



# Spatiotemporal modelling of northern shrimp *Pandalus borealis* distribution patterns throughout Canada's subarctic and arctic regions

Krista D. Baker<sup>1,\*</sup>, Darrell R. J. Mallowney<sup>1</sup>, Samantha Fulton<sup>2</sup>

<sup>1</sup>Northwest Atlantic Fisheries Centre, Fisheries and Oceans Canada, St. John's, Newfoundland and Labrador A1C 5X1, Canada

<sup>2</sup>Freshwater Institute, Fisheries and Oceans Canada, Winnipeg, Manitoba R3T 2N6, Canada

**ABSTRACT:** Northern shrimp *Pandalus borealis* occur throughout Canada's Atlantic Ocean, where they are thought to form a single population spanning from Baffin Bay to the tail of the Grand Bank. Here, they play an important role in the ecosystem as prey for many taxa and have been targeted by a lucrative large-scale fishery since the 1970s. Yet, we still understand little about which (and how) ecosystem and environmental factors influence their distribution and abundance. We used survey data collected over 29 yr throughout 23 degrees of latitude to develop a spatiotemporal model predicting northern shrimp density. We confirmed that both top-down drivers (e.g. predation pressure), as well as bottom-up drivers (e.g. bottom temperature) play important roles in determining both the presence and abundance of northern shrimp. The model was used to predict the density of northern shrimp throughout the entire study area from 2005 to 2022. Our results highlight the importance of understanding ecosystem and environmental dynamics in relation to northern shrimp population patterns and trends within resource assessments.

**KEY WORDS:** Shrimp · *Pandalus borealis* · sdmTMB · Spatial distribution model · Northwest Atlantic

## 1. INTRODUCTION

Northern shrimp *Pandalus borealis* are found and fished throughout the North Atlantic Ocean. Off Canada's northeast coast, northern shrimp are thought to form one large, interconnected population from Baffin Bay to the tail of the Grand Bank off Newfoundland and Labrador (Jorde et al. 2015, Le Corre et al. 2019, 2020, Bourret et al. 2024). Here, the annual landed value of the northern shrimp fishery exceeds CAN \$200 million (DFO unpubl. data). Northern shrimp are fished using large factory freezer trawlers (>30.5 m lengths, known as the 'offshore' fleet), as well as smaller 'inshore' vessels that land fresh catch (DFO 2023). The inshore fleet is comprised of approximately 260 licence holders that generally fish from June to September, and the offshore fleet is made up of 17 licences that fish year-round following

patterns of ice-free conditions (DFO 2023). Fishing efforts focus on depths between 200 and 500 m. During the past 5 yr, exploitation rate indices have ranged from below 5% to above 30% with temporal and spatial variation (DFO unpubl. data). Although there are no size restrictions related to shrimp that can be caught in the fishery, the trawl netting has a minimum mesh size of 40 mm (DFO 2023), and generally the smallest shrimp caught by the fishery are between 15 and 17 mm carapace lengths (DFO 2023, Fulton et al. 2024). Nordmore grates (22 mm or 28 mm) are used to reduce the bycatch of marine mammals, turtles, and groundfish and are mandatory throughout the fishery (DFO 2023).

Patterns in *Pandalus* spp. distribution, abundance, and size have been linked to a variety of features including depth (Squires 1996), temperature (Wieland 2005 — West Greenland), predator abundance

\*Corresponding author: krista.baker@dfo-mpo.gc.ca

(Jónsdóttir et al. 2012 — Iceland, Richards & Hunter 2021 — Gulf of Maine), time of day (Hudon et al. 1992), and fishing pressure (Beita Jiménez 2021) throughout their range. For example, in the Gulf of Maine, while fishing likely contributed to the decline of northern shrimp in the early 2010s, predation by longfin squid *Doryteuthis pealeii* was identified as the most significant driver in the collapse of northern shrimp (Richards & Hunter 2021). Off West Greenland, the negative effect of Greenland halibut *Reinhardtius hippoglossoides* predation tempered northern shrimp population growth predicted by increasing temperatures and reduced Atlantic cod *Gadus morhua* predation in the early 2000s (Wieland et al. 2007). However, in more recent years the overall impact of predation is considered reduced as northern shrimp numbers increase off West Greenland (Kingsley 2014). In the Barents Sea, the abundance of 1 yr old northern shrimp was inversely correlated with Atlantic cod abundance, whereas no correlation was found with shrimp that were 2+ yr old (Aschan & Ingvaldsen 2009). Aschan & Ingvaldsen (2009) attributed this finding to the lack of overlap between Atlantic cod and 2+ yr old shrimp when temperatures were cold, illustrating the complexity of understanding spatial- and temporal-varying patterns and drivers.

Off Canada's northeast coast, despite a long-standing and lucrative fishery, we still understand little about which (and how) environmental factors are influencing northern shrimp distribution and have no accepted, population-wide distribution model to examine trends and patterns over space and time. Species distribution models have wide applicability and can help biologists and managers understand local and regional patterns through time (e.g. Zimmermann et al. 2023), predict future changes in abundance and distribution (e.g. Panzeri et al. 2024), direct conservation efforts (e.g. Grüss et al. 2024), and provide a better understanding of factors influencing the observed patterns (e.g. Evans et al. 2021). For example, spatiotemporal models were used to compare northern shrimp densities in fjords with different management histories off Norway (Zimmermann et al. 2023). Fine-scale spatial variability in shrimp density were found, but no obvious effects related to the contrasting management were observed. To prepare for future climatic changes and manage northern shrimp effectively off Canada, adequate fundamental knowledge and understanding of northern shrimp distributional patterns, as well as their covariates are crucial.

In this study, we used spatiotemporal modelling to explore the influence of environmental features on

northern shrimp distributional patterns using a survey dataset spanning 29 yr and covering more than 23 degrees of latitude. We examined trends in density related to environmental conditions and tested for evidence of local depletion caused by predation. We used the best model to create annual predictions throughout the stock range and examined changes in the overall abundance patterns through time. The results can be used to help inform assessment biologists and resource managers of particularly important environmental and ecosystem covariates to assess when evaluating the current stock status and predicting future stock changes.

## 2. MATERIALS AND METHODS

### 2.1. Data collection

Data for modelling were derived from 2 trawl surveys: (1) the Northern Shrimp Research Foundation (NSRF) survey and (2) Fisheries and Oceans Canada (DFO) multispecies survey. The NSRF survey occurs in the summer, usually between late June and August in spatial assessment units termed Eastern Assessment Zone (EAZ), Western Assessment Zone (WAZ), and Shrimp Fishing Area (SFA) 4 (Fig. 1). The survey is a collaborative survey between NSRF and DFO and collects data annually, since 2005 in SFA 4, 2007 in EAZ, and 2014 in WAZ. The DFO multispecies survey takes place in SFAs 5, 6, and 7 in autumn (usually spanning September to December), and annual data were available from 1995 to 2023.

Both surveys use consistent surveying and sampling designs. The surveys follow a random-stratified sampling design, with the number of stations allocated proportional to the area of each stratum. They use a Campelen 1800 shrimp trawl, with an average wingspread of 16.8 m, a vertical opening of 4 m and codend liner of 12.5-mm mesh (for additional details of survey and gear, see Walsh & McCallum 1997 and Siferd 2015). A trawl-mounted CTD (conductivity, temperature, and depth device) records bottom temperature and depth during each tow (Siferd 2015).

