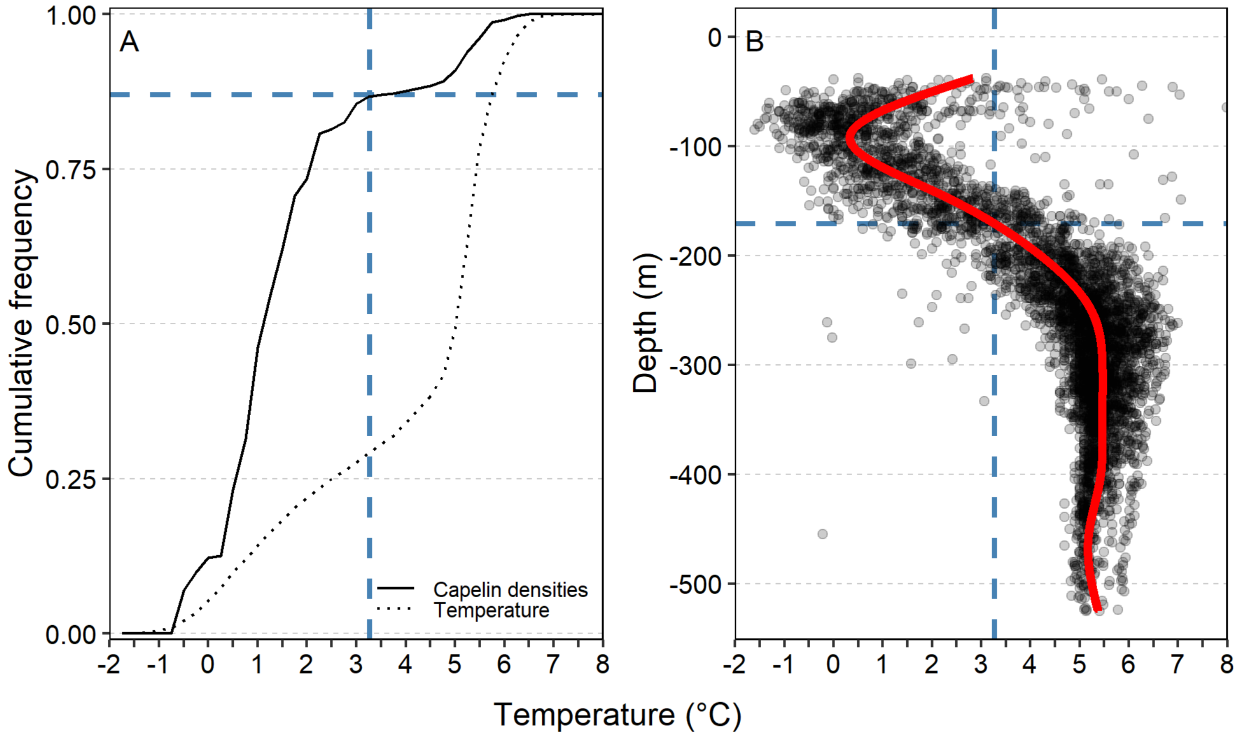

Figure 4: A) Empirical cumulative frequency distribution of observed temperatures and temperatures weighted by capelin densities from the nGSL bottom trawl survey. Dashed blue lines indicate where the cumulative frequency distribution changes sharply (3.3 °C, 87%). B) Depths and associated temperature observed in the nGSL bottom trawl survey. The grey dots represent temperature and depth of all tows for the 1990–2018 period. The red line indicates the predicted temperature by a cubic regression spline using depth as covariate. The dashed blue lines indicate the 3.3 °C and associated depth (171 m) according to the model.

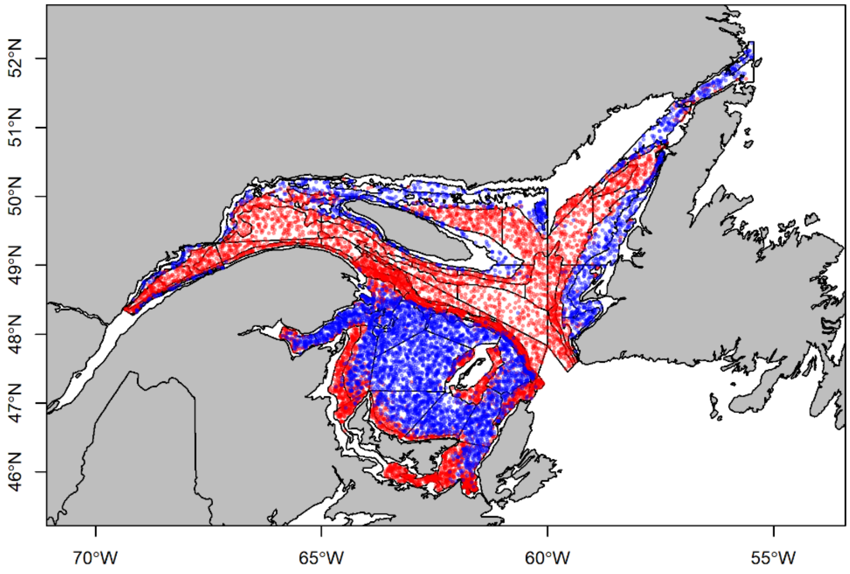

Figure 5: Map of sGSL and nGSL bottom trawl surveys tows performed inside (blue) and outside (red) capelin preferred thermal habitat.

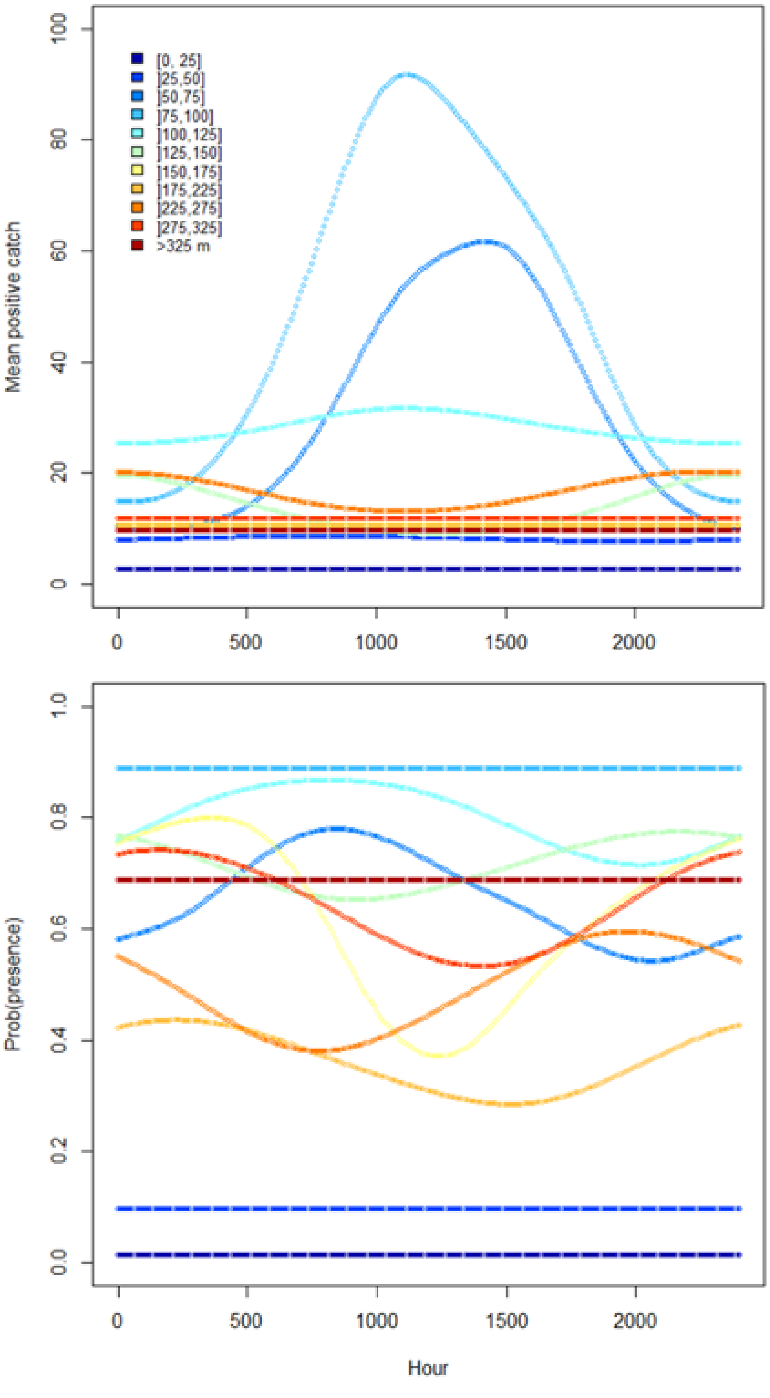

Figure 6: Predicted average capelin positive catches (top) and probability of occurrence (bottom) in the southern Gulf of St. Lawrence bottom trawl survey as a function of the time of day and by depth class.

