**Notes to collaborators:**

This paper is long. I fully expect reviewers to tell me to move a bunch of the methods to supplementary materials. Feel free to mark anything you feel is better suited for supplementary or straight-up unnecessary for inclusion. So much information came out of the modeling process that I felt like a kid in a candy shop when writing the results section, and I had to self-edit over and over again to get something more interesting than a list of a thousand quantitative outcomes. After some consideration, I decided the storyline to follow was

*Cod seasonal spatiotemporal distributions for multiple size classifications indicate strong habitat preferences for certain depths, temperatures, and bottom sediment types. Geographic ranges have contracted, centers of gravity have generally inconsistent directional movement patterns, and there are a few patches of persistent high density despite declining abundance. Combined, this evidence suggests cod distribution follows MacCall’s (1990) basin model of spatial dynamics. It is therefore important to identify cod distribution patterns within each biological stock, across distinct size groups, and across multiple spatial scales to build a comprehensive understanding of how shifting environmental conditions like warming bottom waters will affect the population as a whole.*

I’ve also mentioned that industry stakeholders were supportive of this modeling method, as they would prefer to model the population using data that covers multiple depths and habitat types to, at minimum, provide data-backed insight into potential issues from density-dependent catchability.

I see this paper as the starting point for a bunch of further work. There’s space to write a whole paper on identifying the strongest distribution mechanism within each seasonal-stock-age group grounded in optimal foraging theory and the ideal free distribution model (density-independent, proportional density model, constant density model, basin model). I’ve got to be careful if I do this though, as VAST essentially models interpolated surfaces of density within discrete area-time groupings and then uses that to extrapolate all other measures of spatial and population dynamics. I don’t want to correlate something to a transformation of itself and call it significant.

I’ve also been thinking about building temporally dynamic habitat suitability models for each size class within the study area (we got conditional effects curves out of the model and I did something similar in my dissertation, so it shouldn’t be that hard) and testing how well seasonal cod distributions match the distribution of high-suitability patches. This could directly extend into the quantification of high-suitability habitat area reduction. I’m interested in identifying persistent high-density patches (with something more robust than the eyeballing I’ve done in this paper) and then figuring out what the environmental characteristics of those patches are and what they could tell us about the plasticity of the stocks to changing conditions.

The cod footprint work will also benefit from the publication of the VAST model results. Once we finalize the footprint’s spatiotemporal bounds, we can extract the dynamic environmental characteristics and cod indices of abundance specific to that area. It would be neat to quantify average environmental characteristics (depth, sediment makeup, rugosity, bottom temp, etc.) within the footprint areas, within the cod biological stock boundaries, and at the NEFSC BTS sample points to see how well they all match up. I think that’ll be more powerful than just talking about simple in-or-out hit rates.

**Title:** Spatial density and habitat associations of Atlantic Cod on the Northeastern US Continental Shelf

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**1 Abstract (~175 word limit, currently 175)**

The spatial distribution of the Atlantic cod (*Gadus morhua*) stock is shaped in part by several habitat and oceanographic variables. In this study, Vector Autoregressive Spatio-Temporal (VAST) models were used to combine data from multiple survey programs to hindcast seasonal spatial densities of three size classes of cod within the Northeast US Continental Shelf from 1982 to 2021. Bottom habitat characteristics, bottom water temperature, depth, and basin-averaged climate indices were included as density covariates. Depth, bottom temperature, and gravel sediments were strongly associated with spatial density. The relative abundance of all size classes generally decreased throughout the time series. Model outputs highlighted patches with persistently high spatial density despite range losses and declining abundance. This aligns with the “basin model”, a spatial dynamic frequently reported in collapsed fish stocks. The availability of habitat with suitable depth and temperature will likely be reduced under current projections of bottom water temperature, further endangering the recovery of the stock. Improving our understanding of cod habitat preferences and variation in spatial density will be important for future management efforts.

**Keywords:** Atlantic cod, vector autoregressive spatiotemporal model, spatial density, habitat

**2 Introduction**

Atlantic cod (*Gadus morhua*) are an ecologically, economically, and culturally critical part of New England’s groundfish fishing industry. Atlantic cod population assessments and management efforts are informed by a suite of bottom trawl surveys orchestrated by state and federal agencies, perhaps most notably by the Northeast Fisheries Science Center’s (NEFSC) twice-annual bottom trawl survey. This survey has been an important tool to assess groundfish stocks from Cape Hatteras, NC to Nova Scotia since the early 1960s. However, bottom trawl surveys like the NEFSC’s have reduced efficiency over complex bottom habitats with high bathymetric relief or hard substrate, such as cobble fields or rocky ledges (McElroy et al. 2019; Grabowski et al. 2020). Most bottom trawl survey programs have low sampling effort within shallow or complex habitat areas due to risks to the equipment, and will instead focus on sampling in areas deeper than 18m and with soft and smooth bottom habitats (Johnston and Sosebee 2014).

The limited survey information within complex bottom habitats is concerning to fishing industry stakeholders, fisheries scientists, and fisheries managers alike. Habitat complexity likely interacts with catchability, thereby making it difficult to determine if differences in catch between habitats are truly reflective of relative abundance (Peterson and Black 1994; Grabowski et al. 2020). The challenge that this poses to cod stock assessments can vary by life history phase; several early life history phases of cod are associated with complex bottom habitat areas and therefore are not likely to be sampled well by conventional bottom trawl methods. Age-0 and age-1+ juvenile cod have been found in higher densities over hard substrate or high-bathymetric relief areas, likely as a refuge from predation (Gotceitas and Brown 1993; Gotceitas et al. 1995; Gregory and Anderson 1997; Cote et al. 2004; Lough 2010; Grabowski et al. 2018; Linner and Chen 2022). Though conventional wisdom holds that adult cod prefer colder and deeper offshore waters, recent evidence indicates that shallow inshore areas support a wide size range of cod (Dean et al. 2021). Industry stakeholders also have reported a relatively high density of large cod within inshore hard-bottom habitats of the western Gulf of Maine, possibly indicating a density-dependent reduction in large cod spatial distribution and altered availability to bottom trawl surveys (Grabowski et al. 2020; McElroy et al. 2021). Stakeholders’ observations of increased cod density over complex bottom habitats have created the perception that cod abundance across most of the species' spatial range is much higher than what bottom trawl-informed assessments have suggested, which could strain relationships between scientists, managers, and stakeholders.

A further complication to assessing cod population dynamics is the complex spatial structure of its subpopulations. Since 1972, cod in US waters have been managed as two spatially distinct stock units: the Georges Bank and Gulf of Maine stocks (Serchuk and Wigley 1992). This structure may not have reflected the true biological structure of the cod population, leading to misinterpretations of the population’s spatial variation and magnitude of the productivity (Kerr et al. 2014; Zemeckis et al. 2014). Recent work by the Atlantic Cod Stock Structure Working Group has provided evidence that there are five biological cod stocks in US waters: a Georges Bank stock, a Southern New England stock, an Eastern Gulf of Maine Stock, a spring-spawning Western Gulf of Maine stock, and a winter-spawning Western Gulf of Maine and Cape Cod stock (McBride and Smedbol 2022). The former three stocks inhabit spatially separate areas, and the latter two stocks are sympatric with spatial overlap in the western Gulf of Maine. Each of these spatial areas has a unique composition of static spatial features (e.g., depth, bottom substrate, rugosity) and dynamic environmental characteristics (e.g., bottom water temperature) that are expected to influence the within-stratum distribution and productivity of the associated cod stock (Ames 2004; Zemeckis et al. 2014; Guan et al. 2017a; Dean et al. 2019; Linner and Chen 2022). Tracking the varying spatial dynamics and productivity of cod populations at spatially explicit and biologically relevant scales will be critical to developing useful management strategies (Kerr et al. 2014; Zemeckis et al. 2014; Dean et al. 2019; McBride and Smedbol 2022).

The objective of this study was to build size-specific indices of abundance and seasonal maps of spatial density for Atlantic cod for each of the stock areas using all relevant state and federal groundfish survey data. Surveys available for inclusion in modeling cover inshore, offshore, smooth, and complex bottom habitats, and utilize both bottom trawl and bottom longline methods. Vector Autoregressive Spatio-Temporal (VAST) models were used to combine all survey data into size-specific models of cod spatiotemporal density. VAST models estimate the spatiotemporal density of a target organism conditioned on density covariates and controlling for catchability covariates, and so are useful for estimating the spatiotemporal density of organisms in areas with limited observation data. These estimates of spatial-temporal density can then be used in the calculation of indices of abundance, population centers of gravity, range edges, and habitat associations. VAST models were fitted for three size classes of cod to examine whether cod size influences its distribution, abundance, and habitat use patterns. The output of these models could improve our understanding of cod spatial dynamics, habitat associations, and demographics, which in turn would benefit management efforts.

