NRHA Modeling Approach and Methods Overview

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Basic Rationale/Considerations

Our goal was to develop a comprehensive habitat modeling framework that could 1) be used to assess historical patterns of habitat use for marine species on the Northeast Shelf, and 2) be adapted to generate long-term projections of habitat use based on projected future climate scenarios.

While traditional species distribution models (SDMs) explain patterns of habitat use as a function of environmental predictors, other factors such as biotic interactions can give rise to correlations in the occurrence or abundance of species that are not explained by the environment. By modeling species environmental responses as well as their "residual" covariances in space and time, spatiotemporal joint SDMs (JSDMs) offer benefits over traditional, single species models that do not attempt to control for these factors. These gains can include less biased estimates of species environmental responses and/or the uncertainty around them, the pooling of information across species to improve parameter estimation (i.e., borrowing strength) and the resolution of underlying or "latent" gradients, and the option to predict joint occurrences and/or condition upon the occurrence states or abundances of other species, producing more realistic predictions of species assemblages. Finally, the residual correlations estimated by JSDMs (and/or the partial correlations derived from them) may provide insights on potentially important ecological processes, such as biotic interactions or unmeasured "missing" predictors.

Because basic ecological requirements, species interactions, and habitat use patterns can vary over ontogeny, we chose to model adults and juveniles of each species as distinct groups, based on length at maturity (when data was available).

Due to the dynamic nature of the marine environment, whenever possible we used time-varying measurements for covariates. Rather than including depth as a covariate, we instead sought to incorporate more ecologically-relevant correlates of depth, such as gradients in hydrodynamic stress or in the quality of underwater light, which can be linked mechanistically to organismal function.

Community-level basis function model (CBFM) – a novel approach to joint SDMs

Most existing implementations of joint SDMs represent adaptations of the latent variable model (LVM; Warton et al. 2015, Hui 2016, Ovaskainen et al. 2016) and employ a Bayesian framework that depends

on computationally expensive Markhov chain Monte Carlo (MCMC) sampling for parameter estimation. This computational burden is compounded in a spatio-temporal context, where the estimation of spatially and/or temporally structured latent fields means that model complexity scales rapidly with the number of observational units. As such, fitting spatiotemporal JSDMs to large datasets (such as ours) can involve processing times that make this approach largely impractical.

We (with collaborator Dr. Francis Hui at Australian National University and others) developed a novel approach to fitting JSDMs, the community-level basis function model (CBFM). In lieu of spatially structured latent variables, CBFM employs a pre-specified set of fixed spatial (and/or temporal) basis functions that are common (i.e., shared) across all species. Species' covariances in space, time, and with each other are then modeled via their respective basis function coefficients (i.e., weights or loadings), which are treated as random slopes drawn from a common distribution. This approach can be seen as a parallel of LVM but offers several advantages, including better scaling for datasets with many observations, because the "randomness" is integrated at the species, instead of observation, level. Additionally, the basis function approach relaxes assumptions about stationarity, so that the strength of correlations between two points in spacetime is not just a function of their distance from one another, but also their specific locations. Moreover, because the basis function approach is closely related to generalized additive models (GAMs), CBFM can model species responses to covariates as smooth terms, whereas most existing JSDM frameworks are limited to linear or quadratic/polynomials. This was particularly convenient in the context of NRHA, where the flexibility and data-driven nature of GAMS had made them a method of choice for single-species models, and permitted straightforward comparisons of the two. *REFER TO CBFM MS for additional information……*

Biological response data

We examined abundance data from the NMFS Spring & Fall Bottom trawl surveys for the time period between 2000-2019. This limited timeframe was selected because: (1) recent patterns of habitat use are likely the most informative/relevant for identifying habitat suitability at present or in the future, and, (2) prior to this period, data for many satellite-derived covariates are not available. For assessing out-of-sample predictive performance, the dataset was split, with 15 years used for training (2000-2014) and 5 years held out for testing (2015-2019). The model(s) included response data for NRHA species of

interest, as well as other dominant community constituents (i.e., those with high rates of occurrence) and taxa thought to constitute important prey for species of interest, based on the literature.

While calibration factors have been estimated (i.e., Miller et al. 2010) to account for the 2009 change in vessel and sampling gear from the RFV Albatross IV to the RFV Henry Bigelow, they do not exist for all species and are rarely stage specific. Moreover, in the case of presence-absence models, the calibrated data can induce false "absences" in samples where species were in fact present. To circumvent these issues, we used raw (un-calibrated) count data, estimating a species-specific (and stage-specific where appropriate) "VESSEL" effect to attempt to control for the gear change.