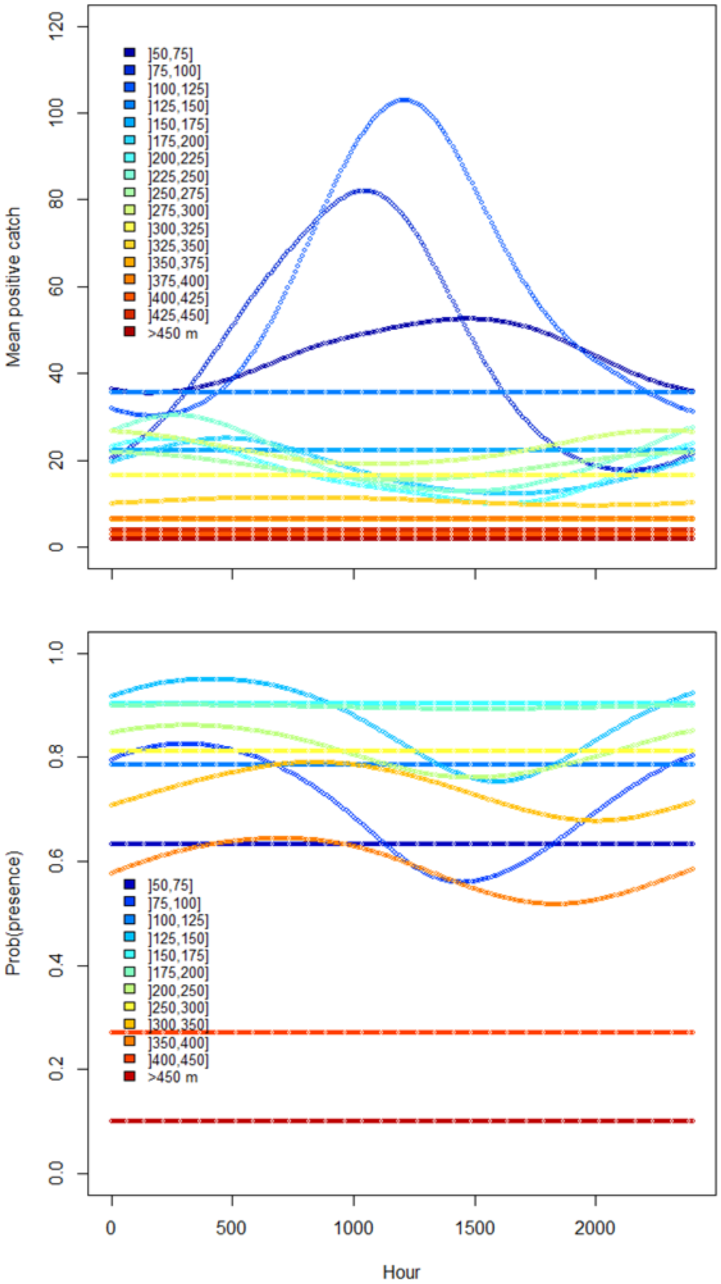

Figure 7: Predicted average capelin positive catches (top) and probability of occurrence (bottom) in the northern Gulf of St. Lawrence bottom trawl survey as a function of the time of day and by depth class. Note that some depth classes were combined for the analysis of the probability of occurrence to achieve convergence in model fitting.

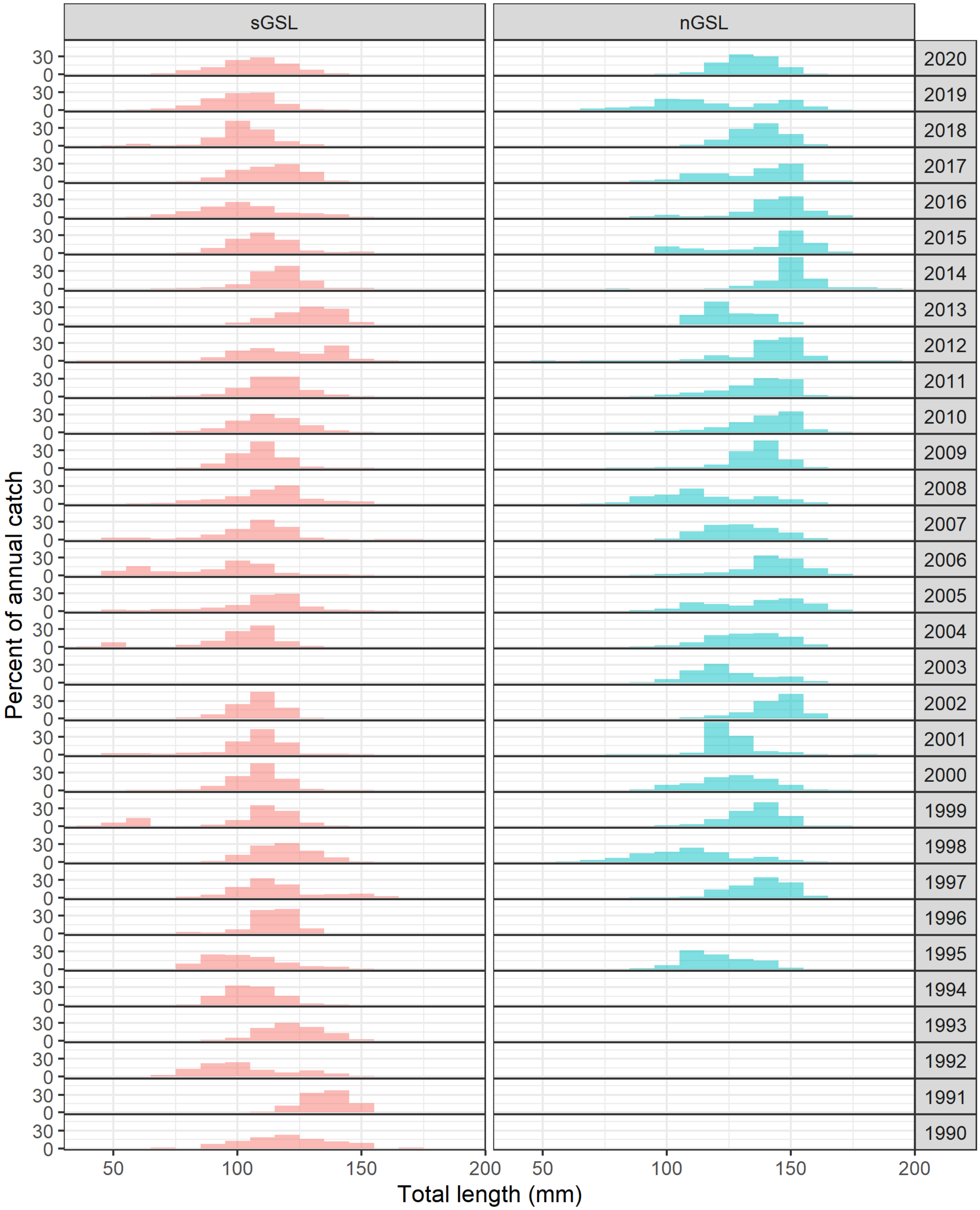

Figure 8: Comparison of annual relative length frequency distributions from the sGSL and nGSL bottom trawl surveys, 1990–2020. Note that length frequencies are not represented for the 1990–1994 nGSL surveys either because not enough (n = 63 in 1990) or no length data was recorded (1991–1994).

