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Integrating diverse marine predator data for robust species distribution models in a dynamic ocean

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Abstract

Species distribution models (SDMs) are an important tool for marine conservation and management, yet guidance on leveraging diverse data to build robust models is limited. We evaluated whether an integrated SDM (iSDM) framework outperforms traditional data pooling or ensemble approaches when synthesizing multiple data types. We trained traditional SDMs and iSDMs using three data types for the blue shark (*Prionace glauca*) in the North Atlantic: fishery-dependent marker tags, observer records, and fishery-independent electronic tags. We compared pooled and ensembled SDMs, built with boosted regression trees, to an iSDM explicitly designed to address data-specific biases while leveraging each dataset's strengths. While all approaches produced robust models, performance varied among data types, with fishery-dependent data consistently yielding more accurate than fishery-independent data. Differences in performance stemmed from models' abilities to capture spatiotemporal dynamics in training data. iSDMs accounting for seasonal variability yielded the most accurate estimates but were computationally intensive, emphasizing the need to align model purpose with integration methods. Our findings reveal key trade-offs in data integration methods, particularly in balancing predictive accuracy and feasibility. As diverse data sources grow, leveraging robust approaches will be vital for improving conservation and management strategies and understanding dynamic species distributions in a changing ocean.

Keywords: boosted regression trees; data integration; highly migratory species; integrated nested Laplace approximation; spatiotemporal dynamics; species distribution models

Introduction

Species distribution models (SDMs) have become a standard tool within ecology to understand species' responses to changing environmental conditions (Guisan and Thuiller 2005, Araújo and Luoto 2007). In the marine environment, SDMs play a key role in conservation and resource management by providing critical insights on species' spatiotemporal distributions that are used to understand habitat use, connectivity, and range shifts in the context of various anthropogenic stressors (Guisan and Thuiller 2005, Robinson et al. 2017). However, recent technological advancements have greatly expanded the volume of data available for SDM training, and, with that, efforts to mobilize more diverse data types (Isaac et al. 2020). For highly mobile species, there are key questions regarding how to combine disparate data sources that often represent only a specific life stage or migration mode within the broader species' distribution (Fletcher et al. 2019, Isaac et al. 2020, Karp et al. 2023). In marine systems, diversity in species occurrence data primarily stems from fishery-dependent or fishery-independent data sources. Spatially referenced fishery-dependent data provide abundance and occurrence information as a product of fishing activity, often in the form of vessel catch logbooks, onboard observer programs, or mark-recapture sampling (Kohler and Turner 2018, Crear et al. 2021). In contrast, fishery-independent data are predominantly collected through surveys that are explicitly designed to minimize biases in estimates of species' abundance (e.g. ship-based hook or net surveys, visual aerial transects) or as part of scientific research projects such as electronic tagging efforts to track movements of free-swimming animals (e.g. acoustic, archival, and satellite tags; Block et al. 2011).

While each data type provides valuable information about the distribution of a species and the biotic and abiotic processes associated with their distributions, all are subject to sampling biases (e.g. gear selectivity, differing spatial, and/or temporal extents; Fithian et al. 2015). For an SDM using a single data type, model outputs will reflect these biases which can result in skewed predictions of species distributions and lead to erroneous mitigation and conservation measures (Pennino et al. 2019, Karp et al. 2023). For example, SDMs created from fishery-dependent observations can reflect fishery-interaction probability rather than true habitat suitability due to the preferential sampling inherent in fishing activity (*sensu* Crear et al. 2021, Karp et al. 2023). Similarly, data from fisheries-independent surveys may only sample a fraction of the distribution of highly migratory species whose movements often span ocean basins and exceed the scope of typical surveys (Paradinas et al. 2023).

Various methods have been proposed to build modeling frameworks that can integrate different data types, i.e. data pooling, ensemble modeling, and joint likelihood approaches (Fletcher et al. 2019, Rufener et al. 2021, Braun et al. 2023b). Data pooling and ensemble modeling techniques have been widely applied for marine species (Oppel et al. 2012, Pikesley et al. 2013, Abrahms et al. 2019, Braun et al. 2023b) and involve either combining data from multiple sources to produce an aggregated dataset for subsequent modeling (i.e. pooling) or averaging predictions from multiple models (i.e. ensembles). In marine ecosystems, where data can vary in quality and be limited in spatial and temporal coverage, combining data sources can be a valuable way to better represent the spectrum of a species' ecology and realized niche as they can leverage advantages inherent in each dataset (e.g. sample size; Braun et al. 2023a). However, despite the relative success of pooling and ensemble approaches to overcome biases inherent in individual models fitted to a particular data type (Braun et al. 2023b), both have their limitations as they lack the capability to explicitly account for uncertainty across datasets or share derived animal-environment relationships across models.

Recently, model-based data integration—termed integrated species distribution models (iSDMs)—has emerged as a means to combine datasets in ways that retain the strengths of each and may lead to more robust models and realistic ecological inference (Fletcher et al. 2019, Isaac et al. 2020). This includes joint likelihood approaches, which facilitate simultaneous modeling of different data sources while explicitly accounting for the differences in the underlying sampling processes (Isaac et al. 2020). These approaches enable a formal integration of different data that can share information across datasets, such as species-environment relationships, regardless of the type of data (e.g. occurrence, abundance; Paradinas et al. 2023). Many joint likelihood approaches are also spatially explicit, in that they formally account for spatial autocorrelation in the data which can be estimated for each data type and shared across models (Simmonds et al. 2020, Ahmad Suhaimi et al. 2021, Barber et al. 2021). Furthermore, joint likelihood approaches have been shown to achieve greater predictive performance when compared to other integration techniques (i.e. data pooling or ensemble modeling; Paradinas et al. 2023) or to models fitted to a single data type (Simmonds et al. 2020). Despite these advantages, iSDM applications in marine systems have been limited, likely due to their complex structure and requisite intensive computational resources (Lezama-Ochoa et al. 2020, Stock et al. 2020).

To date, there have been limited comparative efforts that investigate the predictive performance across different integration modeling approaches using empirical data (Barber et al. 2021, Rufener et al. 2021). With increasing data availability for highly migratory species, quantitative comparisons of modeling approaches are crucial and should use appropriate model performance metrics while ensuring ecologically realistic environmental relationships and predictions. Here, we compare four integration techniques with SDMs built for a heavily-exploited pelagic fish species, the blue shark (*Prionace glauca*), in the North Atlantic. We use fishery-dependent marker tags, fishery observer records, and fishery-independent electronic tag data to fit four integrative modeling approaches in a comparative framework. We then assess model performance and identify tradeoffs among predictive skill, ecological realism, and computational demand associated with each approach to provide insight on how to best leverage diverse data types for modeling species distributions.

Methods

Occurrence data

To assess the performance of different integrated modeling approaches, we used three occurrence datasets for blue sharks in the North Atlantic (Fig. 1), as outlined in Braun et al. (2023a). These datasets consisted of two fishery-dependent data sources, marker (e.g. conventional or "spaghetti") tags and fisheries observer data, along with one fishery-independent data source (i.e. electronic tags). Blue shark marker tag data were obtained from the International Commission for the Conservation of Atlantic Tunas (ICCAT) Secretariat tag database (Ortiz et al. 2023), which is a product of multiple national tagging programs, both scientific and opportunistic, involving commercial and recreational fisheries since 1959 (Kohler and Turner 2018, Ortiz et al. 2023, Braun et al. 2023b). This dataset provides presence observations of tagged blue sharks upon release (Kohler and Turner 2018, Braun et al. 2023b) and an additional presence if the individual was subsequently recaptured (Kohler and Turner 2018). The majority of marker tag releases came from rod and reel gear associated with recreational fisheries (71%), followed by commercial longline fisheries (24%). In contrast, most blue shark recaptures were from longline fisheries (57%), with rod and reel accounting for 36%, and an overall recapture rate of 7.61% since 1959. Although majority of blue shark occurrences in the marker tag dataset came from recreational rod and reel gear, biasing observations toward the Northeast US continental shelf in the summer, releases and recoveries also occurred across the main footprint of the longline fleet in this region (Kohler and Turner 2018, Braun et al. 2023b). The second fishery-dependent dataset represents catch data from the US pelagic longline observer program, which has been in place since the early 1990s, spanning from the Grand Banks to the equator (Larkin et al. 2000, Crear et al. 2021). The observer data consists of set-level catch information of blue sharks within the spatial extent of the fishery. To align with the temporal extent at which environmental data were available (see below), both fishery-dependent datasets were filtered to retain records between 1993 and 2019.