**3 Methods**

**3.1 Survey Data**

Eleven surveys of groundfish abundance were available for use (Table 1). The combined spatial footprint of all surveys covered the waters of the continental shelf along the US coast from Lubec, Maine to Cape Hatteras, North Carolina. Temporal coverage spanned from 1959 to 2022. These surveys utilized different vessels and methods, have variable spatial extents, were completed either annually or seasonally, and had variable temporal coverage (as in, the number of years in which the survey occurred). All surveys reported the number of cod and total weight (kg) of cod caught per tow, and some surveys processed all or a portion of the catch to provide further biological detail (individual length, weight, sex, age, etc.). Survey data were cleaned (see next section), cut to chosen model spatial and temporal domains, and combined into a single dataset.

**3.1.1 Data cleaning and response variable**

To be considered in the model, survey data needed to provide valid information for spatial location, sampling date, and number of cod caught, as well as valid size-identifying biological information for at least a portion of the catch. Cod caught in the surveys were separated into three distinct size classes, as it was expected that habitat utilization and spatial density would vary among size or age groups. Small cod were defined as shorter than 39.1 cm total length or less than 0.58 kg. Medium cod were between 39.1 and 70.2 cm, or between 0.58 and 3.44 kg. Large cod were longer than 70.2 cm or heavier than 3.44 kg. This size structure roughly matches ages 0-2 (pre-spawning), ages 2-5 (variable spawning), and ages 5+ (spawning) cod (Zemeckis et al. 2014; Dean et al. 2019; Dean and Perretti 2022). This assumed age structure represents the average across all years and all spatial areas of the model domains, though time to maturity may be slightly different between time periods and spatial locations (Dean and Perretti 2022). Fish that were unable to be assigned to a size class were not used in the models. Because some fish only had length information and no individual weight information, biomass per size class could not be used as the response variable. Instead, total abundance (count) of each of the size classes was used as the response variable for each sampling event.

**3.2 VAST**

VAST models were used to estimate cod spatial density over time by size class and create joint indices of abundance using the cleaned groundfish survey data. VAST is a framework for implementing spatial delta-generalized linear mixed models (delta-GLMM) and can be structured to provide estimates for multiple categories of interest and spatial strata (Thorson and Barnett 2017; Thorson 2019). As recommended by model developers for abundance-data models, we specified a Poisson-link delta model with lognormal-Poisson distribution. This model family is designed to accept positive continuous data with zeros and use a delta (or “hurdle”) approach to derive spatiotemporal density as a combination of two linear predictors (Thorson 2018). The first linear predictor estimates encounter probability, and the second linear predictor estimates catch rates given a positive encounter probability. Using notation from Thorson (2019), the first linear predictor can be represented as

1.

where is the encounter probability predictor for observation *i* for category at location and time . represents temporal variation for each category and time, represents spatial variation for each location and category, represents spatiotemporal variation for each location, category, and time, represents vessel effects for each vessel and category, and represents the effect of density covariates for each category and time. The second linear predictor is structured the same way but calculates the catch rate predictor. Both linear predictors incorporate fixed and random effects, and spatial and spatiotemporal variation are approximated as Gaussian Markov random fields (Thorson et al. 2015b; Thorson and Barnett 2017; Thorson 2019). Implementation of VAST models requires several further structural and data inclusion decisions, as outlined in Thorson (2019) and below in sections 3.2.1 through 3.2.6.2.

**3.2.1 Spatial domain, smoothing, resolution, and strata**

Though survey data coverage extends to Cape Hatteras, North Carolina, the southern edge of the Atlantic cod range likely does not reach this point. For this model, the spatial extent of the model domain was American waters on the continental shelf from the northern edge of the Gulf of Maine through the mouth of the Chesapeake Bay (Fig. 1). This area was represented as a 2D mesh built on a stochastic partial differential equation (SPDE) approximation to a Gaussian Markov random field with a Matérn correlation function. Geometric anisotropy (directional correlation) is expected in most marine ecosystems (Thorson et al. 2015a) and was therefore included as a fixed effect, though support for its inclusion was also assessed in the model selection process (see Section 3.3). Spatial variables were defined at a pre-determined number of knots. Knots were placed via k-means clustering of the data to minimize the average distance between knots and sampling locations. Sampling locations are expected to have spatial variables equal to the nearest knot, so in effect, the number of knots defines the spatial resolution of spatial density estimates. In this model, the number of knots was set to 200 and the mean distance between nearest-neighbor knot locations was 30.1 km. Assessment of directional correlation found that the distance with approximately 10% correlation was 123.2-157.7 km for the first linear predictor and 42.7-66.0 km for the second linear predictor across all size classes, indicating that this number of knots and the resulting distance between knots provided sufficient spatial resolution.

It is of interest to calculate spatial dynamics and indices of abundance for each of the distinct biological stocks proposed by the Atlantic Cod Stock Structure Working Group, as there is evidence that the complex spatial structure of these biological stocks affects both our understanding of cod spatial dynamics and management efforts (Zemeckis et al. 2014; Guan et al. 2017a; McBride and Smedbol 2022; Linner and Chen 2022). Therefore, a custom extrapolation grid was built as a spatial domain for derived quantities, which had 2000 grid cells (each cell approximately 20.1 km by 20.1 km) spread across four spatial strata. Bilinear interpolation was then used to calculate spatial density within each of these cells. The spatial strata represented the Eastern Gulf of Maine, Georges Bank, Southern New England, and combined winter- and spring-spawning Western Gulf of Maine stocks. The latter two stocks overlapped substantially in space, supporting their treatment as a single spatial stratum. The models also reported results at a basin-wide scale, in which all strata were combined.

**3.2.2 Temporal domain and resolution**

The temporal domain of the models began in 1982 when the adoption of the Interim Groundfish Plan shifted management strategies from regional quotas to minimum size and gear regulations. The last full year of data available at the time of modeling was 2021. Survey data from outside this temporal domain were not used in the model.

Many surveys considered by this modeling effort were conducted twice annually, in the spring and fall. This is a useful sampling design to track seasonal migrations. In the highly-studied Western Gulf of Maine region, cod typically migrate inshore to spawn in the spring, move offshore to feeding areas in the summer and fall, and may move to deep offshore basins to overwinter (Zemeckis et al. 2017). Cod on Georges Bank likely make similar seasonal migrations, with evidence of persistent spring spawning sites within the relatively shallow waters of Georges Shoals and Nantucket Shoals (DeCelles et al. 2017). Because it is supported both by data availability and the behavior of cod, time steps in the model were structured to represent the spring and fall seasons of each year in the time series. Therefore, though there were 40 years of data, there were 80 time steps. The spring season was March through August of any year *x*, and Fall was September through December of year *x* and January and February of year *x*+1. This approach ensured that the fall season time steps were temporally continuous. Therefore, day 1 of a modeled year is March 1st.

**3.2.3 Effort estimates**

VAST requires an effort estimate for each observation. For surveys using bottom trawl methods, area swept is a commonly reported effort measure. Area swept was reported, assumed, or calculated for the surveys included in this modeling effort as information was available (Table 1). Some bottom trawl surveys reported area swept for each tow, and this was therefore used as an effort measure. Several surveys did not report the area swept for each tow but instead reported an average area swept based on gear mensuration and vessel travel distance. Typically, these surveys also validated that effort was within tolerance limits for acceptable tow duration and vessel speed to maintain similarity between tows. For these surveys, this provided average area swept was included as the estimated effort for each observation. Finally, a few surveys reported only optimal gear mensuration and intended distance towed. For these surveys, the estimated average effort per tow was calculated as the intended distance covered by the tow multiplied by the optimal wing spread.

It is recommended that the area swept be set to 1 for sampling gears with an unknown effective area swept (Thorson 2019). Initially, the area swept for the bottom longline and jigging surveys was set to 1. However, this created an issue of scaling and mixed units. Simple leave-one-out sensitivity tests were run to determine the influence of the bottom longline and jigging surveys on the overall cod indices of abundance. Removing the Eastern Gulf of Maine Sentinel jigging survey had little impact on the modeled abundance of all three size classes of cod, so it was excluded from further analysis. Removing the bottom longline survey reduced the abundance of medium and large cod by up to 50% in some years and was therefore retained for further analyses. The description of the bottom longline motivation and methods in McElroy et al. (2019) state that it was developed to match the sampling effort of the NEFSC bottom trawl survey as closely as possible. The bottom longline survey uses a 1 nautical mile groundline soaked for 2 hours across slack tide in an attempt to approximate the same sampling area of the NEFSC bottom trawl survey. The two surveys caught comparable numbers of cod per unit effort across all size classes and seasons (Fig. S1). For these reasons, the average area swept of the NEFSC bottom trawl survey was used as the input for the area swept of the bottom longline survey. It is likely that the true area sampled of the bottom longline survey varies with current velocity and other oceanographic conditions, but a longer time series and further calibration studies are needed to make a true quantitative determination.

**3.2.4 Spatial, temporal, and spatiotemporal effects**

Spatial, temporal, and spatio-temporal effects can be included in both linear predictors. A model selection process was used to justify the use of spatial and spatiotemporal random effects in the first and second linear predictors. The intercept for each linear predictor was defined as a fixed effect for each time step– this ensured independent estimates of abundance for each time step, which is most appropriate for creating abundance indices (Thorson 2019). A temporal correlation component was estimated for the spatio-temporal variation in both linear predictors. This is recommended for indices generated by multiple data sources that do not necessarily sample the same locations in every time step (Thorson 2019). Without this estimation, unrealistic “hot spots” may develop or be carried through the time series when this is inappropriate. Because the models include data from surveys with varied sampling intensity, locations, and temporal coverage, this is an important structuring decision.