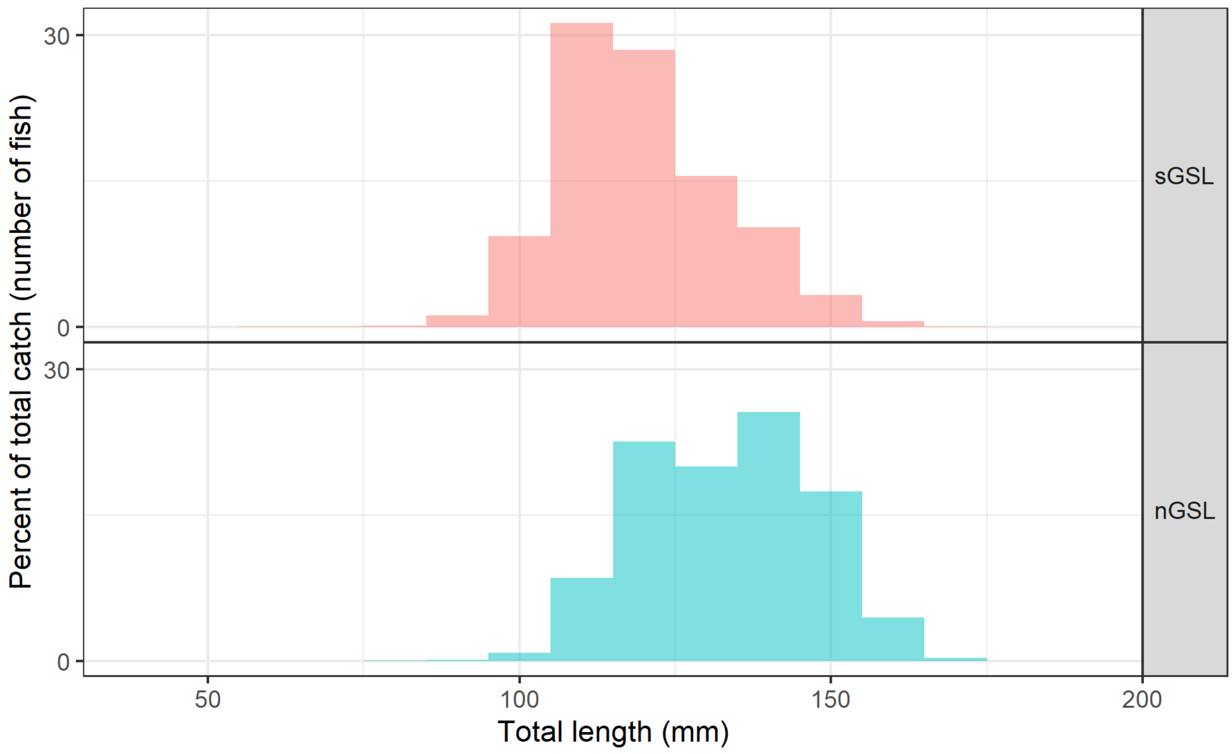

Figure 9: Comparison of capelin relative length frequency distribution from spatially overlapping sGSL and nGSL bottom trawl survey strata, 1995–2020.

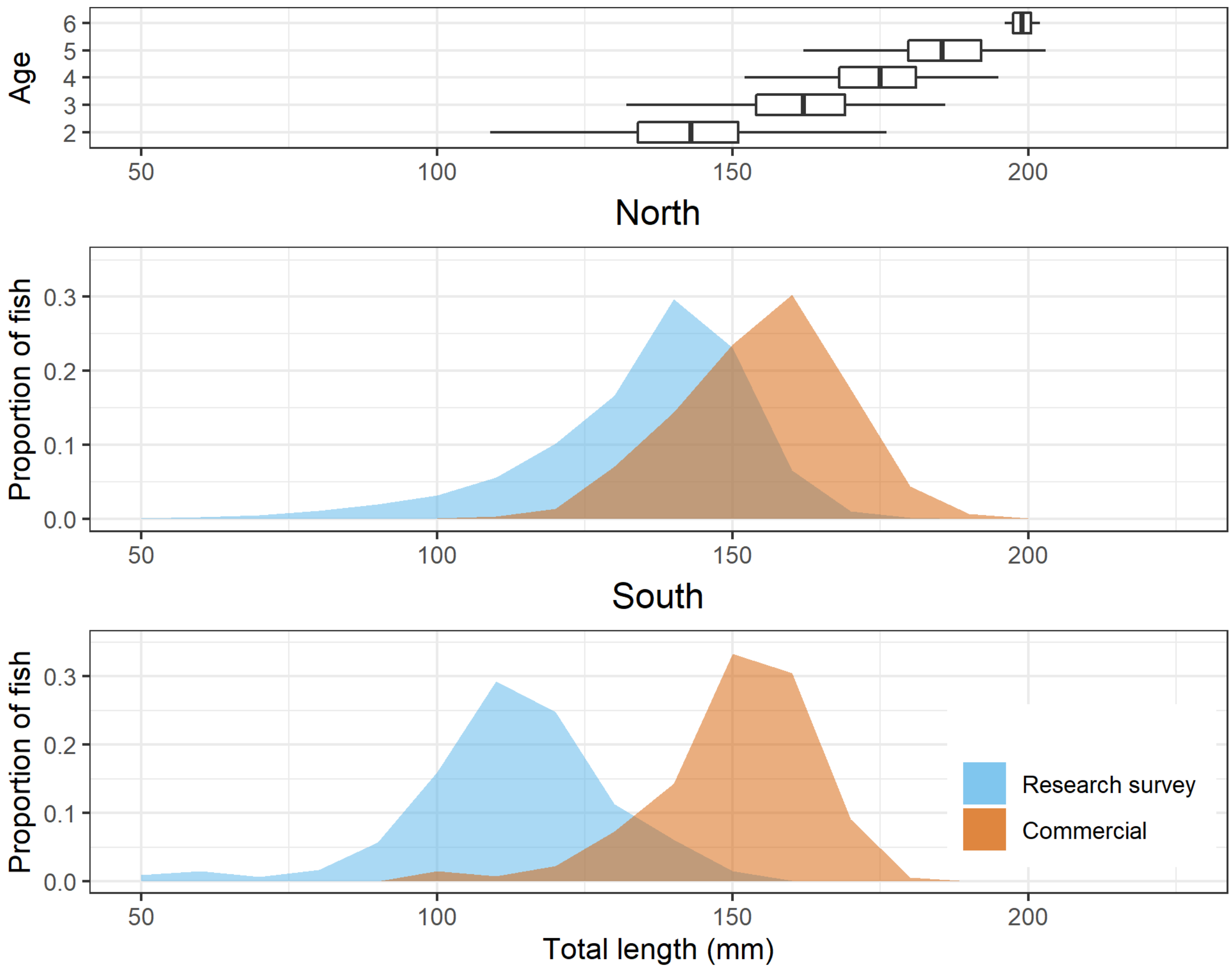

Figure 10: Length at age (top row, 1984–1993 GSL capelin data, Hurtubise 1994) and length distribution for nGSL (middle) and sGSL (bottom) bottom trawl surveys (blue) compared to length distribution in the commercial fishery. For the commercial fishery length distributions, NAFO Divisions 4R and 4S were used when compared with the nGSL survey whereas NAFO 4T commercial fishery data was used when compared with the sGSL survey.