Fishery-independent data consisted of electronic tags deployed on 107 individuals across the North Atlantic from 2006 to 2018 (Fig. 1). Two types of electronic tags were used to track blue shark movements: satellite-linked tags (model

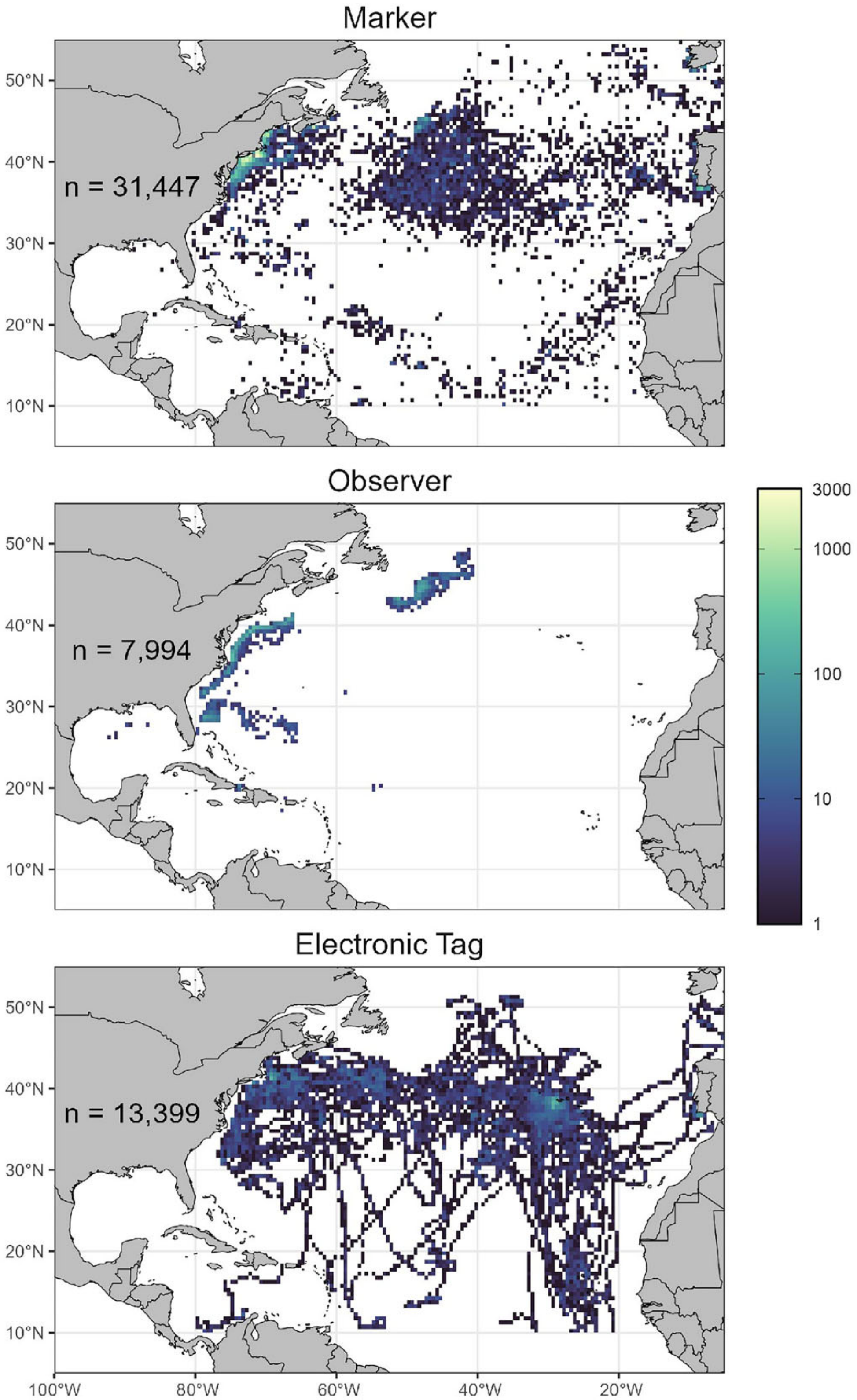

Figure 1. Presence locations for the marker tags (1993–2019), fishery observer data (1993–2019), and the electronic tag data (2006–2018). Note that to protect confidentiality, grid cells for the fishery observer data that contained <3 vessels were removed.

SPOT, Wildlife Computers) and pop-up satellite archival transmitting tags (models PAT and miniPAT, Wildlife Computers). While the magnitude of uncertainty in position estimates varies between tags types (Winship et al. 2012), Braun et al. (2023a) demonstrated SDMs fit separately to each type of tag data exhibited negligible differences in model performance. Therefore, electronic tag data were aggregated to form a single data type in this study. Additional descriptions of the three data sources and details on quality control and filtering are given in the Supplementary Material.

Environmental data

We included three environmental variables as covariates in the models that have previously been shown to be important drivers of habitat use for blue sharks (Braun et al. 2023b): sea surface temperature ("SST"; °C), the spatial standard deviation of SST ("SST_sd"; an index of frontal activity and calculated over a 0.25° resolution), and bathymetry (m). Dynamic surface environmental variables (SST and SST_sd) were sourced from the Global Ocean Physics Reanalysis (GLORYS; Lellouche et al. 2018), a high resolution (1/12° and daily outputs) data-assimilating ocean model served through the Copernicus Marine Environmental Monitoring Service (DOI: https://doi.org/10.48670/moi-00021). GLORYS outputs were averaged to a monthly temporal resolution. The static bathymetry variable was sourced from ETOPO1 (https://www.ngdc.noaa.gov/mgg/global/global.html) at 1-min resolution. Environmental data were extracted for the presence and pseudo-absence (discussed below) locations and times for each data type. To account for location uncertainty inherent in electronic tag data (e.g. Braun et al. 2018), the environment was sampled around each recorded presence by averaging each environmental variable within the estimated location ± the 95% confidence interval surrounding that location (Braun et al. 2023b). All environmental grids used the GLORYS native spatial resolution (1/12°).