For each tow, shrimp are sorted to species then characterized based on maturity and sex (Siferd 2015, Baker et al. 2021, 2024). When shrimp are abundant (i.e. shrimp catches more than approximately 3 kg tow<sup>-1</sup>), subsamples are taken. The carapace length of each shrimp is measured with digital calipers to the nearest 0.01 mm (Siferd 2015). The weights of shrimp defined as 'fishable' in their assessments (>17 mm

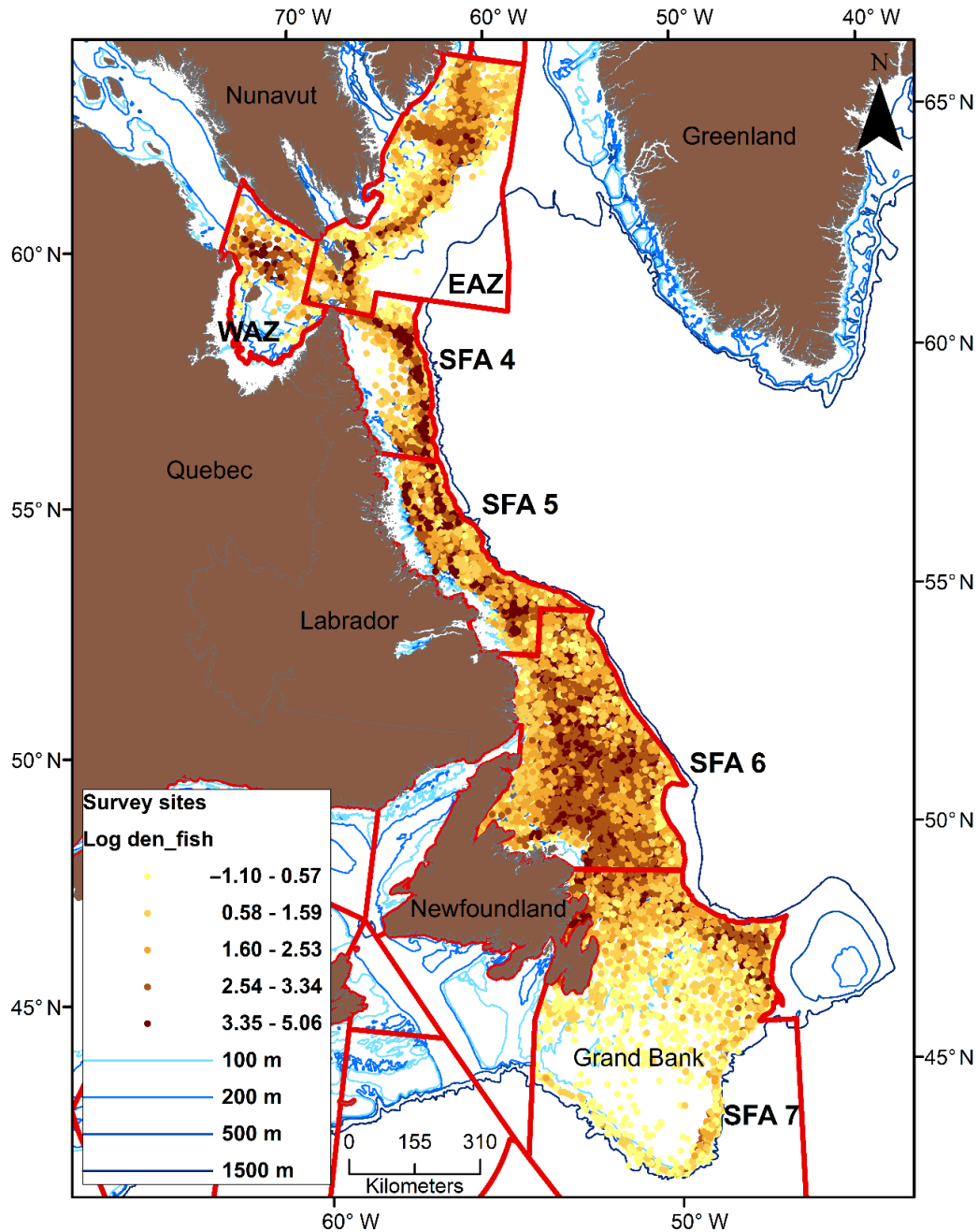


Fig. 1. Locations of trawl sets and observed logged densities of fishable northern shrimp, ('log den\_fish') from the Northern Shrimp Research Foundation surveys (2005 to 2023) and Fisheries and Oceans Canada multispecies surveys (1995 to 2023). Red lines depict assessment areas or shrimp fishing areas (SFAs)

carapace length) (DFO 2023, Fulton et al. 2024) were standardized to densities of  $\text{kg km}^{-2}$  at each tow location.

For each tow, groundfish are also identified to species, then weighed and counted. The weight of Greenland halibut, Atlantic cod, and redfish *Sebastes* spp. in each tow were standardized to densities of  $\text{kg km}^{-2}$ . These taxa represent abundant predators of northern shrimp that have been documented with *Pandalus*

spp. in their diets throughout the study area (Parsons 2005, Fulton et al. 2024).

## 2.2. Data summary

The data consisted of 20 261 sets from annual trawl surveys spanning 1995 to 2023, 23.6 degrees of latitude, and 23.2 degrees of longitude. Standardized

fishable northern shrimp densities ranged widely from 0 to 150 402 kg km<sup>-2</sup> (Table 1), and 12 795 trawl sets contained fishable northern shrimp. The survey sets were in depths of 32 to 1504 m, bottom temperatures of -1.9 to 10.7°C.

### 2.3. Spatiotemporal modelling

We created a spatiotemporal model to identify important covariates of northern shrimp density (kg km<sup>-2</sup>), as well as predict northern shrimp density throughout the study area, following procedures similar to those previously published for striped shrimp *P. montagu* in the northern portion of the study area (see Baker et al. 2024). We used the stochastic partial differential equation (SPDE) approach for Gaussian random fields by building a 1001 knot mesh over the study area, with a minimum edge distance of 25 km (Fig. 2) (Lindgren et al. 2011). We fitted spatiotemporal generalized additive mixed-effect models (GAMM) using the package 'sdmTMB' (Anderson et al. preprint doi:10.1101/2022.03.24.485545) in R version 4.3.0 (R Core Team 2023).

Depth, slope, bottom temperature, and a topographic roughness index (TRI) were considered potentially important environmental covariates in model formulations. Depth was the average bottom depth (m), and bottom temperature (°C) the average bottom temperature recorded by the CTD during the trawl set. Slope was the average slope gradient (°) of the seafloor at the location of the trawl set, calculated from GEBCO raster data (GEBCO Bathymetric Compilation Group 2023). Slope was considered a potential driver of northern shrimp abundance and distribution because it influences hydrological conditions and nutrient availability. TRI was the topographic roughness index of the seafloor at the location of the trawl set, calculated from GEBCO raster data (GEBCO Bathymetric Compilation Group 2023). Similar to slope, TRI was considered a potentially useful covariate because it measures variations in elevation of the seafloor; patterns in nutrient dynamics, species diversity, and general productivity are often linked to bottom topography (Huang et al. 2018).