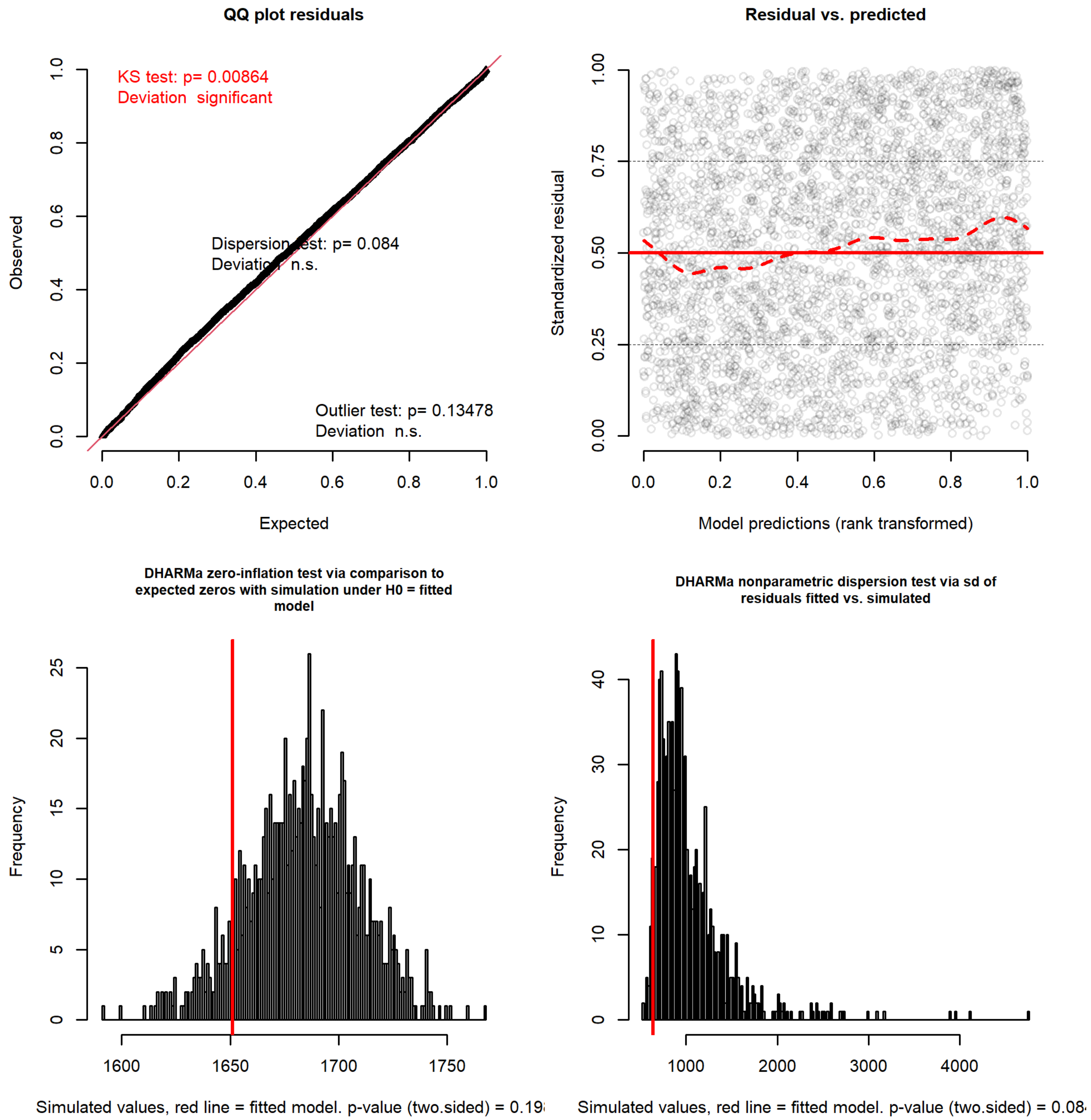

Figure 11: sGSL model 3.1 DHARMa diagnostic plots.

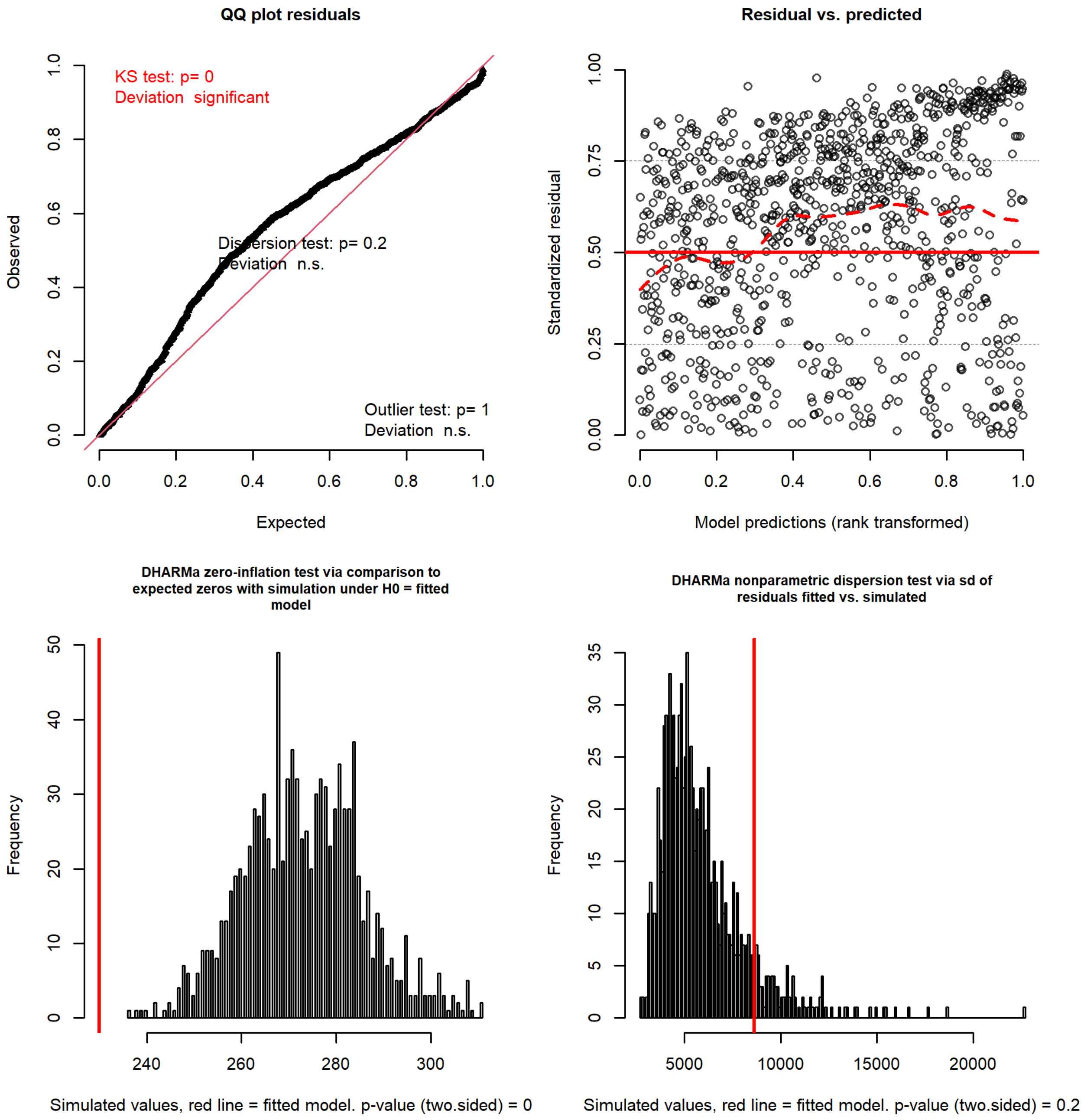

Figure 12: nGSL model 2.1 DHARMa diagnostic plots.