Species distribution models

Blue shark monthly habitat suitability was modeled for each model integration approach as a function of environmental variables using traditional SDM modeling frameworks (i.e. spatially implicit) and Gaussian field models that estimate a spatial process across the study domain (i.e. spatially explicit). Here, spatially implicit and explicit models were fitted with boosted regression trees (BRTs) and the integrated nested Laplace approximation (INLA), respectively. Although the models differ conceptually, both have demonstrated strong predictive performance in modeling the distributions of marine fishes (Brodie et al. 2020, Lezama-Ochoa et al. 2020, Stock et al. 2020, Braun et al. 2023a). BRTs are among the most widely used algorithms for modeling species distributions, valued for their ease of use and ability to handle complex ecological data (Rubbens et al. 2023). BRTs combine the strengths of tree-based models and boosting to optimize partition of variance, which allow them to be highly flexible. Additionally, they are not subject to caveats of commonly used (semi-)parametric statistical models as they are robust to outliers, missing data, collinearity among environmental variables, and the inclusion of irrelevant variables (Elith et al. 2008). Statistical models (e.g. Gaussian field models), however, initially rely on assumptions about the distribution of the underlying data as well as the relationship between the response variable and environmental covariates. A key distinction between BRTs and INLA is how they address spatial and spatiotemporal autocorrelation, which may arise when environmental covariates in the model do not account for all the underlying processes driving species distributions. BRTs do not inherently reduce spatial autocorrelation, but instead focus on improving model fit by sequentially fitting trees to the residuals of previous models, allowing them to capture complex, non-linear relationships in the data (Elith et al. 2008). In contrast, INLA explicitly addresses spatial and spatiotemporal autocorrelation by approximating Gaussian fields as discrete Gaussian Markov random fields (GMRFs; Lindgren et al. 2011), which are incorporated as random effects. The GMRF acts as a spatial or spatiotemporal smoother and reflects the assumption that nearby locations are more similar than distant locations (Lindgren et al. 2011). While the models compared here differ in complexity, this reflects an intentional design choice to contrast a widely used SDM approach (i.e. BRTs) with a more flexible, integrative framework (i.e. iSDM using INLA). This comparison highlights the practical benefits and trade-offs associated with increased model complexity—including the use of joint likelihoods, spatial structure, and dynamic temporal effects—rather than isolating any single difference between model infrastructure.

Much of the recent development in iSDMs have supported applying a Poisson point process modeling (PPM) framework as it provides a flexible approach that can link presence-only occurrence and abundance data (Fletcher et al. 2019, Isaac et al. 2020, Rufener et al. 2021). While statistically sound, PPMs are better suited for predicting distributions over large temporal scales (i.e. climatology over the study period; Isaac et al. 2020). Yet, it is often necessary in marine resource and conservation management to predict mobile species distributions at finer temporal scales (ranging from days to months; Lewison et al. 2015). To solve this, we adopt dynamic SDM approaches that incorporate simulating location data where individuals were likely absent (i.e. "pseudo-absences"), which have been extensively employed in modeling the distributions of pelagic species to capture and predict their dynamic habitat use at fine temporal scales (Barbet-Massin et al. 2012, Hazen et al. 2021). Pseudo-absences were sampled using the background sampling method by randomly drawing, without replacement, from within climatological monthly convex hulls of each dataset (Farchadi et al. 2024). Although the observer data includes observed fishing effort when blue sharks were not detected (i.e. recorded as "absences"), previous studies have demonstrated background sampling results in higher predictive skill and improved ecological realism relative to other pseudo-absence techniques (Hazen et al. 2021), including when compared to using true absences fishery observer data (Braun et al. 2023b). Pseudo-absences were generated for each month, creating a 1:1 presences: pseudo-absences ratio for each dataset, which is consistent with what is recommended in the literature for each model type (Warton and Shepherd 2010, Barbet-Massin et al. 2012, Hazen et al. 2021). To assess the influence of uneven sample sizes on model performance, each integration approach was modeled using both the full datasets and a downsampled version in which each dataset was matched to the smallest sample size (i.e. observer data). This allowed us to evaluate whether observed differences in predictive skill and ecological realism were attributable to dataset size rather than true model differences. Each integration modeling approach was built with the binary response variable of presence: pseudo-absence using a Bernoulli family distribution and logit link function to model the probability of blue shark presence. To ensure that seasonal variation in distribution was captured without constraining ecological relationships to narrow temporal windows, we modeled all months together for each modeling framework. This approach is particularly well suited for highly migratory species like blue sharks, whose movements span broad spatial and temporal scales throughout the year, and aligns with emerging best practices for modeling dynamic marine species distributions to support conservation and management (Hazen et al. 2018, Crear et al. 2021, Welch et al. 2023).

Data pooling and ensemble modeling

For the data pooling approaches, models were trained on a combination of blue shark presences across all three data types and corresponding pseudo-absences. This results in a single model that combines inferences across all the datasets but assumes that the nature of the data is the same across all sources (Fletcher et al. 2019, Paradinas et al. 2023). In contrast, ensemble modeling combined predictions across data-specific models, which allow the separate models to explicitly account for data uncertainties but lack the capability to "learn" environmental relationships across individual models or account for variability among data types (Fletcher et al. 2019, Paradinas et al. 2023). For ensemble modeling, independent models were fitted to each blue shark dataset separately and then equal-weighted, mean model ensembles were created that averaged across the predictions from each of the three data-specific models. Both approaches were fitted with BRTs and were configured with a tree complexity of 5, bag fraction of 0.75, a learning rate of 0.005, and 2000 trees, following Braun et al. (2023a). Although hyperparameter tuning is recommended in order to identify optimal values that maximize predictive skill and minimize overfitting (Elith et al. 2008), hyperparameters were fixed to isolate the effects of the different integration approaches and data types. The resulting models from both approaches describe species-specific "habitat suitability" as continuous values ranging from 0 (low habitat suitability) to 1 (high habitat suitability). All data pooling and ensemble models were fitted with the *gbm.fixed* function in the "dismo" R package (Hijmans et al. 2021).

Joint likelihood modeling

To formally integrate the three different data sources into a single model (i.e. iSDMs), we applied joint likelihood approaches using approximate Bayesian inference through INLA (Rue et al. 2009). INLA provides a computationally efficient alternative to traditional types of Bayesian inference as it uses the stochastic partial differential equation (SPDE) approach to model the underlying spatial process by approximating GMRFs with a Matérn covariance (Lindgren et al. 2011). For these iSDMs, each data source directly informed blue shark habitat suitability through shared parameters in a jointly-estimated likelihood. The general structure of the iSDMs included shared effects for three environmental covariates and the GMRFs. The iSDM for logit-transformed probability of presence of blue shark at location s and time t with data type i ($\eta_{s,t,i}$; note e, m, or o for electronic tag, marker, or observer data, respectively), are as follows, where $s \in S$ is a location in the study area S:

$$\begin{aligned}
\eta_{s,t,e} &= \alpha_e \ + \ f_e\left(SST_{s,t}\right) + f_e\left(SST_{sd_{s,t}}\right) + f_e\left(Bathymetry_{s,t}\right) \\
&\quad + \omega\left(s,t\right), \\
\eta_{s,t,m} &= \alpha_m \ + \ f_m\left(SST_{s,t}\right) + f_m\left(SST_{sd_{s,t}}\right) + f_m\left(Bathymetry_{s,t}\right) \\
&\quad + \gamma_1\omega\left(s,t\right), \\
\eta_{s,t,o} &= \alpha_o \ + \ f_o\left(SST_{s,t}\right) + f_o\left(SST\_sd_{s,t}\right) + f_o\left(Bathymetry_{s,t}\right) \\
&\quad + \gamma_2\omega\left(s,t\right).
\end{aligned}$$

Here, each a refers to to data-specific intercept terms for each linear predictor in the model. The functions $f(SST)$, $f(SST\_sd)$, $f(Bathymetry)$ are shared effects for the three environmental covariates. To allow for possible non-linear relationships, all environmental covariates were modeled using SPDE. This smoothing approach is the same as estimating GMRFs in INLA, however, the covariates' effect is modeled using a Matérn covariance in one dimension (i.e. 1D SPDE; Lindgren et al. 2011). Furthermore, ω is the GMRF describing spatial and spatiotemporal autocorrelation over the study area and is jointly estimated across all three likelihoods. This field is shared across the marker and observer datasets through dataset-specific scaling parameters (γ_1 and γ_2, respectively). Although ω is introduced in the electronic tag model, its estimation is informed by all three datasets through the joint likelihood, allowing each source to shape the shared spatial structure based on its contribution to model fit. This structure follows previous implementations of iSDMs in predator-prey contexts (Barber et al. 2021), where fishery-independent data representing prey (e.g. blue shark) inform predator distribution models (e.g. fishing fleet). In our case, we assume that the spatial dynamics captured by the electronic tags reflect ecological processes that are also relevant to explaining the distribution of blue shark occurrence in the fishery-dependent datasets.