Stage-specific counts were generated using length information collected during the surveys along with estimated length at maturity data (L50s) collected from the literature. For a given tow, each observed length-class bin was classified as either "adult" or "juvenile", and then the counts for each applicable length-class bin were summed for each life stage. Finally, the proportion of measured individuals comprising each life stage was multiplied by the total abundance of each species to obtain stage-specific abundances.

When maturity information was not available for a given species, all individuals were treated as a single group. Likewise, if either life stage of a species had fewer than 500 nonzero counts, the two stages were pooled into a single group. Species with fewer than 500 nonzero counts altogether (i.e., across stages) were not considered in the model. Species were also assigned to functional groups based on water column use (i.e., demersal, pelagic, or benthic in the case of epifaunal or infaunal invertebrates).

Basic modeling framework

Because some species overlap in their use of demersal and pelagic habitats, members of both functional groups were combined in a single model. However, discrete models for demersal and pelagic communities are also being considered and would permit covariate sets to be more custom-tailored for each group (as the number of covariates that can be considered simultaneously in the model is limited). At present, the model includes 97 different species-stages. Benthic invertebrates (primarily molluscs and crustaceans) have not been included in the present model fits but will be added in future runs.

We also opted to combine the Spring and Fall survey data in a single model (instead of modeling each season separately). This was based on the reasoning that species' niches would be more completely

represented by observations spanning a broader range of environmental conditions. In the case of temperatures, this might be particularly important for long-term projections based on climate model outputs. Moreover, although a comparison has not yet been conducted for the latest round of model fits, comparisons of earlier fits indicated that the combined-season model performed comparably (as well or better) than single-season models for out-of-sample prediction.

Models were fitted to both binary presence-absence and abundance (count) response data. The overdispersed nature of counts and high proportion of zeros for some species necessitated a more flexible mean-variance relationship than that of the negative binomial error distribution, so we adopted a "hurdle" approach, modeling presence-absence with binomial error and then count conditional on presence using zero-truncated negative binomial error.

Species responses to continuous predictor variables were modeled as smooth terms using thin-plate regression splines, while the effect of vessel was modeled as a parametric term. In the presented models, the vessel effect is estimated for each species independently; however we are exploring the potential for drawing vessel effects randomly from a shared (i.e., species-common) distribution.

Spatiotemporal covariance was modeled using a tensor product of 30 multi-resolution thin-plate spline (MRTS) spatial basis functions and 3 temporal basis functions (gaussian) that were associated with month of the year (i.e., from 1-12). This allowed for observations falling closer together within a given year to be more closely correlated, helping to control for any seasonal variation that might not be accounted for by measured covariate. Meanwhile, longer-term (i.e., interannual) temporal variability was modeled via a species-specific random intercept for "year", which was drawn from a species-common (i.e., shared) distribution with mean-zero. We explored other alternatives for modeling time, including via an additional set of species-common temporal basis functions, and also as a tensor product (interaction) of spatial and long-term temporal (i.e. year) basis functions, however these more complex approaches tended to lead to overfitting and poorer out-of-sample prediction in both CBFM and single-species GAMs. We are in the process of exploring alternative approaches for modeling temporal covariation that include imposing an autoregressive structure on basis function coefficients and/or allowing them to vary over time.

As a point of comparison, we also fitted "stacked" single-species GAMs using the same covariate set, as well as stacked spatiotemporal GAMS which included a 2-d smooth on latitude and longitude and a

random intercept for year (more complex spatiotemporal structures did not improve out-of-sample prediction performance, and often hindered it).

Uncertainty in species responses to covariates is measured via 95% confidence intervals, with corresponding uncertainty in predictions quantified via 95% prediction intervals. If estimates of uncertainty are available for predictor variables, additional model runs that incorporate this uncertainty (by including the upper/lower bounds of predictors and iterating over different combinations thereof) can be conducted.

Covariates & Covariate Selection

Physicochemical covariates included the following:

Surface temperature (monthly mean)
Bottom temperature (monthly mean)
Surface salinity (monthly mean)
Bottom salinity (monthly mean)
Annual min surface temperature
Annual max surface temperature
Annual min bottom temperature
Annual max bottom temperature
Surface height anomaly (monthly mean)
Bottom stress (95th quantile, static)
PAR (at 0.5* depth - monthly mean, modeled as a tensor product with hue angle)
Hue angle (at 0.5* depth - monthly mean, modeled as a tensor product with PAR)

Temperatures, salinities, and sea surface height were obtained from the GLORYS 12v1 reanalysis (Jean-michel et al. 2021), which provides spatially and temporally continuous data at a spatial resolution of 1/12 degree (~ 9km) daily and corresponds closely to measured observations on the NE shelf (Chen et al. 2021). In addition to monthly mean surface and bottom temperatures and salinities, we also included long-term (annual) temperature extremes (i.e., min and max), which can be important drivers for many taxa (Morley et al. 2018). Sea surface height variations related to circulatory features such as fronts and eddies are often associated with productivity, making them a valuable predictor for many species as well (McHenry et al 2019). If desired, data from other circulation models (i.e., ROMS/HYCOM) could be

substituted here, and it may be worth performing some type of bias correction for these predictors, based on the instantaneous point measurements taken during NMFS surveys.