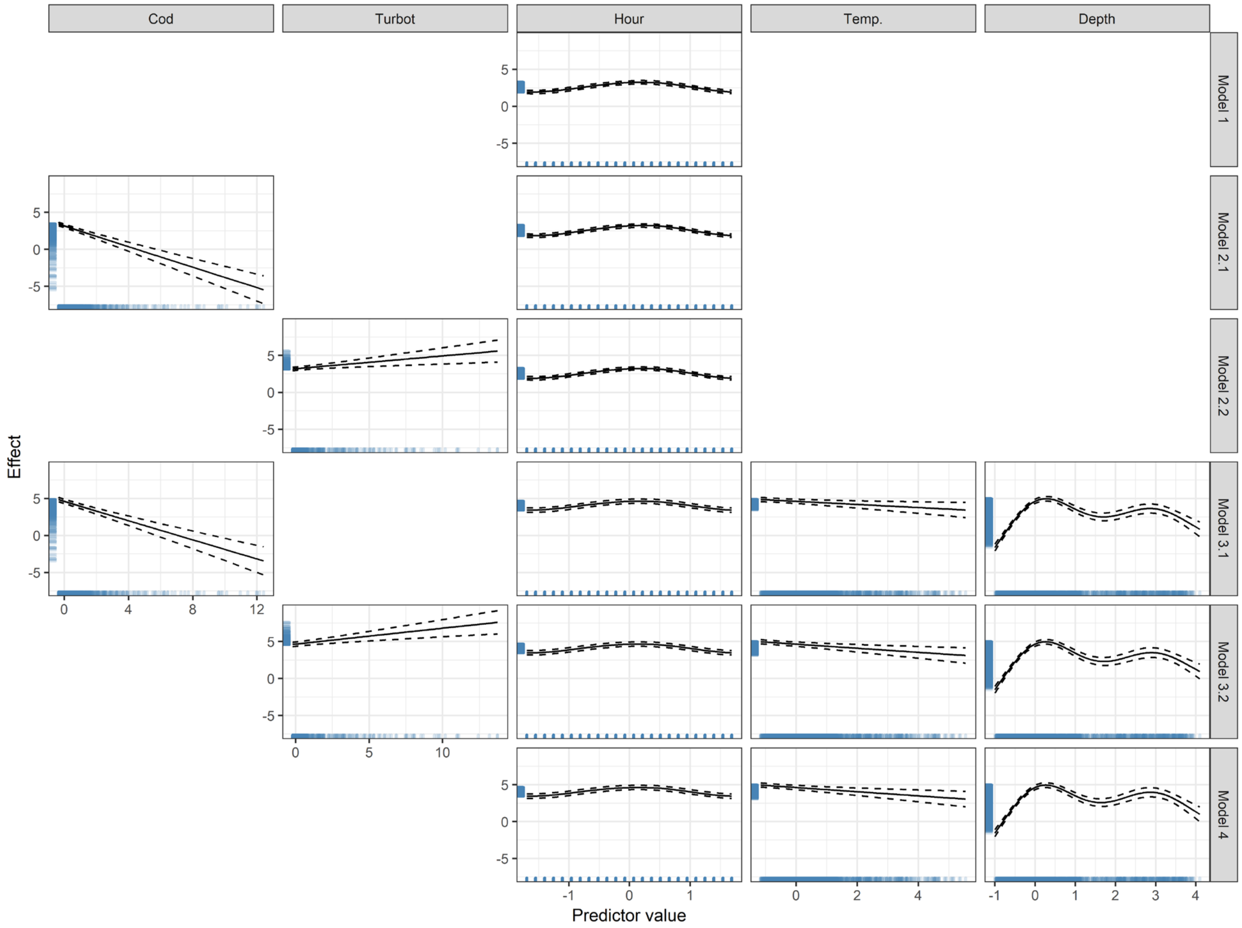

*Figure 13: sGSL capelin model predictor effect plots for each model (rows) and covariate (columns). Effects are on the scale of the linear predictor. Dashed lines represent the 95% confidence intervals (mean predicted value ± 1.96 * standard errors). Distributions of the data for the standardized (mean = 0, variance = 1) predictors are represented as rug plots along the abscissa.*

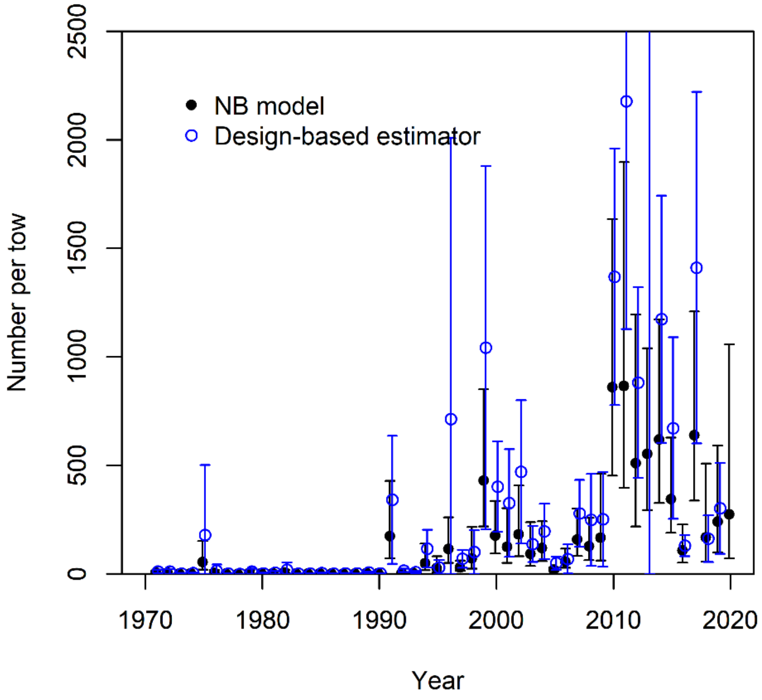

Figure 14: Estimated capelin abundance index for the southern Gulf of St. Lawrence survey using the negative binomial AR(1) model (black) compared to the index based on the traditional design-based estimator (blue). Vertical bars represent 95% confidence intervals.

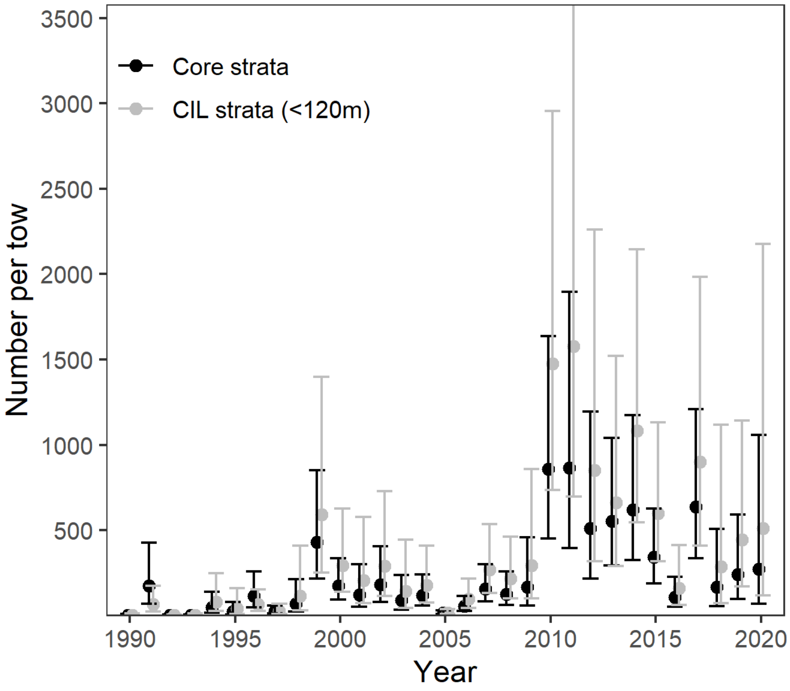

Figure 15: Estimated capelin abundance indices for the southern Gulf of St. Lawrence survey based on core strata and assuming that mean densities in strata covering favoured habitat (CIL strata) estimate mean densities in strata occurring below this habitat. Vertical bars represent 95% confidence intervals. Indices for the southern GSL before 1990 are not shown.

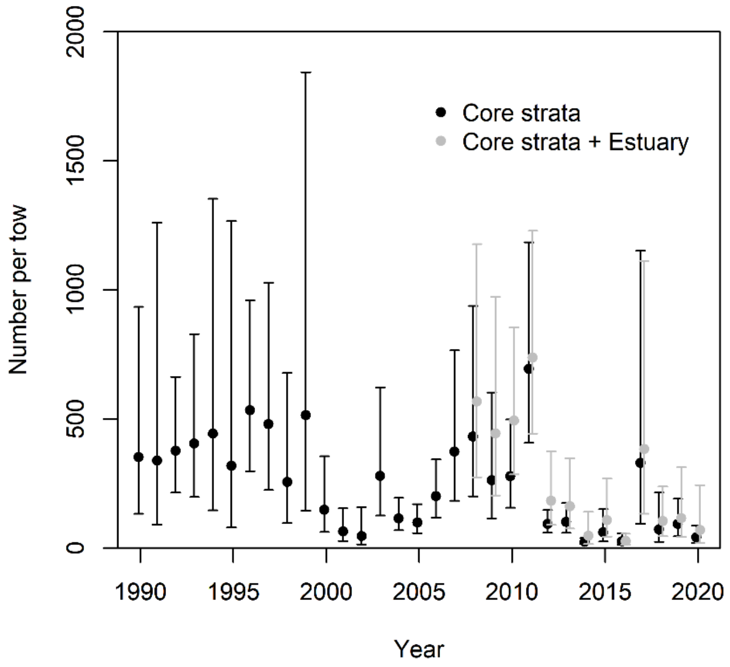

Figure 16: Estimated capelin abundance indices for the northern Gulf of St. Lawrence survey based on all strata (Core strata) that were part of the sampling plan since 1990, and including strata in the Estuary added in 2008.