The model used to estimate the temporal correlation component varied with size class. VAST models for small- and medium-sized cod included sufficient observation data to successfully fit an AR1 process. Attempts to use an AR1 process for the large size class failed to fit. A random walk process was used instead. For all size classes, the temporal correlation component was calculated for the first linear predictor. These results were used as the temporal correlation components of the second linear predictor, rather than calculating a new temporal correlation component for the second linear predictor.

**3.2.5 Vessel effects**

The random variation in catchability among levels of a grouping variable is referred to as “vessel effects” in the VAST model structure. VAST models covariation in vessel effects with a factor model, where variation in catchability between groups is a random effect. Each survey used in this modeling effort has its own set of sampling protocols and vessels, and these differences likely introduce variability in catchability. Therefore, vessel effects were included in the models. Multiple vessels were sometimes used to complete each survey, but most surveys did not specify the vessel used for each sampling event. Thus, we used the survey as the grouping variable rather than the vessel.

**3.2.6 Density Covariates**

VAST allows for the effects of both density and catchability covariates to be included in modeling efforts. Catchability covariates are processes that affect the ability to observe the target organism without necessarily affecting the distribution of the organism. Density covariates are processes that directly affect the distribution of the target organism, regardless of the ability to observe it. Both covariates affect the catch rate of the target organism, but only density covariates are used to predict target organism density within the spatial domain. Therefore, VAST “controls for” catchability covariates and “conditions on” density covariates. VAST is unable to distinguish whether potential covariates should be treated as catchability or density covariates; this must be decided with theoretical insight from an analyst. As mentioned previously, differences in sampling design were included as vessel effects, but explicit catchability covariates were not used.

**3.2.6.1 Environmental variables**

Several environmental variables were tested as potential density covariates. The final model only includes density covariates with significant impact, as determined by a model selection process outlined in section 3.3. Depth strongly influences the distribution and habitat use of Atlantic cod (Lough 2010; Guan et al. 2017b; Li et al. 2018; Linner and Chen 2022). Very few cod are found in waters deeper than 400 m, and the highest densities of cod are found between 10 and 150 m (Lough 2010). Depth at all survey locations was extracted from rasterized GEBCO 15 arc-second bathymetry (GEBCO Compilation Group 2023) and included as a potential density covariate.

There is evidence that cod habitat preferences include large-grain sediments like gravel, cobble, and boulders, making sediment type an important environmental covariate to consider when mapping spatial density (Gotceitas and Brown 1993; Gotceitas et al. 1995; Methratta and Link 2006; Lough 2010; Grabowski et al. 2018; Linner and Chen 2022). The spatial distribution of sediment types through the VAST model’s spatial domain was modeled by Brad Harris and Felipe Restrepo at Alaska Pacific University (Harris and Restrepo, pers. comm.). This model is an expansion of the New England Fishery Management Council Swept Area Seabed Impact (SASI) model, which used sediment observations from many sources to model and classify bottom habitats by sediment particle size (Bachman et al. 2011, 2019). The sediment classes were based on Wentworth (1922): mud, sand, gravel, cobble, and rock (Table S1). The sediment distribution model used an ordinary kriging approach to interpolate the probability of finding any of the five sediment classes within the cells of a 1 km by 1 km resolution grid with the same spatial extent as the VAST model.

There is further evidence that cod prefer habitats with high bathymetric relief, like boulders and steep ledges (Gregory and Anderson 1997; Cote et al. 2004). Bathymetric relief was characterized by rugosity, which is a unitless measure of bottom vertical change over horizontal distance. Using methods outlined in Friedman et al. (2012), rugosity was calculated from the 15 arc-second rasterized bathymetry data over the VAST model’s spatial domain. Rugosity at each survey location was extracted from the resulting rugosity raster.

The previous density covariates are spatially dynamic but temporally stationary. Cod distribution is also often temporally dynamic, as cod have seasonal migrations that likely reflect shifting water temperatures (Lough 2010; Zemeckis et al. 2017; Li et al. 2018). Sea surface temperature (SST) could affect spawning and recruitment success, and so was included as a potential density covariate (Planque and Frédou 1999; Drinkwater 2005; Fogarty et al. 2008; Pershing et al. 2015; Klein et al. 2017). Though most surveys measured and reported SST for every observation, the empirical dataset includes many missing SST values. VAST cannot tolerate missing values in density covariates and removing a large proportion of data was undesirable. Therefore, NOAA’s 1/4° spatial resolution daily Optimum Interpolation SST (OISST) data product was used to fill gaps. OISST daily rasters were pulled from NOAA data sources and SST was extracted at observation locations. OISST values were compared to field measurements, when available, and the two were found to be generally similar.

Bottom water temperatures likely also influence cod distribution and productivity (Drinkwater 2005; Methratta and Link 2006, 2007; Guan et al. 2017b). Models of bottom water temperatures within the NEUS continental shelf were provided by Du Pontavice et al. (2023). The bottom temperature within approximately 5-minute by 5-minute grid cells was calculated at a daily timestep for 1982 to 2020. Bottom temperature data were not modeled for 2021, the final year in the VAST model’s temporal domain. Instead, bottom temperature data from 2020 were used to fill this gap, as it was assumed that bottom temperature trends would remain similar between sequential years. Further, the bottom temperature product did not extend to the inshore areas within the modeled spatial domain. To resolve this limitation, bottom temperature was extrapolated to the shoreline using an ordinary kriging approach.

**3.2.6.2 Climate Indices**

Several climate indices have a relationship to cod recruitment and abundance, as they are associated with long-term warming (Pershing et al. 2015). For this model, North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO) index data were used as spatially static basin-wide climate indices. NAO is a measure of differences in atmospheric pressure at high and low latitudes of the North Atlantic and is expected to affect the intensity and location of wind patterns, heat transport, and moisture transport. AMO measures average anomalies of sea surface temperature in the North Atlantic basin. Data for both climate indices were publicly available in NOAA’s data repositories. Values for both climate indices were extracted for every survey observation at the best available temporal resolution, which was a daily timestep for NAO and a monthly timestep for AMO.

**3.3 Model selection**

The model selection process was conducted separately for each size class and consisted of two steps. The first step compared models with and without anisotropy and/ or spatial and spatiotemporal random effects in the linear predictors as in Ng. et al (2021) and Gaichas et al. (2023). These models did not include any density covariates. AIC was used to compare models, and restricted maximum likelihood (REML) was used in model construction to make comparison via AIC possible (Zuur et al. 2009). For all three size classes, the best model included anisotropy and spatial and spatiotemporal effects in both linear predictors (Table S2).

Before inclusion in model selection, potential density covariates were tested for collinearity. High correlations were found between two pairs: cobble and rock sediment probability, and OISST and bottom temperature. For the first collinear pair, rock sediment probability was removed, and cobble sediment probability was retained in the model. Grab and coring sampling methods (the bulk of sediment samples that support the sediment model) are unlikely to sample large-grain sediments like boulders effectively, and so the lower-quality data that feeds this model will inevitably result in a lower-quality and less reliable model of large-grain sediment distribution (Bachman et al. 2011). For the second pair of collinear variables, OISST was removed as it was expected that the distribution of groundfish like cod would be more directly affected by bottom temperature than sea surface temperature. Once these two collinear relationships were addressed, the remainder of density covariates were not correlated and therefore were tested for inclusion in the final model.

The second step in model selection was to select the most informative combination of potential density covariates. For each size class, a series of drop-one covariate models were run to assess covariate influence via AIC, as in Hansell et al. (2022). If AIC values were within 2 units of each other, the most parsimonious model was selected (Burnham and Anderson 2004). Results from the series of drop-one models for small cod indicated monthly AMO was not a significant density covariate, and so it was excluded from future small cod model runs. For the medium size class, all density covariates were retained. Models without AMO, bottom temperature, or predicted likelihood of cobble density covariates did not converge, highlighting their importance to modeling the spatial density of medium cod. Results from the large size class models indicated that the predicted likelihood of cobble, sand, and mud were not significant density covariates, and so they were excluded from future large cod model runs (Table S3).

**3.4 Final model, diagnostics, and derived quantities**

After the model selection process, the best selected models for all three size classes were run twice; once with Gaussian Markov Random Fields (GMRF) for enhanced fine-scale spatiotemporal interpolation turned on, and once with them turned off. The resulting centers of gravity from model fits were compared. Major differences between centers of gravity from models with and without GMRF turned on would indicate an important density covariate is not being explicitly modeled (Perretti and Thorson 2019; Hansell et al. 2022).

Final models were run with both GMRF and bias correction turned on. Models with bias correction use the “epsilon method” to ensure that the mean and variation of generated indices of abundance are not biased due to their transformation by a nonlinear function in the modeling process (Thorson and Kristensen 2016). Mapping residuals within the spatial domain did not highlight any spatial area as having a consistently poor fit (Fig. S2-S4).