We fitted two iSDMs that explicitly accounted for the temporal process within the GMRFs: one model maintained a constant time spatial effect (iSDM Constant), while the other incorporated seasonally varying spatial effects (iSDM Seasonal). The iSDM Constant model was fitted with a single shared GMRF that is constant across all seasons and years of the training data. The iSDM Seasonal model, however, was fitted with four shared GMRFs, each accounting for the seasonal spatial autocorrelation in the training dataset. Seasonal GMRFs were categorized as fall (September–November), winter (December–February), spring (March–May), and summer (June–August) and followed a cyclic first order autoregressive spatiotemporal structure (AR1) where adjacent seasons (e.g. winter and fall) are more correlated than distant seasons (e.g. winter and summer). All models were fitted through the "inlabru" R package. As no prior information was available, we used default Matérn smoothness ($\nu = 1$) and default Gaussian priors on the hyperparameters that govern the range and marginal standard deviation of the SPDEs (Bachl et al. 2019). These priors are internally determined based on the mesh geometry to provide broad applicability in the absence of strong prior information. Specifically, the prior for the range is centered to correspond to ~20% of the mesh extent, while the prior for the marginal standard deviation is centered around one, with fixed precision of 0.1 (i.e. variance = 10), resulting in weakly informative priors tuned to the spatial scale of the model.

Model performance analysis

We compared the performance of each modeling approach using three metrics: *predictive skill*, *ecological realism*, and *computational demand*. Quantitative metrics were calculated using a 5-fold cross-validation with randomly assigned 80% training—20% testing splits for each fold, repeated 10 times and evaluated across the three metrics. *Predictive skill* denotes the ability of a model to accurately predict the presence or absence of a species on new test data, which were not included in

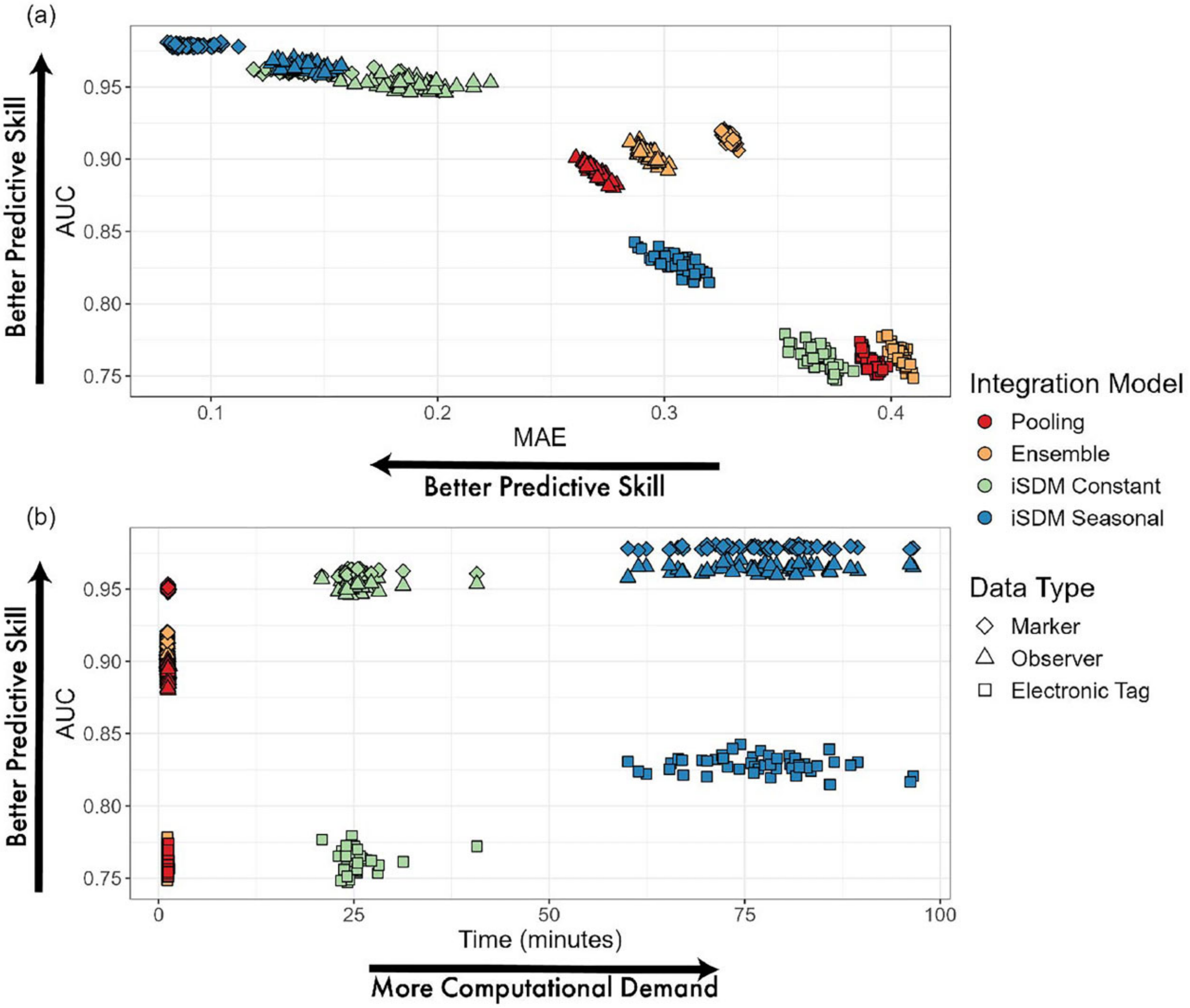

Figure 2. Model performance comparison across: (a) predictive skill and (b) computational demand. Points represent metrics measured for each data type during cross-validation testing iterations within integration models.

the model's training. Predictive skill was assessed using both the Area Under the receiver-operating Curve (AUC) and mean absolute error (MAE). The combined use of AUC and MAE have been recommended for evaluating SDMs as they offer complementary insights into the model's performance while addressing potential limitations associated with their individual calculation assumptions (Konowalik and Nosol 2021). For each iteration of the cross-validation, predictive skill metrics were measured against the entire testing dataset as well as each data type separately to explore the robustness of the model across data sources. We tested the influence of model type on predictive skill (AUC and MAE) using a one-way analysis of variance (ANOVA) (Brodie et al. 2020) in the "stats" R package (R Core Team 2022). Model performance was evaluated using both the full datasets and their downsampled counterparts to assess potential bias arising from uneven sample sizes.

Previous studies have also suggested the importance of *ecological realism* as a validation metric (Hazen et al. 2021, Braun et al. 2023b). Ecological realism is defined as the ability of the models to predict realistic patterns of species distributions focusing on biologically plausible relationships with environmental variables and spatial-temporal dynamics consistent with observed ecological processes (Warren et al. 2020). We qualitatively evaluated each SDM using (i) spatial predictions for an example month (September 2014) compared to known distribution and movement ecology of blue sharks and (ii) partial response curves for each model fitted to the full sample to compare the relationships between blue shark presence and environmental variables across the different methods. September 2014 was selected as a representative month due to its relatively balanced distribution of each data type.