Survey and diel period (Period) were considered potential drivers of shrimp catchability during trawling activities, where survey was a factor representing the summer NSRF survey, or the fall DFO multispecies survey and Period was a factor representing Dark or Light. Set-specific values (recorded onboard

Table 1. Summary of set-specific data used in spatiotemporal modelling of fishable northern shrimp, from Fisheries and Oceans Canada multispecies surveys (1995 to 2023) and Northern Shrimp Research Foundation surveys (2005 to 2023)

	Mean (range)	Range with fishable northern shrimp
Density of fishable northern shrimp (kg km <sup>-2</sup> )	1181 (0–150402)	
Depth (m)	286 (32–1504)	34–1358
Bottom temperature (°C)	2.08 (-1.9–10.7)	-1.6–9.2
Slope (°)	0.95 (0–41.52)	0–27.81
Greenland halibut density (kg km <sup>-2</sup> )	517 (0–21504)	0–21504
Redfish density (kg km <sup>-2</sup> )	1923 (0–358210)	0–235690
Atlantic cod density (kg km <sup>-2</sup> )	227 (0–15009)	0–15009

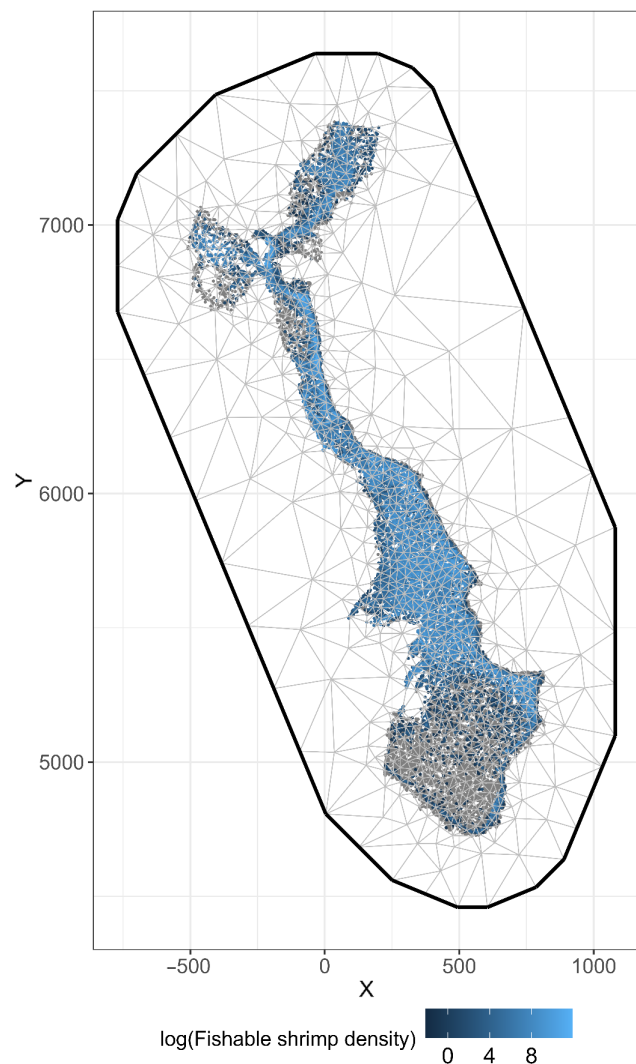


Fig. 2. Stochastic partial differential equation (SPDE) mesh used in fitting the spatiotemporal model. Points represent fishable northern shrimp density (kg km<sup>-2</sup>, logged) available from the Northern Shrimp Research Foundation surveys (2005 to 2023) and Fisheries and Oceans Canada multispecies surveys (1995 to 2023) and used in modelling. X and Y are projected in UTM Zone 22N (km)



at the time of trawling) noted as dull—overcast, bright but hazy, and bright sunlight were classified as 'Light', and dark, moonlight, dusk, and dawn were classified as 'Dark' (Baker et al. 2021). To further explore potential diurnal movement patterns influencing catchability, set-specific time to solar noon and zenith angle were also tested in model formulations in substitution for Period.

The site-specific density of Atlantic cod, Greenland halibut, and redfish in the previous year were considered potentially important ecological covariates in model formulation that could cause local depletion of shrimp by predation. The annual distribution of the predators' densities throughout the study area were estimated using spatiotemporal modelling (Eq. 1). We have represented the model formulations following the 'mgcv' package syntax (Wood 2017).

$$\text{Density}_{\text{FISH}} = s(\text{Depth}) + 0 + \text{Year} \quad (1)$$

where  $\text{Density}_{\text{FISH}}$  was the standardized weight ( $\text{kg km}^{-2}$ ) of Atlantic cod, Greenland halibut, or redfish in a given trawl set. Depth was the average bottom depth (m) of the trawl set and Year was a factor representing the year when the survey occurred. The  $s$  represents the smooth function computed with thin-plate regression splines. The '0' is included in the equation to ensure the intercept does not pertain to a specific level of the factor, in this case year. Both time-invariant spatial and spatiotemporal (assumed to be independent across years) random fields were included. A delta-lognormal model was the best model for redfish, and the delta-gamma models were the best-fitting models for Greenland halibut and Atlantic cod (based on Akaike information criterion—AIC) (Akaike 1973). The models were used to predict the annual density of each predator on a  $5 \text{ km}^2$  grid of depth throughout the study area (GEBCO Bathymetric Compilation Group 2023). These prediction surfaces (Figs. S1–S3 in the Supplement at [www.int-res.com/articles/suppl/m740p079\\_supp.pdf](http://www.int-res.com/articles/suppl/m740p079_supp.pdf)) were used to estimate the density of Atlantic cod, Greenland halibut, and redfish at the trawl sites lagged by 1 yr. Lagged predictions of predators were used because they help identify the possibility of localized depletion of northern shrimp, rather than temporal co-occurrence. These predator densities were log-transformed to reduce the influence of outliers.

Shrimp density models that included a covariate for each predator and spatial-varying coefficient with a mean of zero were considered (Anderson et al. preprint doi:10.1101/2022.03.24.485545). When using spatial-varying coefficients, the relevant predator den-

sities were normalized, where  $x_{\text{scaled}} = (x - \text{mean}(x)) / \text{standard deviation}$ . The addition of spatial-varying coefficients recognized that the effect of species interactions may not be uniform throughout the large study area (Doser et al. 2024). Latent habitat characteristics through time and space were described by Gaussian random fields representing spatial and spatiotemporal autocorrelation. We assumed the spatiotemporal random fields were independent across years. We tested model performance based on the inclusion of anisotropy (both shared and distinct between model components) to account for heterogeneity of the spatial correlation dependent on direction. We considered models with a Tweedie response distribution, as well as delta-gamma and delta-lognormal models.

Model convergence was checked by ensuring the maximum absolute log likelihood gradient with respect to all fixed effects was  $<0.001$ , the Hessian was positive definite, and no random field marginal standard deviations were less than 0.01 (Anderson 2023). The best model was determined based on ability of the model to converge, residual diagnostic checks, and AIC (Akaike 1973). In addition, randomized quantile residuals were examined using Markov chain Monte Carlo sampling to estimate random effects and fixed effects at their maximum likelihood values, using the R package 'sdmTMBextra' (Anderson 2023).

## 2.4. Predictions

The best-fitting model predicting fishable northern shrimp density was used to predict their density throughout the study area from 2005 to 2022, using a  $5 \text{ km}^2$  gridded surface of depth (0 to 750 m) and slope (GEBCO Bathymetric Compilation Group 2023), and assuming Period equal to Light, when catch was maximized. The timeframe of 2005 to 2022 was used due to data availability (bottom temperature) and because it was previously shown (through simulations) that spatiotemporal modelling could accurately hind-cast striped shrimp density in the northern-most areas with shorter timeseries (i.e. WAZ and EAZ) using a smaller data set within this timeframe (Baker et al. 2024). Bottom temperatures were required for the entire prediction surface, so we used Bedford Institute of Oceanography North Atlantic Model (BNAM) monthly bottom temperature predictions at the time of the survey (Wang et al. 2018). Bottom temperatures associated with August were used for EAZ, WAZ, and SFA 4, while bottom temperatures associated with October were used in SFAs 5 to 7.