After final model selection and assessment of diagnostics, seasonal maps of cod spatial density were generated for each size class. These maps are useful on their own to visualize changes in cod spatial density through space and time but can also be used to derive other measures of population and spatial dynamics. Resulting maps were used to derive spring and fall indices of relative abundance for all three size classes of cod, both for individual stock areas and for the entire NEUS population. Seasonal centers of gravity (COG) were also derived within each stock area and for the entire NEUS population. COG measures the density-weighted spatial location of the center of a population. Range shifts were quantified by the derivation of seasonal northeastern and southwestern range edges, represented by the 0.05 and 0.95 quantiles of cod distribution along the northing and easting axes, though these could only be calculated at the spatial scale of the entire modeled domain. It should be noted that the northeastern range edge is not a true quantification of the northern or eastern limits of cod populations in the Gulf of Maine, as the modeled spatial domain excludes significant cod habitats in Canadian waters. The distance between seasonal range edges along a directional axis (e.g., north-south, east-west) was calculated and used alongside range shift metrics as a measure of habitat compression or expansion. Together, these results could indicate whether changes in cod abundance are more likely due to spatial changes in productivity within a consistent range or range shifts. Finally, habitat associations were quantified via conditional response plots. Though these conditional response plots could only be derived for the entire modeled domain and without seasonal distinction, they helped identify which density covariates had the most influence on cod encounter and catch rates.

**4 Results**

For all size classes, the effect of anisotropy was stronger in the first linear predictor than the second, meaning that the encounter rate was similar for longer distances along a directional axis than the positive catch rate. The axis of anisotropy for all size classes generally ran southwest-to-northeast, indicating a greater degree of similarity along the NEUS coastline than along an inshore-offshore gradient (Fig. S5-S8).

**4.1 Small cod**

Small cod densities were highest in nearshore waters along the coast from Massachusetts Bay to Narragansett Bay, particularly in the spring time series (Fig. S6a). The spring index of relative abundance had high interannual variability and a sudden increase in 2003 but consistently indicated that the Western Gulf of Maine and Southern New England stocks contributed the most to the population (Fig. 2a). Stock-specific COGs indicated that changes in the distribution of cod within the Western Gulf of Maine stock had the most influence on the northing component of population COG, but changes in relative productivity between stocks likely influenced the easting component of population COG (Fig. 3a). Thus, spring population COG was typically located around Cape Cod, on the border of the Western Gulf of Maine and George Bank stocks. Spring population COG was highly variable throughout the time series, with no clear directional trend (Fig. 4a, 4g). Spring range edges were also highly variable (Fig. 5a, 5g). The southwestern range edge, represented by the 0.05 quantile of density-weighted distribution, has remained around the same north-south location since the 1990s, but oscillated east-west up to 85 km per year as the highest density patches shifted between Block Island Sound and Cape Cod Bay. The northeastern range edge, represented by the 0.95 quantile of density-weighted distribution, had rapid annual north-south and east-west shifts as relative productivity between the Eastern Gulf of Maine, Western Gulf of Maine, and Southern New England stocks changed. The distance between spring southern and northern range edges has had high interannual variability since 2002, with evidence of north-south range compression beginning in 2016 as the northern range edge has shifted south. The distance between the eastern and western range edges compressed by approximately 62 km from 1982 to 2002 as all stocks but the Western Gulf of Maine saw decreases in productivity. Since 2002, increased productivity near Cape Cod has led to an approximately 17 km increase in east-west range.

In the fall time series, small cod were present at highest densities in nearshore waters from Massachusetts Bay to the southern extent of Nantucket Shoals (Fig. S6b). Temporally ephemeral pockets of high density sometimes occurred at Cashes Ledge and in the waters between Grand Manan Island and Cutler, Maine. The fall index of relative abundance indicated that abundance was lower in the fall than in the spring, and the population has experienced two cycles of increase and decrease over the modeled period—abundance increased from 1982 to 1987, decreased until 1996, increased again until 2009, then rapidly decreased to the present day (Fig. 2b). The Western Gulf of Maine and Eastern Gulf of Maine stocks followed these trends and consistently contributed the most to the population, though the decline in the Western Gulf of Maine population in the final 10 years of the time series was much faster than the decline in the Eastern Gulf of Maine population. The Georges Bank stock contained a similar proportion of the population as the Eastern Gulf of Maine at the beginning of the time series but declined in the 1990s, and its abundance has been low since then. Most stock COGs shifted north and east over the time series (Fig. 3d). Fall population COG was typically located in the Western Gulf of Maine, with a clear northward shift over time (Fig. 4b, 4h). When calculated for the entire modeled spatial domain, population COG shifted on average 1.2 km/ year north. The east-west movement of the fall population COG was less clear, with a period of westward (inshore) movement between 1982-2008, then a rapid return eastward (offshore) from 2009-2019 (Fig. 4b, 4h). This likely reflects changes in relative productivity between stock areas—population COG was farther west when the relative proportion of the population within the Eastern Gulf of Maine was low, and farther east when the Eastern Gulf of Maine contained more of the population (Fig. 2b, Fig. 4b, 4h). Fall southwestern range edges remained in approximately the same place, while northeastern range edges have shifted north and east since the late 1990s as the Eastern Gulf of Maine stock has contained proportionally more of the population (Fig. 5b, 5h). The distance between the north and south range edges decreased by approximately 47 km from 1982 through 1999, and the distance between the east and west range edges decreased by approximately 83 km over the same period. As the proportion of the population within the Eastern Gulf of Maine increased after 1999, the distance between north-south range edges increased by 13 km and the distance between the east-west range edges increased by 142 km.

**4.2 Medium cod**

Model outputs for the spring time series indicated medium-sized cod were consistently present at relatively high densities in all but the deepest sections of the Gulf of Maine and Georges Bank (Fig. S7a). Notable patches of high density include Nantucket Shoals, Stellwagen Bank and Jeffreys Ledge, Cashes Ledge, and the Northeast Peak region of Georges Bank. The index of relative abundance revealed that the population size remained relatively consistent between 1994-2018 but declined to a time-series low in 2021 (Fig. 2c). The Western Gulf of Maine and Georges Bank stocks contributed an approximately equal proportion of medium-sized cod to the population and followed similar abundance trends, while the Eastern Gulf of Maine and Southern New England stocks slowly declined from the late 1980s to the late 1990s. The Southern New England stock abundance has since remained low, but the Eastern Gulf of Maine stock has slightly increased since 2014. The population COG has remained near the northwestern edge of the Georges Bank stock area for the entire modeled period but has consistently shifted north and east since approximately 2011 (Fig. 4c, 4i). The southwestern range edge movement matches that of the Western Gulf of Maine stock COG—consistent northward movement over the modeled period and eastward movement beginning in 2011, resulting in a northward displacement of nearly 75 km and eastward displacement of 30 km (Fig. 5c, 5i). The northeastern range edge has remained at approximately the same east-west location but shifted approximately 100 km south from 1982 to 2011, likely due to declining abundance in the Eastern Gulf of Maine stock. Since 2011, the northeastern range edge has rapidly returned to near its time-series northern extent. Range compressions and expansions matched trends in range edge shifts. The distance between the north and south range edges was consistent from 1982 to 1990, compressed by nearly 80 km from 1990 to 2010, and regained approximately 42 km from 2010 to 2021. The distance between the east and west range edges did not fluctuate as much; it varied little from 1982 to 2011 but compressed by approximately 29 km from 2011 to 2021.

Model outputs for the fall time series resulted in similar patterns of spatial density as that of the spring time series (Fig. S7b). The index of relative abundance was lower in the fall than in the spring and has generally declined since the early 1990s, with the time-series achieving its lowest abundance in 2021 (Fig. 2d). The Western Gulf of Maine and Georges Bank stocks have contributed the most to the population over the time series. Abundance of the Western Gulf of Maine stock was consistent until 2018, at which point it began to decline. Abundance of the Georges Bank stock has declined since the late 1990s. The Eastern Gulf of Maine stock began to decline in the late 1980s, with only a slight rebound beginning in the mid-2010s. The population COG has shifted northward from the northwestern edge of the Georges Bank stock area into the Western Gulf of Maine stock area since approximately 2010 (Fig. 4d, 4j). Fall stock-specific COGs were very similar to spring stock-specific COGs, both in location and directional trends (Fig. 3e). Fall range edges were also similar to spring range edges (Fig. 5d, 5j). Southwestern range edges remained at the same east-west location, but shifted more than 110 km north over the modeled period. Northeastern range edges shifted consistently south until 2011. The slight recovery of the Eastern Gulf of Maine population was likely the driving force behind a return of the northeastern range edge to near its time-series northern maxima by 2021. These range shifts resulted in a north-south range compression of 98 km between 1982 and 2011, with a recovery of only 62 km between 2011 and 2021. East-west range compression was less severe, with evidence of compression intensifying between 2011 and 2020.