As a final metric, we evaluated *computational demand* of each model to assess the trade-offs and feasibility associated with the different modeling approaches as well as a proxy estimate of model complexity (Lezama-Ochoa et al. 2020, Stock et al. 2020). While computational demand can be assessed through multiple metrics (e.g. CPU or memory usage; additional details in Supplementary Material), here we focus on measuring it by the total runtime required for model fitting and prediction. To determine the diminishing returns between model complexity and predictive skill, we used a linear regression to test relationships between runtime and AUC scores for each of the data types.

Results

Overall, each integration approach produced a high performing model; however, results across the three dimensions of performance (predictive skill, ecological realism, and computational demand) varied among approaches (Figs 2 and 3). Analyses using downsampled datasets with equal sample sizes yielded qualitatively consistent results across all integration approaches (Figs S1–S4 and Supplemental Results), confirming that patterns in predictive skill and ecological realism observed with the full datasets were robust to sample size effects. Therefore, we focus here on results from the models trained on the complete datasets. More details on the downsampled results are provided in the supplementary material.

Predictive Skill

All integration approaches demonstrated high predictive skill from the cross-validation procedure with the majority of runs yielding AUC and MAE scores >0.75 and <0.4, respectively (Fig. 2a). Predictive skill, however, differed among data types (ANOVA, $F_2 = 2176$, $P < 0.001$ and $F_2 = 398.8$, $P < 0.001$ for AUC and MAE, respectively) as all the models were able to predict fishery-dependent test data (i.e. marker tag and observer) more accurately than fishery-independent test data (i.e. electronic tags; Fig. 2a). Across integration approaches, marker tags were consistently predicted with greater accuracy compared to the other data types (Fig. 2a and S1a), except for ensemble modeling, which demonstrated marginally better predictive ability for observer data. While all integration approaches demonstrated high predictive skill, iSDM Seasonal outperformed each of the other models when predicting onto the test data while ensemble modeling exhibited the poorest performance. For each data type, iSDM Seasonal AUC scores were ∼3%–7% higher than the average predictive skill across all the models (Fig. 4a). Predictive skill for the other integration approaches was more variable, depending on the data type, with models predicting certain data types more accurately than others (Fig. 4). The greater performance of the iSDM seasonal model was particularly demonstrated for the electronic tag data which exhibited AUC values >5% higher than the average while all other approaches were below the average AUC score.

Ecological realism

Among the integration approaches, the ability to generate ecologically realistic spatial predictions and environmental relationships differed primarily based on the modeling framework (i.e. BRT vs. INLA). For example, blue shark spatial predictions for September 2014 from pooling and ensemble modeling indicated high habitat suitability throughout the Northwest Atlantic continental shelf, extending to the subpolar North Atlantic and coastal regions of northern Africa and Europe, with limited suitable habitat elsewhere (Fig. 3). Both traditional integration approaches using BRTs captured blue shark suitable habitat at (sub-)mesoscale frontal features, which serve as productive foraging grounds for many highly migratory species (Scales et al. 2014, Braun et al. 2019). However, they overpredicted habitat suitability in regions where blue sharks are typically absent during the fall months (e.g. Grand Banks, Gulf of Saint Lawrence, and coastal northern Africa; Braun et al. 2023a, Vandeperre et al. 2014) and underpredicted suitability in areas where blue sharks are frequently observed (e.g. southern North Atlantic and around the Azores Archipelago; Vandeperre et al. 2014; Fig. 3). In contrast, iSDM predictions are closely aligned with blue shark occurrences during September throughout the North Atlantic, including the southern regions, Mid-Atlantic region of the Azores Archipelago, US northeast continental shelf, and along the Grand Banks (Fig. 3). However, iSDM predictions revealed artifacts associated with the construction of the mesh triangulation (Fig. S5).

Furthermore, partial response curves indicated that each integration approach captured similar relationships between blue shark presence observations and the environmental variables (Fig. 5). The ensemble approach, represented as the average response across the data-specific models, exhibited patterns consistent with the other integration approaches, despite single-data-type models exhibiting significantly different environmental relationships (e.g. second row in Fig. 5). While the overall shape of the relationships were comparable, there were notable differences in the magnitude of the marginal effects for individual environmental variables across approaches. Specifically, the pooling and ensemble approaches displayed stronger marginal effects for Bathymetry and SST_sd compared to the iSDMs This pattern is consistent with previous findings that the inclusion of GMRFs can attenuate covariate effects by accounting for unmeasured spatiotemporal variation otherwise absorbed by the environmental predictors (Thorson 2018, Farchadi et al. 2025). As a result, pooling and ensemble models predicted higher suitable habitat in shallower areas and regions characterized by strong frontal features (Fig. 3 and Fig. S6).

Computational demand

Similar to ecological realism, we found that computational demand differed between modeling frameworks as iSDMs were significantly more computationally intensive compared to pooling and ensemble modeling approaches that used BRTs. For example, the iSDM Seasonal model took the longest to fit and predict with cross-validation runs taking between 60 and 100 min whereas BRT model-fitting averaged ∼1 min. Linear regressions demonstrated weak positive relationships between AUC score and time for each data type (Table S1), suggesting increasing model complexity only slightly increased model predictive skill for each data type.

Discussion

In an era of increasing access to growing and diverse data sources, optimizing our capacity to leverage new and existing data types alongside robust analytical methods will play a crucial role in supporting conservation and management decision-making in marine ecosystems (Link et al. 2023). Here, we tested a suite of data-integration approaches using three disparate datasets for a wide-ranging, comparatively data-rich, marine species to better understand the performance of each approach and associated trade-offs in model complexity. We found that model-based integration via joint likelihood approaches (i.e. iSDMs) was the best performing model as measured by predictive skill and ecological realism when accounting for spatial and temporal dynamics. These patterns were consistent across analyses using both full and downsampled datasets, supporting the robustness