### 3. RESULTS

#### 3.1. Spatiotemporal modelling

The best-fitting model predicting fishable northern shrimp density is presented in Table 2, Model 1, where Density was the standardized weight ( $\text{kg km}^{-2}$ ) of fishable northern shrimp caught in a trawl set. Depth was the average bottom depth (m) of the trawl. Slope was average slope gradient ( $^{\circ}$ ) of the seafloor at the location of the trawl set. Temp represented the average bottom temperature ( $^{\circ}\text{C}$ ) recorded during the trawl set. To reduce complexity and over fitting the results, we set thin plate regression splines to a basis dimension of the 5 (i.e.  $k = 5$ ) in the smooth relationships. Period was a factor representing Dark or Light (Baker et al. 2021). Year was a factor representing the year when the survey occurred. Cod (Atlantic cod, logged), GreenlandHalibut (Greenland halibut) and Redfish (redfish, logged) represented the modelled density of each predator taxon in the previous year at the location of the trawl set. Greenland halibut values were scaled so that the effect of Greenland halibut could be included in the model as spatial-varying coefficient with a mean of zero (as well as a regular covariate).

The best model (Table 2, Model 1) included anisotropy to account for heterogeneity of the spatial correlation dependent on direction, but not calculated separately for each model component. The delta-gamma model, where the model was a combination of 2 models: one binomial GLMM with a logit link, and the second component a gamma GLMM with a log link for the positive data. The model included both a spatial (Fig. S4) and a spatiotemporal random field in each model component (Fig. S5). The model residuals met diagnostic tests for normality (Figs. S6 & S7) and displayed no obvious temporal or spatial patterns (Figs. S8 & S9).

Other model iterations considered for predicting fishable northern shrimp density, but not identified in the best-fitting model, included covariates TRI, time to solar noon, zenith angle, and survey, time-varying coefficients for redfish, spatial-varying coefficients for Atlantic cod, redfish, and year, and estimating differing Matérn ranges between random fields and delta-model components (Table 2). The estimated Matérn range for the best model was narrower for the binomial model, compared to the Gamma model (Table 3).

The predicted probability of fishable northern shrimp presence and greatest abundance both peaked at ap-

Table 2. Top 10 models considered in the development of the best model estimating fishable northern shrimp density. All models presented in this table converged and met basic diagnostic checks outlined in Section 2. AIC: Akaike information criterion

No.	Model formulation	AIC
1	$s(\text{Depth}) + s(\text{Slope}) + s(\text{Temp}) + \text{Period} + s(\text{Cod}) + s(\text{scaled\_GreenlandHalibut}) + s(\text{Redfish}) + 0$ + Year; spatial varying = $\sim$ scaled_GreenlandHalibut; anisotropy = TRUE; share range = TRUE, family = delta gamma	192382.9
2	$s(\text{Depth}) + s(\text{Slope}) + s(\text{Temp}) + \text{Period} + s(\text{Cod}) + s(\text{scaled\_GreenlandHalibut}) + s(\text{Redfish}) + 0$ + Year; spatial varying = $\sim$ scaled_GreenlandHalibut; anisotropy = TRUE; share range = FALSE, family = delta gamma	192385.5
3	$s(\text{Depth}) + s(\text{Temp}) + \text{Period} + s(\text{Cod}) + s(\text{scaled\_GreenlandHalibut}) + s(\text{Redfish}) + 0$ + Year; spatial varying = $\sim$ scaled_GreenlandHalibut; anisotropy = TRUE; share range = TRUE, family = delta gamma	192436.0
4	$s(\text{Depth}) + s(\text{Slope}) + s(\text{Temp}) + s(\text{Cod}) + s(\text{scaled\_GreenlandHalibut}) + s(\text{Redfish}) + 0$ + Year; spatial varying = $\sim$ scaled_GreenlandHalibut; anisotropy = TRUE; share range = TRUE, family = delta gamma	192475.5
5	$s(\text{Depth}) + s(\text{Slope}) + s(\text{Temp}) + \text{Period} + s(\text{Cod}) + s(\text{GreenlandHalibut}) + s(\text{Redfish}) + 0$ + Year; anisotropy = TRUE; share range = TRUE, family = delta gamma	192522.5
6	$s(\text{Depth}) + s(\text{Slope}) + s(\text{Temp}) + \text{Period} + s(\text{Cod}) + s(\text{GreenlandHalibut}) + s(\text{Redfish}) + 0$ + Year; anisotropy = TRUE; share range = FALSE, family = delta gamma	192524.7
7	$s(\text{Depth}) + s(\text{Slope}) + s(\text{Temp}) + \text{Period} + s(\text{Cod}) + s(\text{GreenlandHalibut}) + s(\text{Redfish}) + 0$ + Year; anisotropy = TRUE; share range = TRUE, family = delta log-normal	192984.3
8	$s(\text{Depth}) + s(\text{Slope}) + s(\text{Temp}) + \text{Period} + s(\text{Cod}) + s(\text{GreenlandHalibut}) + s(\text{Redfish}) + 0$ + Year; anisotropy = TRUE; share range = TRUE, family = Tweedie	194579.2
9	$s(\text{Depth}) + s(\text{Slope}) + s(\text{Temp}) + \text{Period} + s(\text{Cod}) + s(\text{GreenlandHalibut}) + s(\text{Redfish}) + 0$ + Year + Survey; anisotropy = TRUE; share range = TRUE, family = Tweedie	194581.2
10	$s(\text{Depth}) + s(\text{Slope}) + s(\text{Temp}) + s(\text{Zenith angle}) + s(\text{Cod}) + s(\text{GreenlandHalibut}) + s(\text{Redfish}) + 0$ + Year; anisotropy = TRUE; share range = TRUE, family = Tweedie	194609.5

proximately 300 m depth, at a slope of approximately 12°, and bottom temperature of 2.5°C (Fig. 3). The second notable peaks in the depth, bottom temperature, and slope conditional effect plots are likely the result of sparse sampling at the extreme values of these metrics (Fig. 3). Despite the inclusion of Period in the best model, it had only a small effect on the predicted density of fishable northern shrimp, with catchability slightly higher during Light conditions.

Lagged redfish density showed no clear effect (binomial model) or a slight positive trend (Gamma model) in relation to fishable northern shrimp, until redfish became dense, then a strong negative relationship was found (Fig. 4). Lagged Atlantic cod density illustrated an increasing relationship with the probability of fishable northern shrimp being present. Within well-sampled Atlantic cod densities, Atlantic cod had a positive relationship with fishable northern shrimp density, until Atlantic cod became dense, then a negative relationship was predicted. The overall smooths related to lagged Greenland halibut indicate a slight positive trend related to probability of fishable northern shrimp in well-sampled densities, and a negative trend related to density of northern shrimp; however, the overall effect varied spatially, and the inclusion of a spatial-varying coefficient related to Greenland halibut density improved model performance (Table 2, Fig. 5).

### 3.2. Predictions

The spatiotemporal model predicted that fishable northern shrimp density varied substantially through the study area and between years (Fig. 6). The Grand Bank had consistently low predicted densities of fishable northern shrimp, particularly in most recent years (>2015) (Fig. S10). In contrast, the slope edges and the northern portion of WAZ had consistent high predictions of fishable northern shrimp throughout the time series. Predictions were most uncertain in areas of low abundance (i.e. SFA 7) and poor data availability (WAZ) (Fig. S11).