Sea Bottom Stress (95th quantile, annual) was sourced from the USGS Sea Floor Stress and Sediment Mobility database (Dalyander et al., 2012), with spatial resolutions ranging from 3.5 to 5 km. As time-varying data were not available, this was treated as a static variable. A measure of the strength of hydrodynamic forcing due to waves and currents at the seabed, bottom stress is a close correlate of water depth that has direct physical implications for locomotion, resource acquisition, and energetic costs of marine organisms, and may indirectly reflect other aspects of the benthic environment (e.g., epifaunal or infaunal community composition). Rather than a mean or median, we opted to use 95th quantile values to capture the magnitude of more extreme events, which are often more ecologically relevant determinants of habitat use (Denny et al. 2009).

Water column optical characteristics were estimated from remote sensing data with a horizontal resolution of 4km, following the methods of Lee et al. (2021) and Lee et al. (2005) for hue angle and photosynthetically-active radiation (PAR) at depth, respectively (in collaboration with Dr. ZhongPing Lee at UMass Boston). PAR measures the intensity of light (largely without regard for the spectral distribution), with high values indicating greater levels of illumination, such as those that would be experienced in clearer waters or shallower depths where attenuation by the water column is limited. Alternatively, hue angle quantifies the spectral distribution (i.e., the "color") of light, ranging from roughly 40 deg in shallow, "red" estuarine waters with high levels of dissolved and suspended substances, to 120 deg in oceanic surface waters, and up to 240 deg at the lower end of the photic zone in clear, deep "blue" oceanic waters.

Taken together, these two variables describe the basic quality of underwater illumination, which correlates closely with water depth but has much more direct ecological relevance. Vision is the primary sensory mechanism through which many marine organisms occupying the photic zone perceive and navigate their surroundings, identify resources or capture prey, and detect and avoid predators. The ocular systems of fish and invertebrates exhibit physiological specializations adapted to the intensity and spectral composition of light in the habitats they occupy (de Busserolles et al. 2017, Cortesi et al 2020). To capture the suitability of this "optical habitat", we modeled the interaction between PAR and hue angle via a tensor product smooth, producing a 2-D response surface.

Because most spectral attenuation (and consequently the change in light quality) occurs in the upper levels of the water column, near-surface and bottom values of hue angle, and to a lesser extent PAR, are correlated. To limit the number and collinearity of predictor variables, while also accommodating the fact that our model includes both demersal and pelagic functional groups, we estimated "generalized" optical parameters at the midpoint of the water column (i.e., 0.5 * depth). In the case of discrete demersal and pelagic models (where covariates could be more tailored to the functional group of interest), we estimated these parameters at some fixed near-surface depth (10m for pelagic species) or at the seabed (for demersals).

*Hue angle is closely correlated with remotely sensed Chlorophyll A concentration (a commonly used predictor variable), however exploratory analyses indicated that the former was more informative, and thus we opted to consider only hue angle.

*Benthic habitat characteristics related to substrates (e.g., sediment type or grain size) and topography (topographic position or complexity), can be important predictors for demersal species. These covariates are not included in the present model fits but can/will be in future runs.

Covariates with heavily skewed distributions were log-transformed, and all were standardized (centered and scaled) for numerical stability. Covariate selection is carried out during the model-fitting process, wherein an additional penalty associated with each smooth term serves to shrink the effect of any non-informative covariates to zero, effectively removing them from the model.

*Due to time constraints, the current model runs did not include the additional shrinkage penalty (which extends model run times considerably), however prior experimentation shows this has little to no effect on prediction.

Model Assessment

Out-of-sample prediction performance was assessed by training on 15 years of data (2000-2014) and extrapolating to 5 years (2015-2019). For presence-absence models, classification and discrimination performance were quantified using AUC and Tjur R^2, while predictive deviance and RMSE were used to assess error/precision. For count models, we used pseudo R^2 (the spearman correlation between predicted and observed counts) and RMSE.

PRELIMINARY RESULTS:

Model Checking

Residual checks indicate that with the exception of a few extreme values (~4 sds) overall distributional assumptions were met. There is evidence of a strong pattern for one species in the residual vs fitted values plot. Refer to PLOTS/MODEL_CHECKING to view.