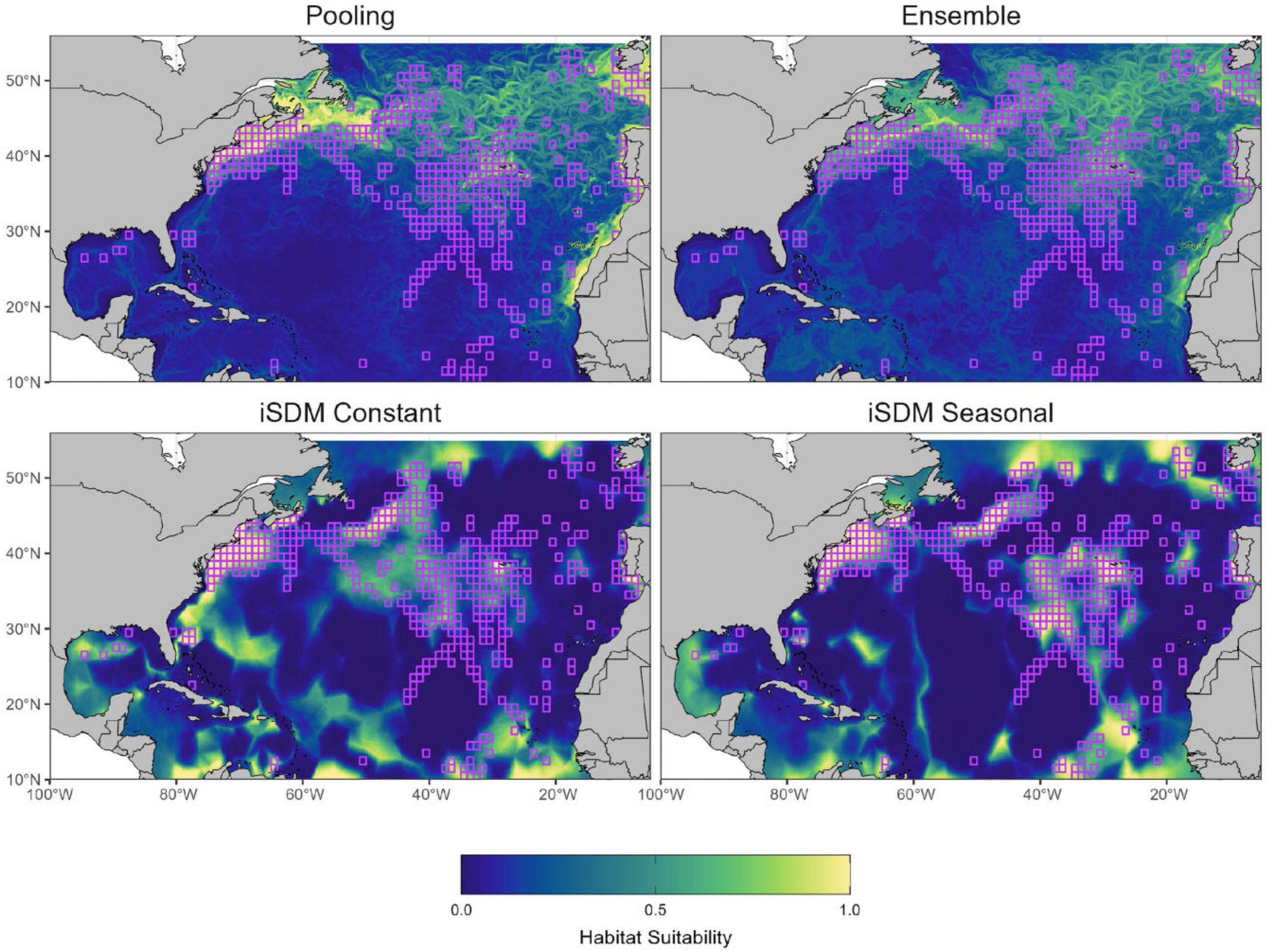

Figure 3. Predicted habitat suitability (from 0 = low to 1 = high) for an example month (September 2014) for each integration approach. Grids are where presences are available during any September in each dataset.

of our findings to sample size effects. Performance of iSDMs that only consisted of a constant temporal spatial effect (i.e. iSDM Constant) exhibited similar or slightly improved performance relative to traditional pooling and ensemble techniques, depending on data type. While explicitly accounting for spatiotemporal dynamics within an integrated model framework further enhances model performance, trade-offs exist regarding the substantial increases in computational demand required for fitting and predicting these models with only marginal improvements in predictive skill. Our results emphasize the importance of use-inspired decisions in the modeling process. Identifying model purpose can guide users on the selection of appropriate data-integration approaches when multiple data sources are available or determine the extent to which spatial and temporal dynamics should be incorporated into the model based on the desired application.

Embracing dynamic models

Data integration represents a promising step forward, as it enables leveraging diverse data types to retain the strength and overcome the bias of each, thereby facilitating more accurate inference regarding a species' distribution. Our study revealed that explicitly accounting for both spatial and temporal dynamics via estimating multiple GMRFs can increase model predictive skill. The majority of studies applying spatially explicit SDMs, whether based on integrated frameworks or single datasets, typically estimate a single GMRF, assuming that the spatial processes driving species distributions are constant over time (e.g. Lezama-Ochoa et al. 2020, Ahmad Suhaimi et al. 2021, Barber et al. 2021, Paradinas et al. 2023). While this assumption may hold for sessile or substrate-associated species with relatively static distributions, the processes that drive the spatial distribution of highly mobile taxa, such as blue sharks, often occur at sub-annual scales, necessitating temporal structure in the model (Isaac et al. 2020).

Here, we demonstrate that accounting for spatiotemporal dynamics in highly migratory species is critical for building accurate, ecologically-realistic models. This was shown for electronic tags where pooling, ensemble, and iSDM Constant models exhibited relatively poor predictive skill, suggesting that the three environmental covariates and the addition of a single GMRF does not adequately explain the variation and inherent biases in the data. In contrast, the iSDM Seasonal model showed improved predictive accuracy, presumably due to the seasonal GMRFs capturing seasonal migration behaviors that were not accounted for by the environmental covariates. Comparisons between the GMRFs of the two iSDM models also revealed potential pitfalls in estimating a single GMRF, evident in the overestimation of spatial field and habi-

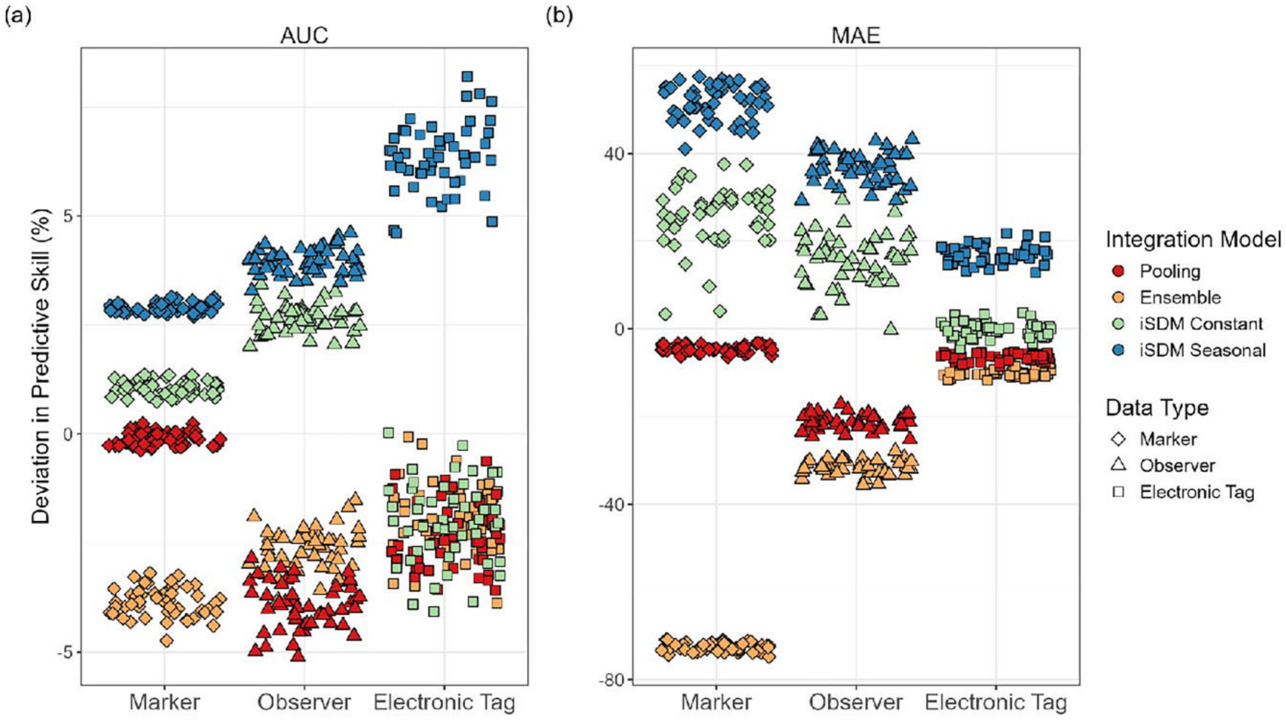

Figure 4. Deviation in predictive skill (%) relative to the all-model average (a) AUC and (b) MAE scores for each data type. Points represent each data type during cross-validation testing iterations within integration models.

tat suitability values in the southwestern North Atlantic (Figs 3 and 6), such as the Sargasso Sea, during the fall. Although presence data were sparse in these areas during the fall season, blue sharks occasionally used them at other times of the year, illustrating how mismatches between the temporal scale of the spatial field and the prediction period can affect model performance. For instance, the iSDM Constant model estimated a single GMRF over the entire study period, which captures long-term climatological spatial structure (temporally static) rather than season-specific dynamics, inflating predicted suitability in these regions. In contrast, the iSDM Seasonal model, which estimates a separate GMRF for each season, assigned lower spatial field values to these areas during fall, reflecting the lack of blue shark occurrences. This underscores a key limitation of static spatial fields in that, without incorporating dynamic temporal structure, models may overestimate suitability in areas used only seasonally or at finer temporal scales, particularly for highly migratory species.