## 4. DISCUSSION

We used data from annual trawl surveys spanning more than 25 yr, 23 degrees of latitude, and 23 degrees of longitude to build a spatiotemporal

Table 3. Fishable northern shrimp density spatiotemporal generalized additive mixed model outputs, with mean estimates as well as confidence intervals around each estimate

Parameters	Binomial model	Gamma model
Matérn anisotropic range (km)	148.2–254.5 @ 119°	89.4–153.6 @ 119°
Dispersion parameter		1.07
Spatial SD	2.32	1.72
Spatiotemporal SD	1.18	1.11
Spatially varying coefficient SD	1.31	0.76

model. The model was used to better understand the factors influencing the distribution and abundance of fishable northern shrimp and create spatial prediction surfaces from 2005 to 2022.

### 4.1. Environmental characteristics

Our results are consistent with previously reported depth preferences for northern shrimp. Northern shrimp are generally found between 20 to 900 m, with larger individuals and shrimp in higher latitudes found in deeper waters (Garcia 2007). In our study area, fishable northern shrimp were found in depths from 34 to 1358 m. Hvingel (1999) reported highest shrimp densities in depths between 150 and 600 m off East Greenland, and in Disko Bay, West Greenland, optimal shrimp habitat was identified in depths between 150 and 350 m with mixed sediments (Krawczyk et al. 2024). In comparison, the probability of finding fishable northern shrimp and their densities peaked near 300 m in our study area.

Temperature is considered a strong determinate of northern shrimp distribution (Shumway et al. 1985), abundance (Garcia 2007), growth (Squires 1996, Bergström 2000), reproductive success (Lund 1988), and survival (Bergström 2000). We found fishable northern shrimp in temperatures as low as  $-1.6^{\circ}\text{C}$ , which coincides with the lowest survivable temperature previously reported (Bergström 2000). In the Barents Sea, egg loss, embryo death, and a reduction in the proportion of females carrying eggs were reported in waters less than  $-1^{\circ}\text{C}$  (Berenboim 1982, Lund 1988). We found northern shrimp in bottom temperatures as high as  $9.2^{\circ}\text{C}$ , which is above their optimal maximum temperature of  $8^{\circ}\text{C}$  (Garcia 2007) but not above the maximum temperature ( $12^{\circ}\text{C}$ ) previously reported (Shumway et al. 1985). Similar to previously reported preferred temperature ranges of  $2\text{--}4^{\circ}\text{C}$  (Le Corre et al. 2024) and  $4\text{--}6^{\circ}\text{C}$  (Squires 1996), in our study area, we found that the probabil-

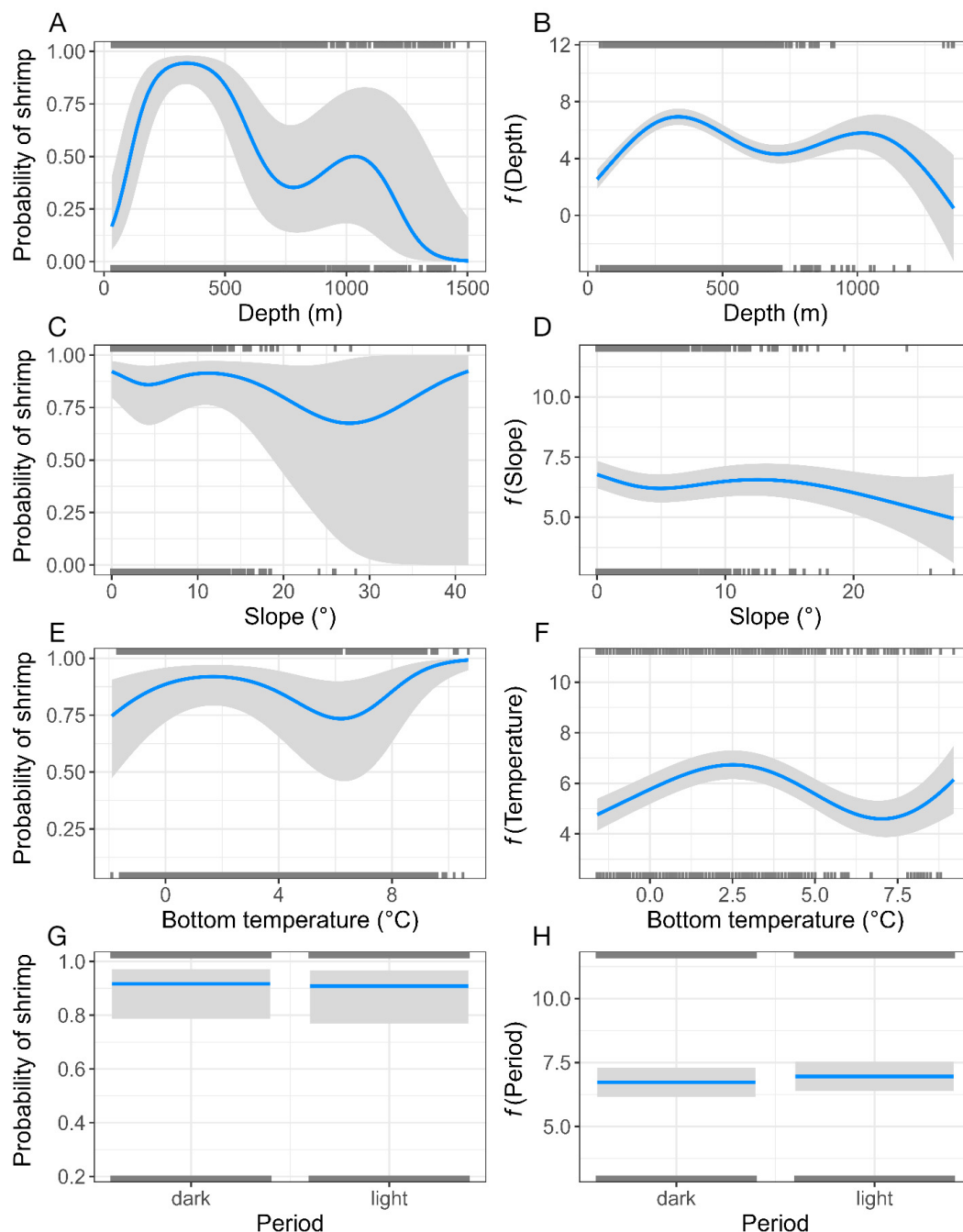


Fig. 3. Fishable (>17 mm carapace length) northern shrimp spatiotemporal delta-gamma model conditional effects plots from the binomial model component (detection probability, left column) and gamma model component (density given detection,  $\text{kg km}^{-2}$ , right column) for environmental covariates. (A–B) Depth (m), (C–D) slope (°), (E–F) bottom temperature (°C), and (G–H) period. Conditional effects are depicted based on setting other categorical variables to their most common levels and other continuous variables to their median values. Rug lines: available predictor data; blue lines: means; shaded ribbons: 95% confidence intervals. Confidence intervals include uncertainty associated with the intercept

ity of finding fishable northern shrimp and their densities peaked in bottom temperatures between 2 and 3°C.