**4.3 Large cod**

In the spring time series, large cod were present at highest densities at the Northeast Peak region of Georges Bank and around the edges of Wilkinson Basin on Stellwagen Bank, Jeffreys Ledge, and Cashes Ledge (Fig. S8a). The index of relative abundance peaked in 2003 and declined to a time-series low by 2021 (Fig. 2e). The Georges Bank stock has contributed the most to the population, followed by the Western Gulf of Maine stock. Both stocks have experienced similar trends in abundance over time. The population COG was typically in the area of Georges Shoal, halfway between the regions of high density. Population COG has moved consistently north and east since the early 1990s (Fig. 4e, 4k). The spring southwestern range edge shifted nearly 103 km northward over the time series and nearly 60 km eastward since 2011 (Fig. 5e, 5k). The northeastern range edge remained stationary in an east-west direction but shifted approximately 69 km south over the time series. This shifts resulted in a severe habitat compression; distance between the north and south range edges decreased by 171 km over the time series, and distance between the east and west range edges decreased by 133 km.

The density patterns of large cod in fall were similar to those in spring, but with lower density south of Cape Cod and in the shoals of Georges Bank (Fig. S8b). Abundance was lower in the fall than in the spring, with a peak abundance in 1989 and time-series low abundance in 2021 (Fig. 2f). Trends in abundance were strongly influenced by the Georges Bank and Western Gulf of Maine stocks. The Georges Bank stock increased in abundance through the early 2000s, after which point it began to decline. Interannual variability of the Western Gulf of Maine stock size was high but has not declined at the same rate as that of the Georges Bank stock, which increased its influence on population spatial dynamics in the later years of the time series. Trends in fall stock-specific COG movement were very similar to spring stock-specific COG movements (Fig. 3f). Fall range edges indicated a rapid northward population shift and compression; the southwestern range edge moved over 100 km north and the northeastern range edge moved 38 km south over the time series Range edges did not move in a consistent east-west direction over the time series. This resulted in a 130 km north-south habitat compression, with some evidence of east-west compression beginning in 2016.

**4.4 Habitat associations**

Depth, bottom water temperature, and the probability of encountering gravel were the most influential habitat covariates for all three size classes of cod for both linear predictors (Figs. 6-7). All size classes had a clear unimodal relationship between depth and presence rate (first linear predictor), with an optimum depth between 40 and 65 meters and a monotonically decreasing presence rate past the optimum (Fig. 6b, 6j, 6s). The relationship between depth and positive catch rate (second linear predictor) was inconsistent across size classes (Fig. 7b, 7j, 7s). Small cod positive catch rate was highest in extreme shallows and decreased rapidly until approximately 60m, after which the rate of decrease was slower. Medium cod positive catch rate was also highest in extreme shallows and decreased until approximately 320m, after which it slowly increased. It should be noted that samples are sparse in waters deeper than 320m (>0.08% of all data), so these results may not be accurate. Large cod positive catch rates did not fluctuate much with depth, though the optimum was at approximately 45m.

All size classes also had a clear unimodal relationship between bottom water temperature and presence rate, with optimum bottom temperature between 5.6 and 6.9°C and monotonically decreasing presence rate with warming bottom temperatures (Fig. 6a, 6i, 6r). There was a unimodal relationship between bottom temperature and positive catch rate for small cod, with optimum bottom temperature at approximately 7.7°C (Fig. 7a). Medium cod had a bimodal relationship between bottom temperature and positive catch rate, with local maxima at both ~1°C and ~10°C (Fig. 7i). Large cod positive catch rate was highest at approximately 1°C and decreased with increasing bottom temperatures (Fig. 7r). Few samples were taken in areas and times where bottom water temperature was below 2°C (> 0.15% of all data), so the relationship between linear predictors and temperature may not be accurate at these extreme cold temperatures.

The probability of encountering gravel had a monotonically positive relationship with presence rate across all size classes (Fig. 6c, 6k, 6t) and a monotonically positive relationship with positive catch rate for medium and large size classes (Fig. 7k, 7t). For small cod, areas with a probability of encountering gravel beyond 65% had a slight decrease in positive catch rate (Fig. 7c). The remaining habitat covariates had limited influence on the two linear predictors and generally inconsistent results across size classes.

**4.5 Unidentified drivers of spatio-temporal effects**

Seasonal population COGs for all size classes were compared with and without Gaussian Markov Random Fields (Fig. S9). Models for the small size class showed little difference in COGs between the two model types, implying that most major drivers of small cod COG variability are likely explicitly included in the models (Fig. S9a-b, g-h). The medium size class models consistently predicted COGs an average of approximately 20 km further east with GMRF turned on (Fig. S9i-j). There was also a temporal trend in the difference in northings between the GMRF On and Off models for this size class; in the first 20 years of the time series (1982-2001), GMRF On models predicted COG an average of 12-13 km farther north than the GMRF Off models. However, in the latter 20 years (2002-2021), this was reduced to only 2-3 km difference (Fig. S9c-d). These results suggested that much of the variability in COG for this size class was driven by sources not explicitly identified in the model, and that the unidentified driver may have a temporally variable influence. For the large size class, both GMRF On and GMRF Off models consistently showed a similar northward shift in population COG (Fig. S9e-f). However, eastings were not as consistent between models. This error also had a temporal trend, with smaller differences in the first 20 years of the time series than in the latter 20 years (Fig. S9k-l). This finding was particularly evident in the fall time series. Again, this indicated that the model does not explicitly incorporate at least one major driver of large cod seasonal COG variability, and that this unidentified driver may have temporally variable influence.

**5 Discussion**

Currently, groundfish population assessments rely heavily on data gathered with bottom trawl surveys. Despite evidence of increased cod abundance in areas with complex bottom habitats, locations with large-grain sediments or high rugosity are avoided or sampled at low frequency with bottom trawls due to the risks of damaging equipment. This is concerning to fishing industry stakeholders, who believe that limiting information from complex habitats will not accurately reflect cod spatial distribution or abundance (Grabowski et al. 2020). Sampling across all habitat types and utilizing dynamic stratification, in which areas of similar habitat characteristics and likelihood of encountering cod are grouped into strata for sampling and later inclusion in assessment efforts, would address this concern and enhance confidence in model estimates of fish stocks. However, these strata cannot be built without accurate information on cod spatial density for all habitats within their spatial range.

VAST models provide a flexible but robust framework to better assess groundfish populations across all habitat types within their spatial ranges. Here, VAST has allowed for the estimation of spatial, temporal, and spatiotemporal correlation of cod abundance, as well as the inclusion of vessel effects, to facilitate the combination of observation data from multiple sources with varied protocols. The model of cod spatial density created in this project utilized observation data from a suite of gear types and survey platforms, which bridged some of the data gaps inherent to models built with only bottom trawl survey data. Density covariates were used to interpolate cod spatial density in un- or under-sampled areas. The quality of model outputs is, in part, reliant on the quality of environmental and habitat data as density covariates. Though we used the best available data for density covariates, there is room for improvement in the confidence of underlying nearshore bottom water temperature data and sediment distribution data. Regardless, this modeling process may be better regarded by industry stakeholders than models built with only bottom trawl observation data.

VAST results highlighted the persistence of small patches with relatively high spatial density. Density values within these patches varied with population size but remained elevated as compared to the rest of the spatial domain. This is consistent with the basin model of geographic distribution theory, in which density-dependent habitat selection leads to distribution contraction into “optimal” habitats (as predicted by the optimal foraging theory and the ideal free distribution model, Fretwell and Lucas 1969) when populations are in decline (MacCall 1990). Atlantic cod stock distributions across regions, size ranges, and time periods have been identified as likely following density-dependent habitat selection processes, especially in periods of population decline (Swain and Wade 1993; Rose and Kulka 1999; Blanchard et al. 2005; Tamdrari et al. 2010; Pershing et al. 2015; Thorson et al. 2016; Li et al. 2018). It is likely that direct environmental forcing or behavioral mechanisms that support density-dependent habitat selection have condensed cod to spatiotemporally variable optimal habitat patches, and areas outside these patches are now less suitable for sustained occupation.

As abundance declines, density within these patches decreases at a much slower rate than in other areas, resulting in greater proportions of the overall cod population contained within these relatively small successful patches. The continued success of these patches despite declining overall population sizes is further evidence for the basin model, and hints at a source-sink dynamic where high-density patches are likely natal areas for cod that range more widely in the study area (Kritzer and Cadrin 2012). Genetic research has already identified many of these patches as important spawning grounds, which has informed the new stock structure utilized in management (Kovach et al. 2010; Zemeckis et al. 2014; Clucas et al. 2019; McBride and Smedbol 2022). Further analysis could determine the degree to which environmental forcing (through spatiotemporally dynamic conditions like bottom water temperatures) and intraspecific interactions shape cod distributions within each stock area.

Range shifts towards more northerly and deeper waters have been observed in many North Atlantic marine species (Perry et al. 2005; Nye et al. 2009; Pinsky et al. 2013; Fredston et al. 2021). These climate-mediated shifts are associated with range expansions and increases in abundance for some northwest Atlantic fishes like summer flounder (Nye et al. 2009) and George’s Bank stocks of haddock (Wang et al. 2024). For cod, model results generally indicate a northward and offshore shift in the population center of gravity, range contraction, and decline in abundance over the time series. These changes in spatial dynamics are occurring simultaneously with temperature-linked reductions in reproduction and growth (Planque and Frédou 1999; Drinkwater 2005; Fogarty et al. 2008; Pershing et al. 2015), which emphasizes the role of habitat preferences for colder waters in contributing to range contractions and decreasing abundance, particularly in the inshore and southern areas of cod’s spatial range.