While our results corroborate previous studies that have shown iSDMs can maintain strong predictive performance, their ability to explain spatiotemporal variation can be limited on how information is shared among the datasets (Simmonds et al. 2020, Ahmad Suhaimi et al. 2021). A key assumption in our modeling framework is that the spatiotemporal patterns associated with the fisheries-dependent data can be inferred from the fishery-independent data (i.e. electronic tags informing marker and observer) via the shared spatial field. Although our analysis demonstrated the effectiveness of this approach in maintaining a high predictive skill for both iSDMs, previous studies have demonstrated that iSDMs may not improve predictive skill if the shared spatial process does not effectively account for dataset-specific biases (Simmonds et al. 2020), making it challenging to determine the most appropriate way to share information across data sources (Figueira et al. 2024). Alternative methods, such as explicitly estimating additional GMRFs tailored to each data type, have yielded promising results by accounting for unknown biases that may not be adequately explained by covariates or a single shared GMRF (Simmonds et al. 2020). Furthermore, incorporating non-stationary dynamics may improve model performance as it may result in more precise predictions and reduce bias (Ward et al. 2022). For example, adding temporal non-stationarity in spatial covariance (i.e. range parameter changes over time) helped increase model performance for certain groups of groundfish along the US west coast (Ward et al. 2022). While these approaches may increase model performance, adding additional parameters and model complexity may increase computational demands with only marginal increases in performance. Striking a balance between incorporating greater dynamism into models and managing computational demands are a core challenge for all ecological modeling efforts, including SDMs Therefore, identifying the model's purpose and envisioning its use may serve as an initial step in designing and developing the "best" models for the desired application.

Balancing performance and flexibility in integration

Although our analysis suggests that iSDMs perform best for modeling the distributions of this highly migratory species, traditional pooling and ensemble modeling approaches performed well across the tested dimensions. Given the abundance of effective options, users may find it challenging to decide which integration approach to employ, a decision contingent on the model's purpose and intended application (Brodie et al. 2020). SDM practitioners facing biased data sources (e.g. fishery-dependent or community science data) without available covariates or information (e.g. priors; see Ahmad Suhaimi et al. 2021) to account for such unexplained variation (e.g.

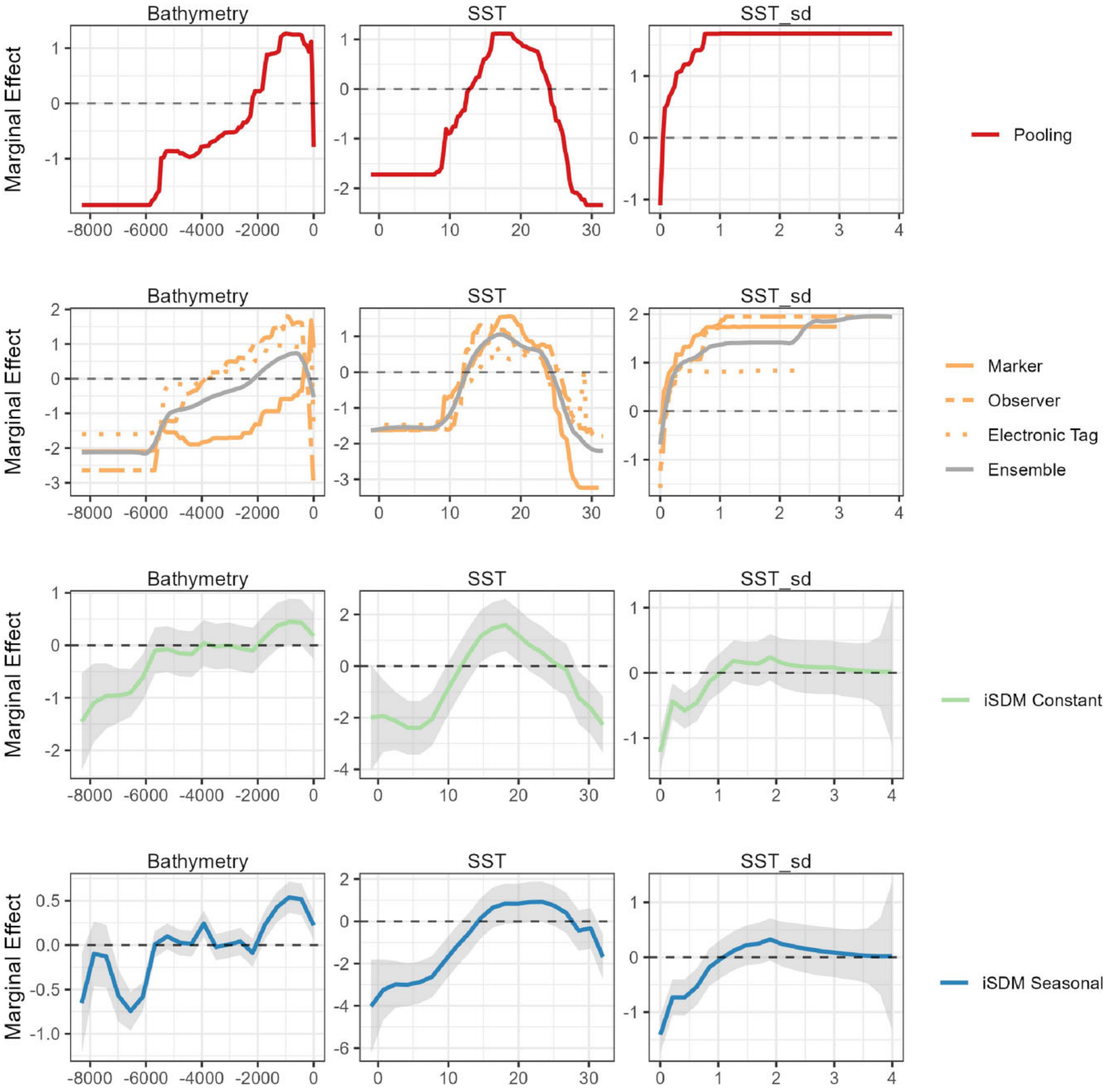

Figure 5. Partial response curves for each model. The gray line in the Ensemble plots represents the average response which was made using a loess function. Shading for iSDM Constant and Seasonal curves represent the 95% credible interval bounds. Dashed lines at 0 represents the point where the covariate contributes neither positively nor negatively to blue shark habitat suitability.

ecological or fishery processes; Stock et al. 2020) may find iSDMs to be the most suitable option. However, the sensitivity of joint likelihood models to the extent of variation explained by the GMRFs, as demonstrated by this study and prior research (Simmonds et al. 2020, Ahmad Suhaimi et al. 2021), suggests that users should employ similar techniques for assessing model performance to determine the most appropriate model structure—spatial or spatiotemporal—and tailor it accordingly. Furthermore, iSDM approaches allow for traditional statistical inference on their predictions unlike the pooling and ensemble approaches in this study that used machine learning modeling frameworks (i.e. BRTs). Therefore, iSDMs may be preferred for applications where estimates of model uncertainty are decidedly important as uncertainty in habitat suitability can be estimated across the spatial domain as well as in the species response curves. For instance, uncertainty maps can aid in identifying the most suitable locations for developing marine protected areas, where data deficiencies exist (Jansen et al. 2022), or communicating model uncertainty when predicting under novel or extrapolated environmental conditions (Karp et al. 2023). Uncertainty associated with the species response curves can help inform establishing biological thresholds that indicate when biological functions become impaired under certain environmental conditions (Liu et al. 2014).