Very little research has focused on the effect of slope on northern shrimp distribution and abundance. We found a relatively small effect size of slope,

but the inclusion of slope within the model improved the model performance. There was little variation of slope in the data, with few sets on slopes greater than 20°. Although the study area consists of canyons and banks with steep slopes, trawls cannot target steep slopes, limiting our ability to truly understand the



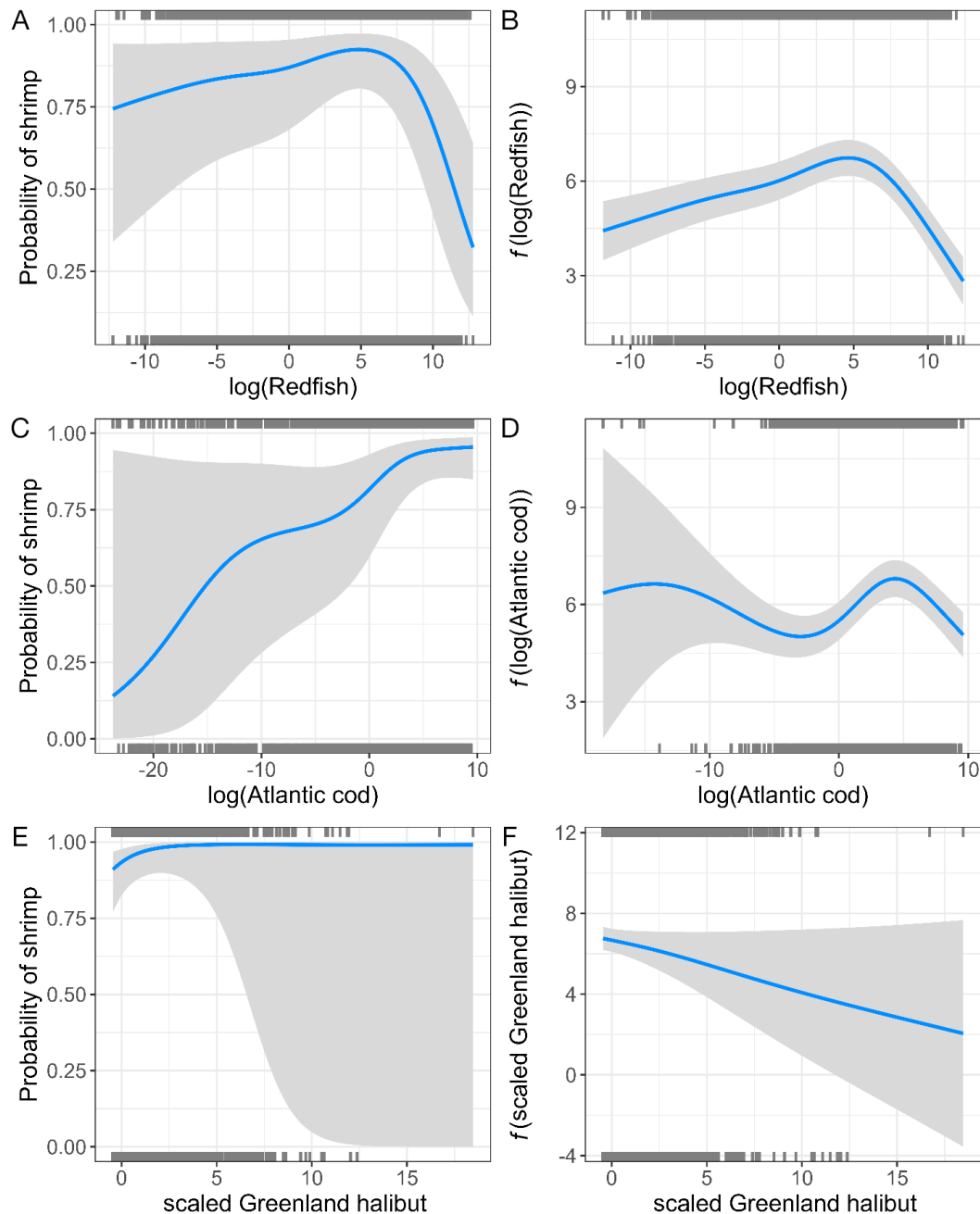


Fig. 4. Conditional effects plots of covariates of fishable northern shrimp presence and density based on spatiotemporal delta-gamma models. (A–B) Logged redfish, (C–D) logged Atlantic cod, (E–F) scaled Greenland halibut densities ( $\text{kg km}^{-2}$ ). Conditional effects are depicted based on setting categorical variables to their most common levels and other continuous variables to their median values. Left column represents the binomial model component (detection probability) and right column represents density given detection. Rug lines: available predictor data; blue lines: means; shaded ribbons: 95% confidence intervals. Confidence intervals include uncertainty associated with the intercept

effect of slope beyond relatively flat surfaces. Nevertheless, our results illustrate that slope may play an important role in northern shrimp's spatial distribution, with peaks near slopes of  $12^\circ$ . Slopes can create heterogeneity on otherwise relatively flat seafloors and result in changes to hydrological conditions (e.g.

current), available organic content, and available prey, all of which are known to influence northern shrimp distribution and abundances (Shumway et al. 1985). Although other studies have indicated that bottom type and habitat heterogeneity influence pandalid shrimp abundance (e.g. Schick 1991), TRI was not