Intense surface and bottom water warming signals within the Northeast US continental shelf 2008-2011 may have signaled a regime shift into warmer waters (Friedland et al. 2020). It should be noted that this period was frequently an inflection point for fall indices of abundance and COGs. Models without fine-scale interpolation were also less able to track rapid COG shifts beginning in this period. As the northwest Atlantic, and specifically the Gulf of Maine-Georges Bank ecoregion, warm at a rapid rate (Pershing et al. 2015), it should be expected that the spatial dynamics of cod will change rapidly. Thus, it is imperative that climate signals be included in population assessment methods. Model outputs indicate that a consequence of warming waters will be a condensed spatial distribution of cod into increasingly smaller patches of suitable habitat. Successful management efforts will need to consider the potential negative effects of reduced patch size and overall suitability of the Northeast US continental shelf under warming conditions to cod recruitment and survival. Environmental forcing may strongly affect the small size class, as its distribution is concentrated within shallow nearshore waters most vulnerable to increasing bottom water temperatures (Kavanaugh et al. 2017). The benthic characteristics and temperatures of high-density patches of small cod should be of particular concern to managers, as juvenile mortality rates have been hypothesized as more important to cod population growth than adult survival and fecundity (Wright 2014).

Several areas closed to groundfishing are among the persistent high-density patches. For example, large cod were consistently present at high densities in the Western Gulf of Maine Closed Area. Small cod were consistently present at high densities in nearshore waters within and around the Great South Channel Habitat Management Area. The continued decline of the population despite the creation of areas closed to fishing and increased fishing regulations points to a multitude of compounding problems beyond fishing alone. However, previous research has noted that even slight fishing pressure compounded with abiotic stressors will extend the rebuilding process (Pershing et al. 2015), and that fishing pressure may have increased selection for “sedentary” fish unlikely to colonize suitable habitats outside of closed areas (Sherwood and Grabowski 2010). The complicated interplay of cod population dynamics, stock structure, habitat preferences, and a dynamic environment make assessing the status of the population and enacting effective management very challenging. The results of this study are clear evidence that the needs and spatial dynamics of biological stocks and age classes are variable, and this must be accounted for when proposing measures to rebuild the population.

**Table Captions**

**Table 1** Description of the 11 surveys available to model groundfish spatiotemporal distribution. Included for each survey are details for gear type, cod biological stock areas covered by the survey (EGOM: Eastern Gulf of Maine, GBK: Georges Bank, SNE: Southern New England, WGOM: Western Gulf of Maine), years in which the survey was conducted, seasons in which the survey is conducted, and method of calculating area swept.

**Figure Captions**

**Figure 1** Spatial domain of cod VAST models with biological stock spatial strata (EGOM: Eastern Gulf of Maine, GBK: Georges Bank, SNE: Southern New England, WGOM: Western Gulf of Maine). Areas with year-round groundfishing closures are filled with crosshatches. Lines indicate the 50, 100, and 200 m isobaths, with darker lines representing deeper isobaths. Ecologically important regions are annotated on the map.

**Figure 2** Indices of relative abundance derived from model outputs. Results are reported in millions and separated by season (columns) and size class (rows).

**Figure 3** Spatial location of stock centers of gravity within the modeled domain. Maps were created using a WGS84 projection and UTM Zone 19N coordinate reference system. Stock area boundaries are represented by black lines; see figure 1 for more detail on each stock area. Results are separated by size class (columns) and season (rows). The southern portion of the Southern New England biological stock area is not represented so that more detail can be seen in center of gravity shifts. Darker, more saturated colors represent stock centers of gravity earlier in the time series and lighter, less saturated colors represent stock centers of gravity later in the time series. Red gradients represent the Eastern Gulf of Maine (EGOM), greens represent Georges Bank (GBK), blues represent Southern New England (SNE), and purples represent the Western Gulf of Maine (WGOM).

**Figure 4** Population centers of gravity over the time series. Population centers of gravity represent the center of cod size class- and season-specific density surfaces without considering the boundaries of biological stock areas. Results were calculated using a WGS84 projection and UTM Zone 19N coordinate reference system. Eastings are therefore reported as kilometers from the western edge of the reference frame, and northings as kilometers from the southern edge of the reference frame. Results are separated by season (columns) and size class (rows). Northings are reported in frames a-f and eastings are reported in frames g-l.

**Figure 5** Population range edges over the time series. Results were calculated using a WGS84 projection and UTM Zone 19N coordinate reference system. Eastings are therefore reported as kilometers from the western edge of the reference frame, and northings as kilometers from the southern edge of the reference frame. Results are separated by season (columns) and size class (rows). Northings are reported in frames a-f and eastings are reported in frames g-l.

**Figure 6** Conditional effects for density covariates on the first linear predictor (presence/ absence) within the a) small cod, b) medium cod, and c) large cod models. Conditional effects report the partial effects of each density covariate to linear predictors when all other density covariates are held fixed.

**Figure 7** Conditional effects for density covariates on the second linear predictor (positive catch rate) within the a) small cod, b) medium cod, and c) large cod models. Conditional effects report the partial effects of each density covariate to linear predictors when all other density covariates are held fixed.

**Supplementary Captions**

**Table S1** Substrate names, grain sizes, and Wentworth scale-based class names for substrate classifications in the sediment distribution model.

**Table S2** Parameters and AIC results for model structures tested for each size class. Delta AIC represents the difference between AIC values for the selected best model and all other models.

**Table S3** Parameters and AIC results for drop-one covariate models tested for each size class. Delta AIC represents the difference between AIC values for the selected best model and all other models.

**Figure S1** Range of seasonal catch (abundance) per unit effort across size classes for the NEFSC Bottom Longline Survey (NEFSC BLLS; red) and NEFSC Bottom Trawl Survey (NEFSC BTS; blue) during years in which both surveys were conducted (2014-2021).

**Figure S2** Spatial residuals (p-value) in each time step for the small cod VAST model grid. Results are split into spring and fall time series. P-values <0 and >0.1 are shown in a dark red to light red color gradient, and p-values <0.9 and >1.0 are shown in a light blue to dark blue color gradient. Maps were created using a WGS84 projection and UTM Zone 19N coordinate reference system.

**Figure S3** Spatial residuals (p-value) in each time step for the medium cod VAST model grid. Results are split into spring and fall time series. P-values <0 and >0.1 are shown in a dark red to light red color gradient, and p-values <0.9 and >1.0 are shown in a light blue to dark blue color gradient. Maps were created using a WGS84 projection and UTM Zone 19N coordinate reference system.

**Figure S4** Spatial residuals (p-value) in each time step for the large cod VAST model grid. Results are split into spring and fall time series. P-values <0 and >0.1 are shown in a dark red to light red color gradient, and p-values <0.9 and >1.0 are shown in a light blue to dark blue color gradient. Maps were created using a WGS84 projection and UTM Zone 19N coordinate reference system.

**Figure S5** Representation of anisotropic distances for a) small, b) medium, and c) large cod as compared to the model spatial domain. This is the distance necessary to achieve a 10% decline in correlation between sites for both linear predictor 1 (yellow) and linear predictor 2 (blue) along a directional axis. Anisotropic distances are represented here as ellipses, where the rotation of the ellipse is the direction of the major axis. Ellipses are arbitrarily centered at the centroid of the model spatial domain. Maps were created using a WGS84 projection and UTM Zone 19N coordinate reference system.

**Figure S6** Log-transformed spatial density for small cod at each modeled time step for a) spring and b) fall time series. Cooler colors (purples and blues) indicate lower spatial density and warmer colors (greens and yellows) indicate higher spatial density. Biological stock areas are outlined in black; see Figure 1 for the names of each biological stock area. Maps were created using a WGS84 projection and UTM Zone 19N coordinate reference system.

**Figure S7** Log-transformed spatial density for medium cod at each modeled time step. Cooler colors (purples and blues) indicate lower spatial density and warmer colors (greens and yellows) indicate higher spatial density. Biological stock areas are outlined in black; see Figure 1 for the names of each biological stock area. Maps were created using a WGS84 projection and UTM Zone 19N coordinate reference system.

**Figure S8** Log-transformed spatial density for large cod at each modeled time step. Cooler colors (purples and blues) indicate lower spatial density and warmer colors (greens and yellows) indicate higher spatial density. Biological stock areas are outlined in black; see Figure 1 for the names of each biological stock area. Maps were created using a WGS84 projection and UTM Zone 19N coordinate reference system.