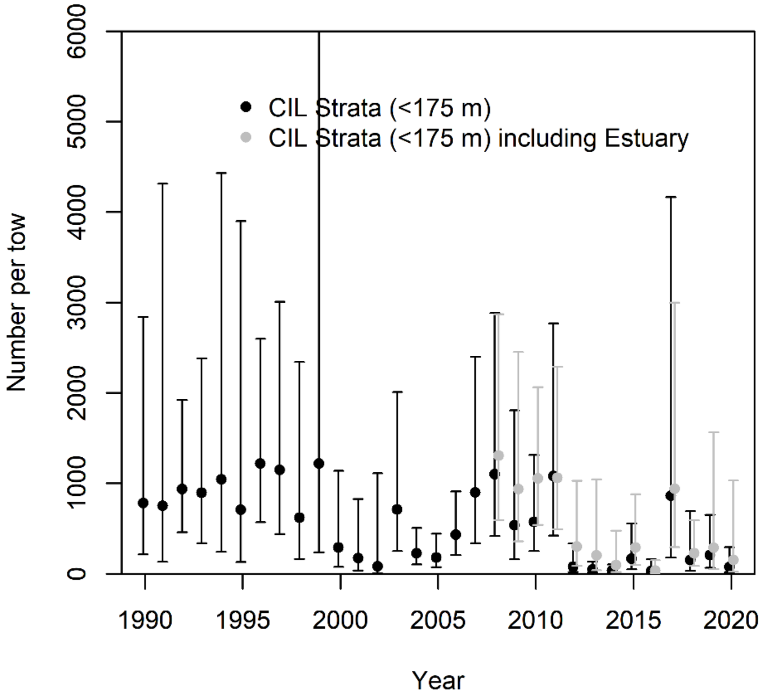

Figure 17: Estimated capelin abundance indices for the northern Gulf of St. Lawrence survey assuming that mean densities in strata covering favoured habitat (CIL strata) estimate mean densities in strata occurring below this habitat. Separate series are shown based on all strata that were part of the sampling plan since 1990, and including strata in the Estuary added in 2008.

APPENDIX 1

Abundance trends for main capelin demersal predators.

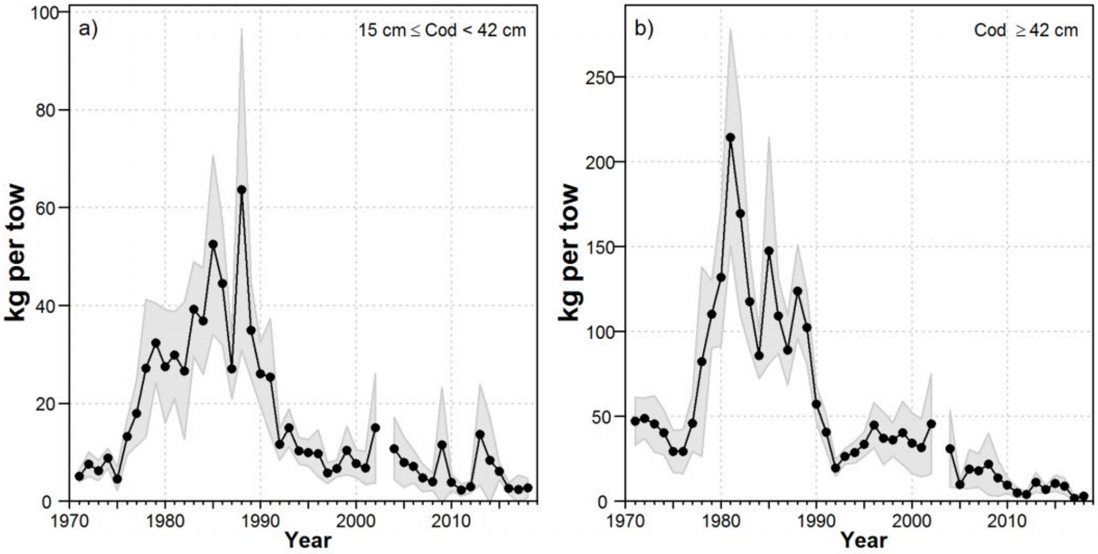

Figure A18: September research survey biomass indices (kg per tow; mean and approximate 95% confidence intervals) for Atlantic Cod 15–42 cm length (left panel, a) and of commercial length (≥ 42 cm; right panel b) from the southern Gulf of St. Lawrence. From DFO 2019a

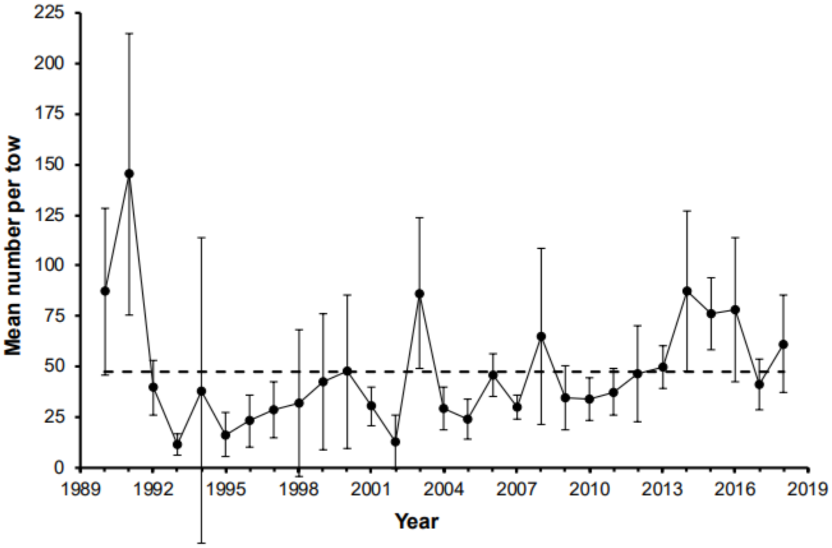

Figure A19: Mean number of cod per tow from DFO survey in 4RS. The error bars indicate the 95% confidence interval. The dotted lines indicate the average for the 1990–2017 period. From DFO (2019b).