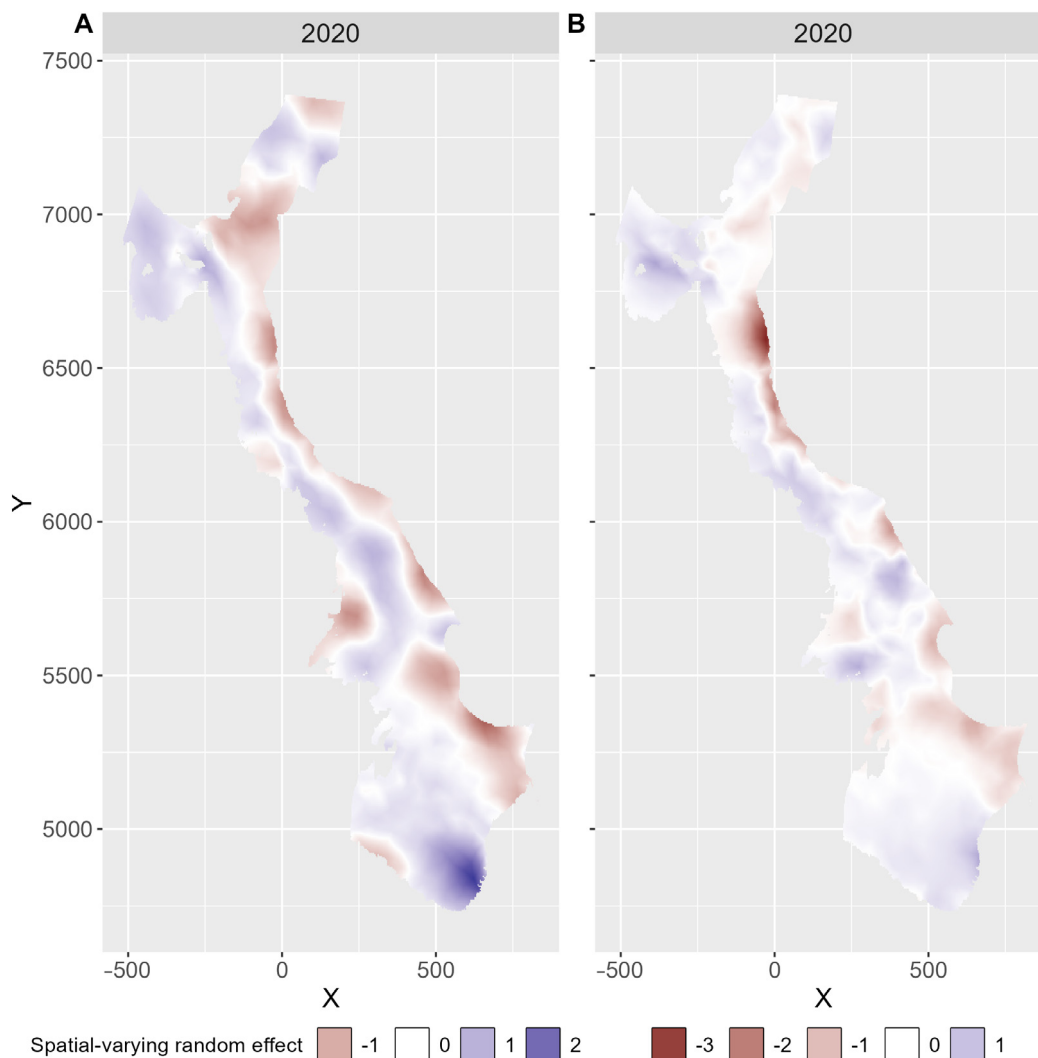


Fig. 5. Spatial random fields associated with the lagged scaled Greenland halibut smooth coefficient in the (A) binomial model and (B) Gamma (link = log) model predicting fishable (> 17 mm carapace length) northern shrimp (A) presence and (B) density. X and Y are projected in UTM Zone 22N (km)

deemed a good predictor of shrimp distribution and abundance in our modelling. This does not necessarily mean that bottom topography is unimportant for shrimp dynamics, but this metric might have simply been too coarse in scale throughout the study region to adequately capture its effect on small-scale shrimp distribution and abundance patterns.

#### 4.2. Time of day

Although the inclusion of the factor representing light conditions (i.e. Period) improved model performance, the effect size was relatively small. The small effect verified that catches were somewhat higher in light conditions compared to dark, indica-

ting the movement of shrimp off the seafloor bottom during dark hours. *Pandalus* spp. complete diel migrations in the pursuit of prey (Barr 1970, Hudon et al. 1992). Northern shrimp were found to be 6.33 times more abundant in day catches compared to night (Fr chet te et al. 1983), and male striped shrimp *P. montagui* were 1.5 times more abundant in catches during daylight hours, compared to nighttime (Baker et al. 2021). Similar to our findings, Barr (1970) also found that movement patterns were related to the light conditions, with the amount of time spent on bottom related to the length of night-like conditions. The lack of a strong effect size in our findings is not surprising. As northern shrimp grow, they change sex from males to females. Our research focused on fishable (i.e. large) northern shrimp, and the model was

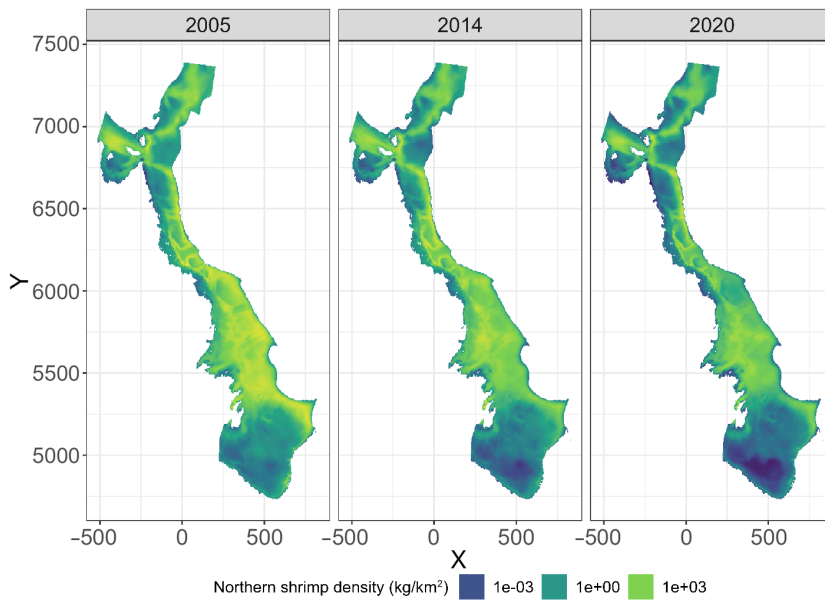


Fig. 6. Prediction surfaces of fishable northern shrimp density ( $\text{kg km}^{-2}$ ), presented on logged scale, based on a spatiotemporal model. Three years representing the first year of predictions (2005), the first year with full survey coverage (2014), and the most recent year with full survey coverage when predictions are possible (2020) are shown. Predictions of survey years (2005 to 2022) are presented in Fig. S10 in the Supplement. X and Y are projected in UTM Zone 22N (km)

strongly influenced by the heaviest, largest shrimp (i.e. large females). Female northern shrimp are not thought to complete diel migrations to the same extent as males (i.e. smaller shrimp) (Barr 1970, Hudon et al. 1992, Bergström 2000).

#### 4.3. Predators

Predation is a strong top-down driver of northern shrimp population trends throughout their range (Wieland et al. 2007, Richards & Hunter 2021), so we expected consistent negative relationships between northern shrimp and lagged predator density.

Redfish are known for their dense, but patchily distributed, biomass. The conditional effect trend associated with lagged redfish density resembles what we would expect from local depletion events caused by predation. There was no clear relationship or an increasing relationship with the probability and density of northern shrimp, indicating co-occurrence based on habitat quality or preferential habitat selection based on prey availability, until redfish became particularly dense, after which, a significant, clear negative relationship was found. This suggests that at particularly high densities, these predators begin to have strong negative, localized effects on fishable

northern shrimp density in the following year. Redfish diet is notoriously difficult to describe because most redfish either regurgitate their prey or fully evert their stomachs when brought to the surface in trawls, and as such it is unknown how much shrimp comprise of their diet throughout the study area and how that amount changes spatially or temporally. However, redfish have been documented as an important predator of northern shrimp off West Greenland (Pedersen & Rigét 1993), and on the Flemish Cap, redfish were deemed to be responsible for the removal of a high proportion of the shrimp population between 2005 and 2012 (Pérez-Rodríguez et al. 2017). There, shrimp consisted of 15–20% of mature redfish diet and 10% of immature redfish diet (Pérez-Rodríguez et al. 2017). In the Gulf of St. Lawrence, redfish shifted their diet from primarily zooplankton to pandalid shrimp and fish, as the redfish grew to sizes of 25 to 30 cm (Brown-Vuillemin et al. 2022). The redfish

population off Canada's Atlantic coast is currently undergoing a population explosion (Brown-Vuillemin et al. 2022, Baker et al. 2024; Fig. S12), and the potential impact of these growing redfish on *Pandalus* spp. populations should be thoroughly explored.