**Figure S9** Population centers of gravity for all size classes of cod over the time series with (red) and without (blue) Gaussian Markov Random Fields (fine-scale interpolation between knots). Population centers of gravity represent the center of cod size class- and season-specific density surfaces without considering the boundaries of biological stock areas. Results were calculated using a WGS84 projection and UTM Zone 19N coordinate reference system. Eastings are therefore reported as kilometers from the western edge of the reference frame, and northings as kilometers from the southern edge of the reference frame. Results are separated by season (columns) and size class (rows). Northings are reported in frames a-f and eastings are reported in frames g-l.

**References**

Ames, E.P. 2004. Atlantic Cod Stock Structure in the Gulf of Maine. Fisheries **29**(1): 10–28. doi:10.1577/1548-8446(2004)29[10:ACSSIT]2.0.CO;2.

Bachman, M., Auster, P.J., Coakley, J., DePiper, G., Ford, K.H., Livermore, J., Packer, D., Quartararo, C., Stevenson, D., Valentine, P.C., Verkade, A., Restrepo, F., and Smeltz, T.S. 2019. Fishing Effects Model Northeast Region.

Bachman, M., Auster, P.J., Demarest, C., Eayers, S., Ford, K.H., Grabowski, J.H., Harris, B., Hoff, T., Lazzari, M., Malkoski, V., Packer, D., Stevenson, D., and Valentine, P.C. 2011. Omnibus Essential Fish Habitat (EFH) Amendment 2 Final Environmental Impact Statement Appendix D: The Swept Area Seabed Impact (SASI) approach.

Blanchard, J.L., Mills, C., Jennings, S., Fox, C.J., Rackham, B.D., Eastwood, P.D., and O’Brien, C.M. 2005. Distribution-abundance relationships for North Sea Atlantic cod (*Gadus morhua*): observation versus theory. Can. J. Fish. Aquat. Sci. **62**(9): 2001–2009. doi:10.1139/f05-109.

Burnham, K.P., and Anderson, D.R. 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociological Methods & Research **33**(2): 261–304. doi:10.1177/0049124104268644.

Clucas, G.V., Lou, R.N., Therkildsen, N.O., and Kovach, A.I. 2019. Novel signals of adaptive genetic variation in northwestern Atlantic cod revealed by whole‐genome sequencing. Evolutionary Applications **12**(10): 1971–1987. doi:10.1111/eva.12861.

Cote, D., Moulton, S., Frampton, P.C.B., Scruton, D.A., and McKinley, R.S. 2004. Habitat use and early winter movements by juvenile Atlantic cod in a coastal area of Newfoundland. Journal of Fish Biology **64**(3): 665–679. doi:10.1111/j.1095-8649.2004.00331.x.

Dean, M.J., Elzey, S.P., Hoffman, W.S., Buchan, N.C., and Grabowski, J.H. 2019. The relative importance of sub-populations to the Gulf of Maine stock of Atlantic cod. ICES Journal of Marine Science **76**(6): 1626–1640. doi:10.1093/icesjms/fsz083.

Dean, M.J., Hoffman, W.S., Buchan, N.C., Cadrin, S.X., and Grabowski, J.H. 2021. The influence of trawl efficiency assumptions on survey-based population metrics. ICES Journal of Marine Science **78**(8): 2858–2874. doi:10.1093/icesjms/fsab164.

Dean, M.J., and Perretti, C. 2022. Time-varying maturity in US cod stocks. Working Paper 12.

DeCelles, G.R., Martins, D., Zemeckis, D.R., and Cadrin, S.X. 2017. Using Fishermen’s Ecological Knowledge to map Atlantic cod spawning grounds on Georges Bank. ICES Journal of Marine Science **74**(6): 1587–1601. doi:10.1093/icesjms/fsx031.

Drinkwater, K.F. 2005. The response of Atlantic cod (*Gadus morhua*) to future climate change. ICES Journal of Marine Science **62**(7): 1327–1337. doi:10.1016/j.icesjms.2005.05.015.

Du Pontavice, H., Chen, Z., and Saba, V.S. 2023. A high-resolution ocean bottom temperature product for the northeast U.S. continental shelf marine ecosystem. Progress in Oceanography **210**: 102948. doi:10.1016/j.pocean.2022.102948.

Fogarty, M., Incze, L., Hayhoe, K., Mountain, D., and Manning, J. 2008. Potential climate change impacts on Atlantic cod (*Gadus morhua*) off the northeastern USA. Mitigation and Adaptation Strategies for Global Change **13**(5–6): 453–466. doi:10.1007/s11027-007-9131-4.

Fredston, A., Pinsky, M., Selden, R.L., Szuwalski, C., Thorson, J.T., Gaines, S.D., and Halpern, B.S. 2021. Range edges of North American marine species are tracking temperature over decades. Global Change Biology **27**(13): 3145–3156. doi:10.1111/gcb.15614.

Fretwell, S.D., and Lucas, H.D. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica **19**: 45–52.

Friedland, K.D., Morse, R.E., Manning, J.P., Melrose, D.C., Miles, T., Goode, A.G., Brady, D.C., Kohut, J.T., and Powell, E.N. 2020. Trends and change points in surface and bottom thermal environments of the US Northeast Continental Shelf Ecosystem. Fisheries Oceanography **29**(5): 396–414. doi:10.1111/fog.12485.

Friedman, A., Pizarro, O., Williams, S.B., and Johnson-Roberson, M. 2012. Multi-Scale Measures of Rugosity, Slope and Aspect from Benthic Stereo Image Reconstructions. PLoS ONE **7**(12): e50440. doi:10.1371/journal.pone.0050440.

Gaichas, S.K., Gartland, J., Smith, B.E., Wood, A., Ng, E., Celestino, M., Drew, K., Tyrell, A.S., and Thorson, J.T. 2023. Assessing small pelagic fish trends in space and time using piscivore stomach contents. Can. J. Fish. Aquat. Sci.: cjfas-2023-0093. doi:10.1139/cjfas-2023-0093.

GEBCO Compilation Group. 2023. GEBCO 2023 Grid. doi:10.5285/f98b053b-0cbc-6c23- e053-6c86abc0af7b.

Gotceitas, V., and Brown, J.A. 1993. Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. Oecologia **93**(1): 31–37. doi:10.1007/BF00321187.

Gotceitas, V., Fraser, S., and Brown, J.A. 1995. Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. Marine Biology **123**(3): 421–430. doi:10.1007/BF00349220.

Grabowski, J.H., Cadrin, S.X., Giacalone, V., Gouhier, T., Kerr, L.A., Odell, J., Pershing, A.J., Sherwood, G.D., Stokesbury, K.D.E., and Trussell, G.C. 2020. Strengths and Weaknesses of the Northeast Fisheries Science Center’s Bottom Trawl Survey.

Grabowski, J.H., Conroy, C.W., Gittman, R.K., Kelley, J.T., Sherman, S., Sherwood, G.D., and Wippelhauser, G. 2018. Habitat Associations of Juvenile Cod in Nearshore Waters. Reviews in Fisheries Science & Aquaculture **26**(1): 1–14. doi:10.1080/23308249.2017.1328660.

Gregory, R.S., and Anderson, J.T. 1997. Substrate selection and use of protective cover by juvenile Atlantic cod *Gadus morhua* in inshore waters of Newfoundland. Mar. Ecol. Prog. Ser. **146**: 9–20. doi:10.3354/meps146009.

Guan, L., Chen, Y., Staples, K.W., Cao, J., and Li, B. 2017a. The influence of complex structure on the spatial dynamics of Atlantic cod (*Gadus morhua*) in the Gulf of Maine. ICES Journal of Marine Science **74**(9): 2379–2388. doi:10.1093/icesjms/fsx064.

Guan, L., Chen, Y., and Wilson, J.A. 2017b. Evaluating spatio-temporal variability in the habitat quality of Atlantic cod (*Gadus morhua*) in the Gulf of Maine. Fish. Oceanogr. **26**(1): 83–96. doi:10.1111/fog.12188.

Hansell, A.C., Becker, S.L., Cadrin, S.X., Lauretta, M., Walter Iii, J.F., and Kerr, L.A. 2022. Spatio-temporal dynamics of bluefin tuna (*Thunnus thynnus*) in US waters of the northwest Atlantic. Fisheries Research **255**: 106460. doi:10.1016/j.fishres.2022.106460.

Johnston, R., and Sosebee, K. 2014. History of the United States Bottom Trawl Surveys, NAFO Subareas 4-7.

Kavanaugh, M.T., Rheuban, J.E., Luis, K.M.A., and Doney, S.C. 2017. Thirty‐Three Years of Ocean Benthic Warming Along the U.S. Northeast Continental Shelf and Slope: Patterns, Drivers, and Ecological Consequences. JGR Oceans **122**(12): 9399–9414. doi:10.1002/2017JC012953.

Kerr, L.A., Cadrin, S.X., and Kovach, A.I. 2014. Consequences of a mismatch between biological and management units on our perception of Atlantic cod off New England. ICES Journal of Marine Science **71**(6): 1366–1381. doi:10.1093/icesjms/fsu113.

Klein, E.S., Smith, S.L., and Kritzer, J.P. 2017. Effects of climate change on four New England groundfish species. Rev Fish Biol Fisheries **27**(2): 317–338. doi:10.1007/s11160-016-9444-z.