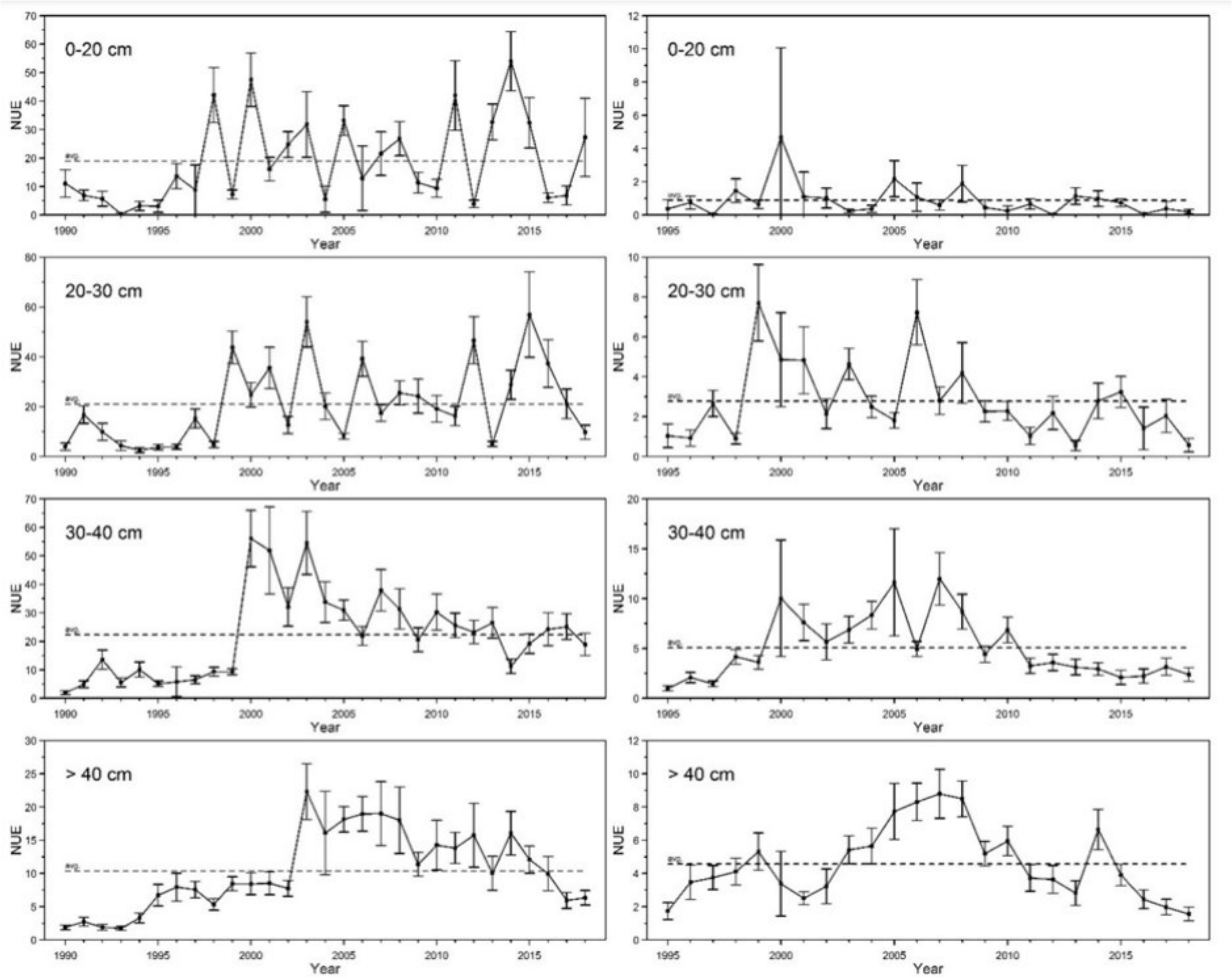

Figure A20: Abundance indices (mean number per tow) for Greenland Halibut for the different size categories observed in the nGSL DFO survey (Left) and in the MSP survey (Right). The dotted lines indicate the average of each series. From DFO (2019c).

APPENDIX 2

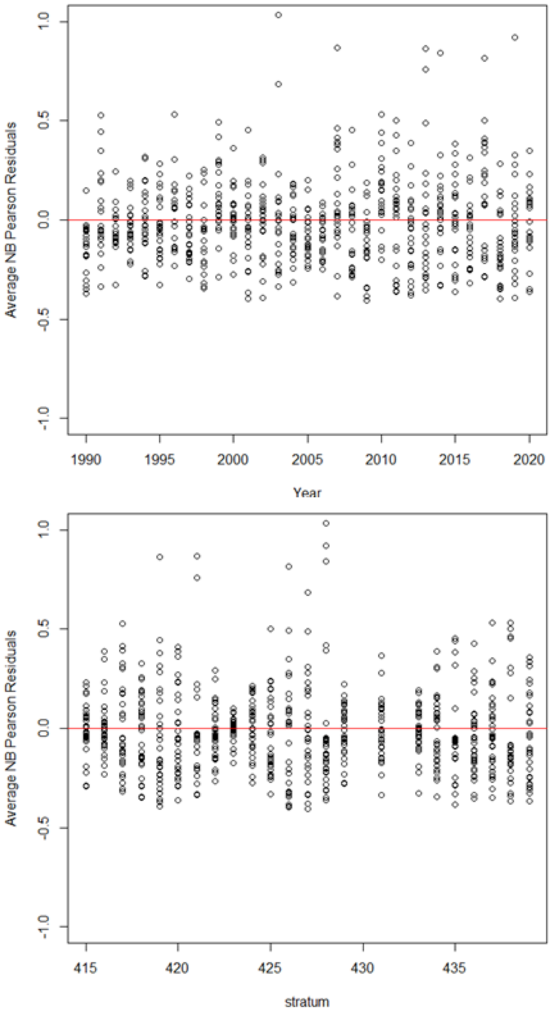

Figure A21: Average Pearson residuals for the southern Gulf of St. Lawrence survey negative binomial AR(1) model, all strata, as a function of year (top) and stratum (bottom).

Table A4: Results output table from the generalized additive modelling of southern Gulf of St. Lawrence survey positive catches as a function of the time of day and depth class (fdclass).

Family: gaussian Link function: identity

Formula: log(catch) ~ fdclass + s(time, bs = “cc”, by = fdclass)

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	0.9645	0.9379	1.028	0.30391	
fdclass25	1.1344	0.9465	1.199	0.23083	
fdclass50	2.2707	0.9412	2.413	0.01592	*
fdclass75	2.7389	0.9433	2.903	0.00373	**
fdclass100	2.3719	0.955	2.484	0.01308	*
fdclass125	1.6007	0.9718	1.647	0.09969	.
fdclass150	1.4	0.9711	1.442	0.14957	
fdclass175	1.3816	1.001	1.38	0.16765	
fdclass225	1.8306	0.9766	1.874	0.06101	.
fdclass275	1.5095	0.9733	1.551	0.12106	
fdclass325	1.3044	0.9785	1.333	0.18265	

Signif. codes: 0 “***” 0.001 “**” 0.01 “*” 0.05 “.” 0.1 “ ” 1

Approximate significance of smooth terms:

	edf	Ref.df	F	p-value	
s(time):fdclass0	1.19E-05	4	0	1	
s(time):fdclass25	3.87E-01	8	0.052	0.296	
s(time):fdclass50	4.03E+00	8	4.74	<2.00E-16	***
s(time):fdclass75	3.38E+00	8	1.951	2.09E-09	***
s(time):fdclass100	6.89E-01	8	0.097	0.233	
s(time):fdclass125	1.27E+00	8	0.215	0.106	
s(time):fdclass150	1.33E-07	8	0	1	
s(time):fdclass175	5.41E-05	8	0	0.546	
s(time):fdclass225	8.63E-01	8	0.127	0.198	
s(time):fdclass275	6.48E-04	8	0	0.352	
s(time):fdclass325	2.10E-04	8	0	0.528	

Table A5: Results output table from the generalized additive modelling of southern Gulf of St. Lawrence survey probability of occurrence as a function of the time of day and depth class (fdclass).

Family: binomial Link function: logit

Formula: pres ~ fdclass + s(time, bs = “cc”, by = fdclass)

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-4.2962	0.7198	-5.969	2.39E-09	***
fdclass25	2.0525	0.7251	2.831	0.00464	**
fdclass50	4.9533	0.7294	6.791	1.11E-11	***
fdclass75	6.3574	0.7486	8.492	<2.00E-16	***
fdclass100	5.7031	0.7767	7.343	2.09E-13	***
fdclass125	5.2277	0.8065	6.482	9.04E-11	***
fdclass150	4.8221	0.8083	5.966	2.43E-09	***
fdclass175	3.7192	0.8509	4.371	1.24E-05	***
fdclass225	4.2633	0.81	5.264	1.41E-07	***
fdclass275	4.8944	0.8153	6.003	1.94E-09	***
fdclass325	5.0814	0.8239	6.168	6.94E-10	***

Signif. codes: 0 “***” 0.001 “**” 0.01 “*” 0.05 “.” 0.1 “ ” 1

Approximate significance of smooth terms:

	edf	Ref.df	Chi.sq	p-value	
s(time):fdclass0	4.57E-05	8	0	0.444	
s(time):fdclass25	3.06E-05	8	0	0.5711	
s(time):fdclass50	3.15E+00	8	23.121	6.19E-06	***
s(time):fdclass75	2.21E-02	8	0.008	0.7216	
s(time):fdclass100	1.43E+00	8	3.144	0.0911	.
s(time):fdclass125	9.20E-01	8	1.121	0.2892	
s(time):fdclass150	2.32E+00	8	5.274	0.0677	.
s(time):fdclass175	7.74E-01	8	1.015	0.2603	
s(time):fdclass225	1.22E+00	8	2.144	0.1553	
s(time):fdclass275	1.06E+00	8	2.264	0.1038	
s(time):fdclass325	8.69E-04	8	0	0.7862	

Table A6: Results output table from the generalized additive modelling of northern Gulf of St. Lawrence survey positive catches as a function of the time of day and depth class.