Atlantic cod are documented predators of northern shrimp (Parsons 2005, Hedeholm et al. 2017, Jónsdóttir 2017). Fulton et al. (2024) found *Pandalus* spp. present in all Atlantic cod stomachs examined from EAZ, WAZ, and SFA 4 in 2022 during the NSRF survey and indicated that of the 12 predator taxa examined, Atlantic cod had the largest mean number of northern shrimp in their stomachs, with up to 12 shrimp found in a single stomach. Similarly, off Iceland, stomach content analysis identified northern shrimp as a consistent, important part of Atlantic cod diet (Jónsdóttir 2017), and on the Flemish Cap, Atlantic cod was deemed the main source of mortality before the fishery started (i.e. <1993) (Pérez-Rodríguez et al. 2017). There, shrimp made up 25–30% of the diet for immature Atlantic cod and mature cod up to 85 cm and 15–20% of the diet of large Atlantic cod (85–140 cm) (Pérez-Rodríguez et al. 2017). Hedeholm et al. (2017) found Atlantic cod up to 60 cm fed on northern shrimp off Greenland but lacked diet samples from large Atlantic cod in the area where most shrimp consumption was reported for all smaller

sizes. Our conditional effect plots indicate very few data points and wide confidence intervals at low Atlantic cod densities. However, once data become more prevalent (i.e. Atlantic cod numbers increase), the trends become more distinct and the general relationship between number of northern shrimp and Atlantic cod density are similar to those predicted for redfish; as Atlantic cod density increases, there is a general positive trend, indicating habitat co-occurrence and/or preferential distribution where prey (i.e. northern shrimp) are abundant. Once Atlantic cod become particularly dense, there is a negative relationship, possibly indicating predation pressure becoming too strong for northern shrimp to maintain large densities. Similarly, Wieland et al. (2007) also found that Atlantic cod had very little impact on northern shrimp population numbers off West Greenland when Atlantic cod was not abundant but had negative impacts on northern shrimp populations when highly abundant.

Greenland halibut have been identified as important predators of northern shrimp throughout their range (Pedersen & Rig  t 1993, Solmundsson 2007, Wieland et al. 2007, Dwyer et al. 2010). For example, off West Greenland a significant negative correlation between Greenland halibut biomass and northern shrimp recruit survival was identified (Wieland et al. 2007). However, in general, Greenland halibut tend to be more generalized, opportunistic feeders of shrimp (Dwyer et al. 2010), and consumption of northern shrimp is lower compared to Atlantic cod (Wieland et al. 2007, Fulton et al. 2024). Off West Greenland, consumption of northern shrimp by Greenland halibut was 10 times lower than consumption by Atlantic cod (Grunwald 1998, within Wieland et al. 2007). In WAZ, EAZ, and SFA 4, Greenland halibut had the highest diversity of prey items in their stomachs compared to the other 11 predator taxa examined, but the proportion of stomachs containing northern shrimp varied by area, with northern shrimp being dominant in EAZ and SFA 4 but not in WAZ (Fulton et al. 2024). Our model predicted a co-occurrence between Greenland halibut and northern shrimp and a steady negative relationship between Greenland halibut density and northern shrimp density in the following year. In contrast to redfish, Greenland halibut do not form large dense schools but can still have top-down impacts on northern shrimp populations. While Greenland halibut may not cause strong local depletion events, they have the ability to gradually influence population numbers over a large scale.

The overall effect of Greenland halibut density in our study was not consistent in space, and the inclusion of a spatial-varying coefficient related to Green-

land halibut density improved the model performance. The largest negative effects were found in slope areas and along the northeast corner of the Grand Bank. Conversely, relatively smaller effects were found in WAZ and closer to shore. These results highlight the importance of testing for spatial-varying coefficients and our underlying assumptions related to effects of potential predictors.

#### 4.4. Spatial-varying coefficients

The northern shrimp population spans multiple ecozones (Spalding et al. 2007) with the potential for large variabilities in available environmental characteristics, potential predators, and prey sources. This large distribution and ecosystem variability increases the complexity of spatial distribution modelling and can raise uncertainty regarding the stationarity and uniformity of species-environment relationships. Such scenarios emphasize the need for evaluating whether the effect of covariates vary with space (Doser et al. 2024). Unlike many spatial distribution models, we did not assume that our coefficients (i.e. smooths) were constant through space and time and were able to confirm that the inclusion of a spatial-varying coefficient related to the Greenland halibut density improved model performance. The overall effect of predators would be expected to be influenced by a variety of other unmeasured factors, including alternate prey availability. The inclusion of a spatial-varying coefficient allows for this variation to be incorporated within the model without direct knowledge or measurements of the underlying drivers of this spatial variation.

Thorson et al. (2023) reviewed the use of spatial-varying coefficients in species distribution models and noted that although spatial-varying coefficients were rarely used, they had wide applicability in species distribution modelling and greatly improve our understanding of habitat use, population dynamics, and the descriptive power of species distribution models. Similarly, Doser et al. (2024) advocated for more widespread use of spatial-varying coefficients in species distribution models by illustrating how they can provide additional information regarding complex fine-scale and large-scale drivers of habitat suitability and inform nuanced conservation management. Here, we further show the benefit of including spatial-varying coefficients in species distribution modelling to more thoroughly understand the non-stationary effect of covariates, particularly the effect of predation.

#### 4.5. General trends and patterns

Our modelling illustrates a general decreasing trend in abundance of northern shrimp throughout the study area, most pronounced in the southern areas, specifically the Grand Bank (Fig. 6). This area is relatively shallow and often considered a 'spill-over area' where northern shrimp densities have generally been low, unless biomass throughout the entire study area is particularly high (~early 2000s). It would be expected that any large-scale declines in population trends might be more pronounced in lower quality habitats. Le Corre et al. (2020) noted high settlement of northern shrimp larvae on the Grand Bank and contributed the discrepancy between settlement patterns and densities to high predation rates of juvenile shrimp from diverse and abundant groundfish in the area. Our results show that Atlantic cod abundance is relatively high here (Fig. S3). In addition, throughout the study area, the 3 predators have exhibited increasing abundances (Figs. S1–S3, S12).

Our analyses focused on environmental and ecological drivers of fishable northern shrimp, but northern shrimp is the target of a directed fishery which could be influencing abundance patterns and trends. The stock status of both SFA 6 and 7 are deemed 'critical' and as a result, fishing is closed in SFA 7 and exploitation rates in SFA 6 usually target 10% or less (DFO 2023, unpubl. data). The highest exploitation rates are consistently recorded in SFAs 4 and 5, but even there, they are generally below 30% (Fulton et al. 2024, Le Corre et al. 2024, DFO unpubl. data). It may be expected that as predators increase, the likelihood of a notable fishing effect on population dynamics may grow in areas with low northern shrimp densities.

#### 5. CONCLUSIONS

Our research illustrates that the spatial distribution and abundance of northern shrimp off Canada's sub-Arctic and northeast coast are driven by both top-down drivers (i.e. predation from Atlantic cod, redfish, and Greenland halibut), as well as environmental conditions, such as temperature, slope, and depth. Biologists should include the monitoring of these covariates within assessments for a better understanding of current and future changes in northern shrimp patterns and trends, and to appropriately inform fisheries management.

**Acknowledgements.** We thank the DFO technicians and biologists, as well as industry partners and Canadian Coast Guard crew members, who were responsible for ensuring

surveys ran smoothly and shrimp data were properly collected and archived. We also thank Darren Sullivan and Sheila Atchison for cleaning DFO and NSRF data; Katherine Skanes for writing original script to organize/clean the DFO data in preparation for analyses; William Coffey for updating the script to ensure survey data was accurate; and Dr. Nicolas Le Corre for running the script to create the dataset used in the analyses.

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*Editorial responsibility: Jean-Sebastien Lauzon-Guay,  
Dartmouth, Nova Scotia, Canada*  
*Reviewed by: K. Wieland and 2 anonymous referees*

*Submitted: December 27, 2023*  
*Accepted: July 4, 2024*  
*Proofs received from author(s): July 16, 2024*