Kovach, A., Breton, T., Berlinsky, D., Maceda, L., and Wirgin, I. 2010. Fine-scale spatial and temporal genetic structure of Atlantic cod off the Atlantic coast of the USA. Mar. Ecol. Prog. Ser. **410**: 177–195. doi:10.3354/meps08612.

Kritzer, J., and Cadrin, S. 2012. Spatial Ecology of Atlantic Cod in the Gulf of Maine. Newburyport, Massachusetts.

Li, Z., Ye, Z., Wan, R., Tanaka, K.R., Boenish, R., and Chen, Y. 2018. Density-independent and density-dependent factors affecting spatio-temporal dynamics of Atlantic cod (*Gadus morhua*) distribution in the Gulf of Maine. ICES Journal of Marine Science **75**(4): 1329–1340. doi:10.1093/icesjms/fsx246.

Linner, R.M., and Chen, Y. 2022. Implications of stock structure in understanding juvenile Atlantic cod (*Gadus morhua*) habitat suitability in the Gulf of Maine. Regional Studies in Marine Science **54**: 102473. doi:10.1016/j.rsma.2022.102473.

Lough, R.G. 2010. Juvenile cod (*Gadus morhua*) mortality and the importance of bottom sediment type to recruitment on Georges Bank. Fisheries Oceanography **19**(2): 159–181. doi:10.1111/j.1365-2419.2010.00535.x.

MacCall, A.D. 1990. Dynamic geography of marine fish populations. University of Washington Press, Seattle, WA.

McBride, R.S., and Smedbol, R.K. 2022. An Interdisciplinary Review of Atlantic Cod (*Gadus morhua*) Stock Structure in the Western North Atlantic Ocean. NOAA Technical Memorandum.

McElroy, W.D., Blaylock, J., Shepherd, G.R., Legault, C.M., Nitschke, P.C., and Sosebee, K.A. 2021. Comparison of a bottom longline survey and a bottom trawl survey for 2 groundfish species in the Gulf of Maine to evaluate habitat-related availability of large fish. FB **119**(4): 231–242. doi:10.7755/FB.119.4.3.

McElroy, W.D., O’Brien, L., Blaylock, J., Martin, M.H., Rago, P.J., Hoey, J.J., and Sheremet, V.A. 2019. Design, Implementation, and Results of a Cooperative Research Gulf of Maine Longline Survey, 2014-2017. NOAA Technical Memo.

Methratta, E., and Link, J. 2006. Seasonal variation in groundfish habitat associations in the Gulf of Maine–Georges Bank region. Mar. Ecol. Prog. Ser. **326**: 245–256. doi:10.3354/meps326245.

Methratta, E.T., and Link, J.S. 2007. Ontogenetic variation in habitat association for four groundfish species in the Gulf of Maine–Georges Bank region. Mar. Ecol. Prog. Ser. **338**: 169–181. doi:10.3354/meps338169.

Ng, E.L., Deroba, J.J., Essington, T.E., Grüss, A., Smith, B.E., and Thorson, J.T. 2021. Predator stomach contents can provide accurate indices of prey biomass. ICES Journal of Marine Science **78**(3): 1146–1159. doi:10.1093/icesjms/fsab026.

Nye, J., Link, J., Hare, J., and Overholtz, W. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Mar. Ecol. Prog. Ser. **393**: 111–129. doi:10.3354/meps08220.

Perretti, C.T., and Thorson, J.T. 2019. Spatio-temporal dynamics of summer flounder (*Paralichthys dentatus*) on the Northeast US shelf. Fisheries Research **215**: 62–68. doi:10.1016/j.fishres.2019.03.006.

Perry, A.L., Low, P.J., Ellis, J.R., and Reynolds, J.D. 2005. Climate Change and Distribution Shifts in Marine Fishes. Science **308**(5730): 1912–1915. doi:10.1126/science.1111322.

Pershing, A.J., Alexander, M.A., Hernandez, C.M., Kerr, L.A., Le Bris, A., Mills, K.E., Nye, J.A., Record, N.R., Scannell, H.A., Scott, J.D., Sherwood, G.D., and Thomas, A.C. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science **350**(6262): 809–812. doi:10.1126/science.aac9819.

Peterson, C., and Black, R. 1994. An experimentalist’s challenge: when artifacts of intervention interact with treatments. Mar. Ecol. Prog. Ser. **111**: 289–297. doi:10.3354/meps111289.

Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L., and Levin, S.A. 2013. Marine Taxa Track Local Climate Velocities. Science **341**(6151): 1239–1242. doi:10.1126/science.1239352.

Planque, B., and Frédou, T. 1999. Temperature and the recruitment of Atlantic cod. Canadian Journal of Fisheries and Aquatic Sciences **56**(11): 2069–2077.

Rose, G.A., and Kulka, D.W. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. Canadian Journal of Fisheries and Aquatic Sciences **56**(S1): 118–127.

Serchuk, F.M., and Wigley, S.E. 1992. Assessment and Management of the Georges Bank Cod Fishery: An Historical Review and Evaluation. Journal of Northwest Atlantic Fishery Science **13**: 25–52. doi:10.2960/J.v13.a3.

Sherwood, G.D., and Grabowski, J.H. 2010. Exploring the life-history implications of colour variation in offshore Gulf of Maine cod (*Gadus morhua*). ICES Journal of Marine Science **67**(8): 1640–1649. doi:10.1093/icesjms/fsq094.

Swain, D.P., and Wade, E.J. 1993. Density-Dependent Geographic Distribution of Atlantic Cod (*Gadus morhua*) in the Southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **50**(4): 725–733. NRC Research Press. doi:10.1139/f93-083.

Tamdrari, H., Castonguay, M., Brêthes, J.-C., and Duplisea, D. 2010. Density-independent and -dependent habitat selection of Atlantic cod (*Gadus morhua*) based on geostatistical aggregation curves in the northern Gulf of St Lawrence. ICES Journal of Marine Science **67**(8): 1676–1686. doi:10.1093/icesjms/fsq108.

Thorson, J.T. 2018. Three problems with the conventional delta-model for biomass sampling data, and a computationally efficient alternative. Can. J. Fish. Aquat. Sci. **75**(9): 1369–1382. doi:10.1139/cjfas-2017-0266.

Thorson, J.T. 2019. Guidance for decisions using the Vector Autoregressive Spatio-Temporal (VAST) package in stock, ecosystem, habitat and climate assessments. Fisheries Research **210**: 143–161. doi:10.1016/j.fishres.2018.10.013.

Thorson, J.T., and Barnett, L.A.K. 2017. Comparing estimates of abundance trends and distribution shifts using single- and multispecies models of fishes and biogenic habitat. ICES Journal of Marine Science **74**(5): 1311–1321. doi:10.1093/icesjms/fsw193.

Thorson, J.T., and Kristensen, K. 2016. Implementing a generic method for bias correction in statistical models using random effects, with spatial and population dynamics examples. Fisheries Research **175**: 66–74. doi:10.1016/j.fishres.2015.11.016.

Thorson, J.T., Rindorf, A., Gao, J., Hanselman, D.H., and Winker, H. 2016. Density-dependent changes in effective area occupied for sea-bottom-associated marine fishes. Proc. R. Soc. B. **283**(1840): 20161853. doi:10.1098/rspb.2016.1853.

Thorson, J.T., Shelton, A.O., Ward, E.J., and Skaug, H.J. 2015a. Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for West Coast groundfishes. ICES Journal of Marine Science **72**(5): 1297–1310. doi:10.1093/icesjms/fsu243.

Thorson, J.T., Skaug, H.J., Kristensen, K., Shelton, A.O., Ward, E.J., Harms, J.H., and Benante, J.A. 2015b. The importance of spatial models for estimating the strength of density dependence. Ecology **96**(5): 1202–1212. doi:10.1890/14-0739.1.

Wang, Y., Gao, J., and McCurdy, Q. 2024. Density-dependent habitat selection and warming determine the spatial distribution of haddock (*Melanogrammus aeglefinus*) on Georges Bank. ICES Journal of Marine Science **81**(5): 961–971. doi:10.1093/icesjms/fsae054.

Wentworth, C.K. 1922. A Scale of Grade and Class Terms for Clastic Sediments. The Journal of Geology **30**(5): 377–392. doi:10.1086/622910.

Wright, P.J. 2014. Are there useful life history indicators of stock recovery rate in gadoids? ICES Journal of Marine Science **71**(6): 1393–1406. doi:10.1093/icesjms/fsu100.

Zemeckis, D.R., Liu, C., Cowles, G.W., Dean, M.J., Hoffman, W.S., Martins, D., and Cadrin, S.X. 2017. Seasonal movements and connectivity of an Atlantic cod (*Gadus morhua*) spawning component in the western Gulf of Maine. ICES Journal of Marine Science **74**(6): 1780–1796. doi:10.1093/icesjms/fsw190.

Zemeckis, D.R., Martins, D., Kerr, L.A., and Cadrin, S.X. 2014. Stock identification of Atlantic cod (*Gadus morhua*) in US waters: an interdisciplinary approach. ICES Journal of Marine Science **71**(6): 1490–1506. doi:10.1093/icesjms/fsu032.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.