Data pooling and ensemble modeling have traditionally been attractive approaches for integrating marine species data, namely due to their flexibility and ease of use. Pooling and en-

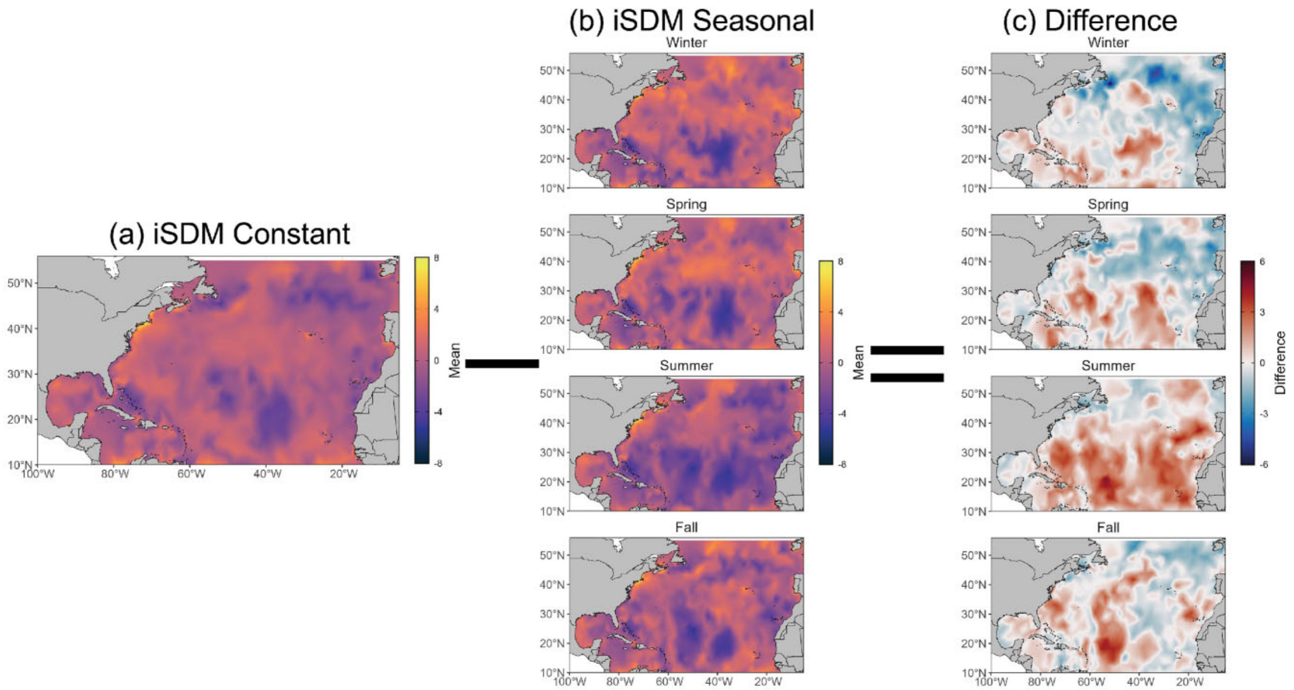

Figure 6. The posterior mean of the estimated GMRFs for the (a) iSDM Constant, (b) iSDM Seasonal, and (c) the difference between the two for each season in the North Atlantic. Warmer colors in the difference plot indicate areas where iSDM Constant estimated greater spatial effect values, while cooler colors indicate areas where iSDM Seasonal estimated greater spatial effect values. Note the range of the color scales for (a) and (b) differ.

semble modeling give users greater flexibility in model structure, such as (semi-)parametric or machine learning models that have been explicitly developed for SDMs (Abrahms et al. 2019, Braun et al. 2023b). iSDMs, however, are largely restricted to semiparametric approaches, which may limit users' choice of which algorithm may be best suited for their data or their model purpose (Brodie et al. 2020). Pooling and ensemble approaches are generally less computationally intensive, especially when using models that are structurally less complex (such as BRTs), which are appealing traits when scientific capacity is limited, timelines to decisions are short, or both (Brodie et al. 2020). Lastly, ensemble modeling may be the only suitable approach when original data are unavailable or confidential, and predictions from existing SDMs are the only accessible information for a particular region (Woodman et al. 2019).

Conclusions

Accurately determining and understanding species distributions is a key requirement for conservation and spatial resource management (Crear et al. 2021). For exploited species like the blue shark, accurate and ecologically realistic SDMs can better assess spatiotemporal exposure to anthropogenic threats such as fisheries, offshore energy development, habitat loss, and climate change and variability (Friedland et al. 2021, Braun et al. 2023a). As shifts in highly migratory species' distributions in the North Atlantic are expected to continue, adapting management strategies for climate-readiness and resilience will be enhanced with the ability to anticipate the effects of climate change (Braun et al. 2023a). In this endeavor, use-inspired SDMs can serve as foundational infrastructure to fulfill such imperative conservation and management goals, allowing managers to be more adaptive to dynamic ocean conditions (Robinson et al. 2017, Crear et al. 2021, Braun et al. 2023a). However, questions of how to use the ever-increasing volume of diverse datasets remain. Here, we demonstrate the trade-offs in the current generation of integrating disparate data sources between informal and formal data integration approaches and provide guidance for SDM practitioners in real-world applications, particularly for highly migratory species. While iSDMs that explicitly account for spatiotemporal dynamics outperformed more traditional approaches, our analysis points to the value of data integration, regardless of approach, as it allows leveraging disparate data sources to create more robust inferences and characterization of the patterns and processes that drive species' space use (e.g. second row in Fig. 5; Fletcher et al. 2019, Isaac et al. 2020, Braun et al. 2023a). As environmental conditions become increasingly novel amidst ongoing climate change and variability (Alexander et al. 2020), iSDMs are well positioned to give practitioners the infrastructure to readily accommodate diverse historical and contemporary datasets, fostering a more holistic understanding of the impacts of climate change on marine species.

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Author contributions

N.F.: Conceptualization, Methodology, Formal analysis, Investigation, Visualization, Writing—original draft, Writing—review & editing. C.D.B: Conceptualization, Methodology, Data Curation, Investigation, Supervision, Project administration, Funding acquisition, Writing—review & editing. M.C.A: Conceptualization, Methodology, Data Curation, Investigation, Supervision, Writing—review & editing. N.L.O: Methodology, Investigation, Writing—review & editing. M.G.P: Methodology, Investigation, Writing—review & editing. P.A.: Collection of data, Writing—review & editing. T.H.C.: Collection of data, Writing—review & editing. J.F.: Collection of data, Writing—review & editing., N.Q.: Collection of data, Writing—review & editing. G.B.S.: Collection of data, Writing—review & editing. D.W.S.: Collection of data, Writing—review & editing. S.R.T: Collection of data, Writing—review & editing. F.V.: Collection of data, Writing—review & editing. R.L.L.: Conceptualization, Methodology, Investigation, Supervision, Project administration, Funding acquisition, Writing—review & editing

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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Data availability

Code and simulated sample data for running the analysis is available at: https://github.com/nfarchadi/BlueShark_ISDM/. Marker tag data used in this research are publicly available from the International Commission for the Conservation of Atlantic Tunas (ICCAT) Secretariat tag database at https://iccat.int/en/accesingdb.html. The fishery dependent observer dataset used in this study are considered confidential under the US Magnuson-Stevens Act. Qualified researchers may request these data from the NOAA Pelagic Observer Program office by contacting popobserver@noaa.gov. We requested data representing all pelagic longline sets between the years 1993 and 2019. For inquiries regarding the electronic data, contact the corresponding author.

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