Predictive Performance

Considered across the species pool, the CBFM presence-absence fit had somewhat greater classification (AUC) and notably better discrimation (Tjur R^2) performance than single-species spatiotemporal GAMS (and much more so than GAMS that did not consider space and time), with comparable levels of error (RMSE). The median AUC was 0.93 (ranging from 0.78 - 0.99), the median Tjur R2 was 0.50 (0.1 - 0.75), and median RMSE was 0.28 (0.09 - 0.42). Refer to PLOTS/MODEL_PERFORMANCE to view.

INSERT COUNT MODEL PERFORMANCE HERE….

For example species (Summer flounder and winter flounder):

Summer Flounder: AUC = 0.94 and 0.93, Tjur R2 = 0.62 and 0.30, RMSE = 0.34 and 0.22, for adults and juveniles, respectively.

Winter Flounder: AUC = 0.95 and 0.96, Tjur R2 = 0.66 and 0.65, RMSE = 0.30 and 0.26, for adults and juveniles, respectively.

ADD COMMUNITY-LEVEL PERFORMANCE METRICS HERE IF POSSIBLE…

Predictor Significance

Across the two models (P/A and count), no covariate was significant for fewer than 31 spp. In both models, optical parameters were significant for the greatest number of spp (92 and 75 spp, for P/A and count, respectively), followed by bottom shear stress (75 and 61 spp, respectively). Every species had at least 2 significant predictors. Refer to PLOTS/ALL_SPECIES/PREDICTOR_SIGNIFICANCE to view

Species Response to Predictors

Vessel effects were significant for 47 spp in the P/A model and 54 spp in the count model, and were reasonably similar (i.e.,correlated) across the two count models (Spearman's R = 0.75). The work of Miller et al 2010 indicate that the Henry Bigelow (HB) is generally more efficient than the Albatross (AL).

Consistent with this, the estimated effect of vessel (with AL being the baseline) was positive for the vast majority of species. There were, however, a few exceptions to this that require additional exploration. We are looking into the possibility of drawing vessel effects from a species-common, non-zero mean distribution which may enhance their estimation (they are presently estimated independently at the species level). To provide an additional point of comparison, we can also run equivalent fits omitting the vessel effect and using the pre-calibrated count data.

For smooth terms, the majority of estimated smooths appear reasonable and resemble the characteristic "niche" model (however there are some particularly "wiggly" smooths that deserve further exploration, and may require adjustments to wiggliness penalties, etc). Note that the tensor product for optical parameters (hue angle and PAR) is plotted as a 2-dimensional response surface, where PAR is on the Y axis and Hue angle is on the X axis, with the color gradient fill reflecting the overall effect magnitude. Higher values of PAR correspond with greater levels of illumination. Low hue angles typically indicate an optical environment on the "redder" (more estuarine or coastal) end of the spectrum, whie higher angles correspond to a "bluer" (more offshore) environment.

Refer to PLOTS/ALL_SPECIES/SPECIES_RESPONSE to view by predictor type (note the y-axis scale varies by sp. to exaggerate the shape of the response).

Refer to PLOTS/EXAMPLE_SPECIES/SPECIES_RESPONSE to view by species (note the y-axis scale is fixed so that effect magnitudes are comparable across predictors).

Variance Partitioning

Variance partitioning plots show the proportion of variance explained by each of the environmental predictor variables, by species.

Refer to PLOTS/ALL_SPECIES/VARIANCE_PARTITIONING to view plots for the entire community or PLOTS/EXAMPLE_SPECIES/VARIANCE_PARTITIONING to view subsets for summer and winter flounder.

Predictions

Visually, predictions of abundance were consistent with observations across the 20-year period, and appeared to resolve seasonal differences well.

Refer to PLOTS/EXAMPLE_SPECIES/PREDICTIONS to view

ADD PLOTS TO PLOTS/ALL_SPECIES/PREDICTIONS WHEN READY

Correlations

Residual correlations reflect the estimated residual covariance between species, or correlations in presence/absence or abundance that are not explained by species responses to the predictor variables. These may reflect the effects of missing predictor variables, dispersal processes, or biotic interactions. Partial correlations are obtained by inversion of the residual correlation matrix and control for indirect effects (e.g., if two species are positively correlated due to their shared negative correlations with another species) and therefore are considered to be a better indicator of "direct" biotic interactions. Still, correlations should be interpreted with caution/skepticism.

Across the community, the most noticeable general pattern is a tendency for strong positive correlations between adults and juveniles of the same species, which may reflect their common responses to unmeasured environmental variability but may also be indicative of dispersal processes/limitations..

Refer to PLOTS/ALL_SPECIES/CORRELATIONS to view the full matrices for the entire community

Refer to PLOTS/EXAMPLE_SPECIES/CORRELATIONS to view subsets for summer and winter flounder