Family: gaussian Link function: identity

Formula: log(catch) ~ fdclass + s(time, bs = "cc", by = fdclass)

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	3.7761	0.19	19.876	<2.00E-16	***
fdclass75	-0.1089	0.2263	-0.481	0.630355	
fdclass100	0.194	0.2414	0.804	0.421667	
fdclass125	-0.199	0.2385	-0.834	0.404212	
fdclass150	-0.67	0.2298	-2.915	0.003581	**
fdclass175	-0.908	0.2409	-3.769	0.000167	***
fdclass200	-0.9875	0.2306	-4.283	1.89E-05	***
fdclass225	-0.7989	0.2262	-3.531	0.000419	***
fdclass250	-0.8578	0.2211	-3.879	0.000107	***
fdclass275	-0.6603	0.2231	-2.96	0.0031	**
fdclass300	-0.9656	0.2279	-4.237	2.32E-05	***
fdclass325	-1.4208	0.2439	-5.826	6.23E-09	***
fdclass350	-1.9176	0.2713	-7.068	1.92E-12	***
fdclass375	-1.9087	0.3008	-6.345	2.53E-10	***
fdclass400	-2.7145	0.3588	-7.566	4.98E-14	***
fdclass425	-2.4244	0.3992	-6.073	1.40E-09	***
fdclass450	-3.0772	0.3959	-7.773	1.02E-14	***

Signif. codes: 0 "***" 0.001 "**" 0.01 "*" 0.05 "." 0.1 " " 1

Approximate significance of smooth terms:

	edf	Ref.df	F	p-value	
s(time):fdclass50	1.10E+00	8	0.179	0.158251	
s(time):fdclass75	2.43E+00	8	0.961	0.000357	***
s(time):fdclass100	2.41E+00	8	0.839	0.001118	**
s(time):fdclass125	3.05E-07	8	0	1	
s(time):fdclass150	4.13E-07	8	0	1	
s(time):fdclass175	1.65E+00	8	0.385	0.036659	*
s(time):fdclass200	2.43E+00	8	0.766	0.002264	**
s(time):fdclass225	2.25E+00	8	0.829	0.001013	**
s(time):fdclass250	1.36E+00	8	0.264	0.087432	.
s(time):fdclass275	1.32E+00	8	0.257	0.089813	.
s(time):fdclass300	5.12E-07	8	0	1	
s(time):fdclass325	6.42E-01	8	0.093	0.245219	
s(time):fdclass350	9.76E-06	8	0	0.576478	
s(time):fdclass375	7.26E-06	8	0	0.564095	
s(time):fdclass400	5.40E-07	8	0	0.82631	
s(time):fdclass425	3.65E-07	8	0	0.817549	
s(time):fdclass450	7.27E-06	8	0	0.748861	

Table A7: Results output table from the generalized additive modelling of northern Gulf of St. Lawrence survey probability of occurrence as a function of the time of day and depth class.

Family: binomial Link function: logit

Formula: pres ~ fdclass + s(time, bs = “cc”, by = fdclass)

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	0.5444	0.3314	1.643	0.100481	
fdclass75	0.3811	0.3744	1.018	0.308726	
fdclass100	0.7594	0.4369	1.738	0.082166	.
fdclass125	1.4629	0.4445	3.291	0.000997	***
fdclass150	1.6804	0.4447	3.779	0.000158	***
fdclass175	1.6131	0.4801	3.359	0.000781	***
fdclass200	0.9429	0.4092	2.304	0.021208	*
fdclass250	0.9193	0.395	2.328	0.019936	*
fdclass300	0.4916	0.4124	1.192	0.233145	
fdclass350	-0.1977	0.4497	-0.44	0.660234	
fdclass400	-1.5364	0.511	-3.006	0.002643	**
fdclass450	-2.7436	0.6542	-4.194	2.74E-05	***

Signif. codes: 0 “***” 0.001 “**” 0.01 “*” 0.05 “.” 0.1 “ ” 1

Approximate significance of smooth terms:

	edf	Ref.df	Chi.sq	p-value	
s(time):fdclass50	3.32E-03	8	0.001	0.8197	
s(time):fdclass75	1.81E+00	8	5.057	0.0398	*
s(time):fdclass100	1.99E-05	8	0	0.8414	
s(time):fdclass125	1.92E+00	8	7.036	0.0128	*
s(time):fdclass150	7.13E-03	8	0.002	0.8231	
s(time):fdclass175	1.32E-01	8	0.125	0.3835	
s(time):fdclass200	1.45E+00	8	3.244	0.0865	.
s(time):fdclass250	5.17E-03	8	0.004	0.4781	
s(time):fdclass300	1.31E+00	8	2.359	0.1468	
s(time):fdclass350	9.60E-01	8	1.584	0.178	
s(time):fdclass400	6.07E-03	8	0.001	0.9476	
s(time):fdclass450	3.54E-04	8	0	0.8091	

APPENDIX 3

Comparison of original and subsetted datasets for capelin catchability analyses.

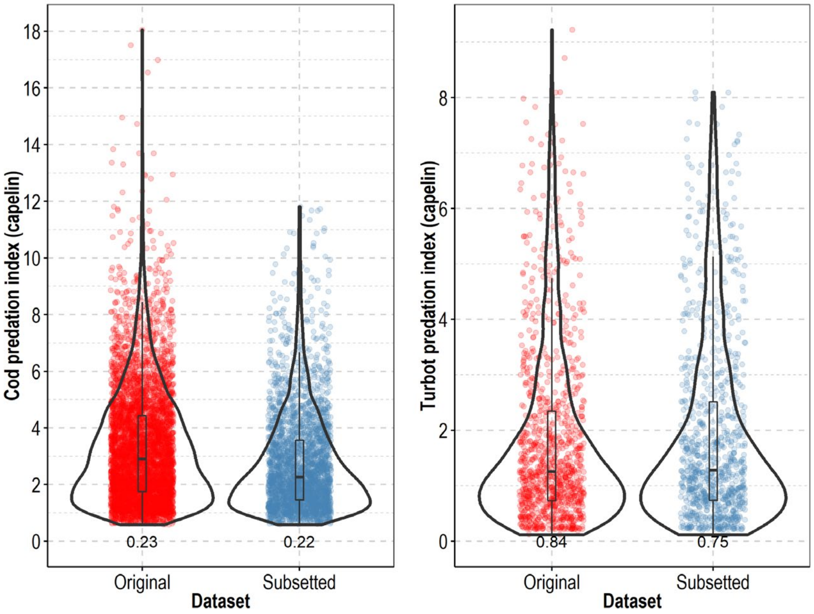

Figure A22: Box and violin plots of sGSL capelin predation indices comparing original and subsetted datasets to meet model assumptions. Predation indices of value zero were removed to have a better idea of the distributions. The proportion of zeros is indicated below each predation index.

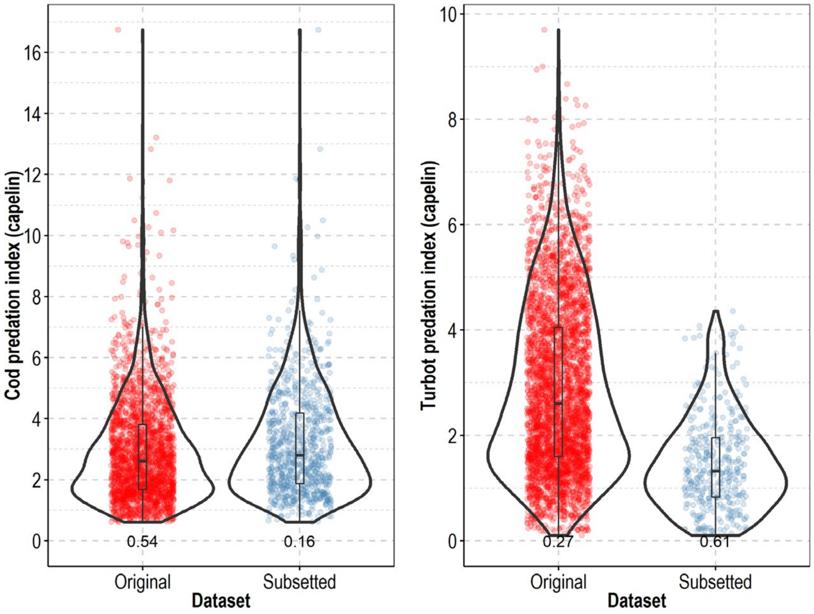

Figure A23: Box and violin plots of nGSL capelin predation indices comparing original and subsetted datasets to meet model assumptions. Predation indices of value zero were removed to have a better idea of the distributions. The proportion of zeros is indicated below each predation index.