

Improving species distribution model forecasts under novel ocean conditions

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February 24, 2025

Introduction

Climate variability and change is impacting marine ecosystems and the services they provide to the communities, businesses, and fisheries that rely on them (Doney et al. 2012, Scheffers et al. 2016, Bryndum-Buchholz et al. 2019). Globally, oceans are experiencing gradual climate trends (e.g., long-term warming) as well as climate-induced extreme events (e.g., heatwaves, cold snaps) that can push ecosystems into novel environmental states, straining social-ecological systems (Samhuri et al. 2021, Schlegel et al. 2021, Free et al. 2023). Over the past decade, episodic ocean warming events, known as marine heatwaves (MHWs), have increased in frequency, intensity, and size compared to a historical baseline (Oliver et al. 2018, 2021), leading to significant ecological, socio-economic, and human health impacts globally (Smith et al. 2021). Recent work has focused on characterizing the spatial and temporal redistribution of species in response to MHWs (Welch et al. 2023); however, species' responses to each MHW event can vary significantly (Welch et al. 2023, Farchadi et al. 2024), challenging traditional ocean management and spatial planning approaches (Samhuri et al. 2021, Welch et al. 2024).

Species distribution models (SDMs) are a popular tool to understand and predict how species' spatiotemporal distributions or abundances change in response to environmental conditions (Hazen et al. 2018, Milanese et al. 2020, Barnes et al. 2022, Braun et al. 2023a). Recent studies have used SDMs to evaluate MHW-driven redistribution of marine predators (Welch et al. 2023) and pelagic fishing fleets (Farchadi et al. 2024), providing critical insights into the ecological and socioeconomic impacts of MHWs. Despite the utility of SDMs in supporting ocean management and conservation efforts (Robinson et al. 2017, Hazen et al. 2018), their performance can decline under extreme climate events (Muhling et al. 2020, Karp et al. 2023, Allyn et al. 2024), a challenge that is exacerbated by the increasing prevalence of novel environmental conditions (Smith et al. 2022). Model performance often depends on how well the training data captures the full gradient of a species' environmental preferences and whether novel conditions created by extreme events generate new areas of suitable habitat (Thuiller et al. 2004, Yates et al. 2018). Model inaccuracies may also stem from inherent biases in the training data, such as sampling process, observer bias, and analytical errors, which, if ignored, can generate misleading species-environmental relationships and lead to erroneous predictions of species distributions (Fletcher et al. 2016, 2019).

In marine fisheries, SDMs have largely relied on single data type approaches, typically derived from either

a fishery-independent source, such as standardized survey efforts and electronic tags (Kleisner et al. 2017, Lezama-Ochoa et al. 2023), or fishery-dependent data, like vessel catch logbooks and observer programs (Crear et al. 2021, Karp et al. 2023). Although fishery-independent data is generally considered a less biased representation of a species' distribution (Braun et al. 2023b), associated high costs and logistical challenges often limit the spatiotemporal coverage of these datasets (Dennis et al. 2015). Fishery-independent data can be particularly sparse in a given area for highly migratory pelagic species, which tend to have extensive and dynamic ranges (Block et al. 2011) and spend considerable time at depth (Braun et al. 2023c). In contrast, fishery-dependent data can provide greater spatial and temporal coverage and is common for many important fishery species. Fishery-dependent data have been used to predict how species may interact with a fishery (Crear et al. 2021), identify target and bycatch hotspots (Hazen et al. 2018), assess climate-induced fleet displacements (Farchadi et al. 2024), and analyze spatiotemporal dynamics of catch-per-unit-effort (Muhling et al. 2019). However, these data can be biased due to preferential sampling by fishers, which can mask underlying drivers of species distributions and are more prone to reporting errors (Karp et al. 2023).

Fisheries-independent and -dependent data together may offer complementary information on species distributions. Recent studies have shown that integrated SDMs (iSDMs), which simultaneously model different data sources while explicitly accounting for the differences in the sampling processes (Isaac et al. 2020), can yield more accurate predictions of species distributions (Paradinas et al. 2023) with greater predictive skill compared to models fitted to a single data source (Simmonds et al. 2020, Ahmad Suhaimi et al. 2021). While various approaches to combine data types have been shown to yield robust SDMs, most studies have assessed these methods under constant environmental conditions (e.g., k-fold cross-validation; Simmonds et al. 2020, Ahmad Suhaimi et al. 2021, Braun et al. 2023b). Thus, it remains unknown whether leveraging diverse data types enhances model performance under novel environmental conditions such as during MHWs.

There is an increasing body of literature examining the performance of SDMs under climate change and variability (Muhling et al. 2020, Barnes et al. 2022, Brodie et al. 2022, Karp et al. 2023). As marine systems continue to face increasingly novel and uncertain conditions, quantitative comparisons of model forecasting performance are crucial to provide accurate and forward-looking information for marine conservation and management (Thorson 2018). Here, we compare three modeling approaches that vary in their approaches to leverage multiple data types and spatial dependence treatments for an important fishery species, albacore tuna (*Thunnus alalunga*), during a period of unprecedented MHWs in the northeast Pacific Ocean (NEP) to assess each model's capacity to accurately forecast albacore distributions under MHW conditions. We discuss our results in the context of current SDM techniques, highlighting how to combine diverse data sources to advance species distribution modelling in a changing climate.

Methods

Summary

To compare SDM approaches, we modeled albacore tuna habitat suitability in the NEP using two fishery-dependent (vessel logbook data) and independent (electronic archival tags) albacore occurrence datasets spanning from 1995 - 2019. We compared three models that varied both in their approaches to how they leverage diverse data types and account for spatial dependence (Table 1). These models included two dynamic environmental variables, monthly mean sea surface temperature (SST) and mixed layer depth (MLD), that were sourced from a high-resolution, data-assimilating ocean model and one static variable representing bathymetry (Supporting Information). We compared the performance of each model under novel conditions (i.e., MHWs) across two dimensions: *predictive skill* and *ecological realism*. Models were fit to training data from 1995 - 2013 and retrospectively forecasted at monthly timesteps from 2014 - 2019, a time period when the NEP experienced multiple large and intense MHWs.

Albacore Occurrence Data

We used two previously published occurrence datasets for albacore tuna in the NEP (Figure 1): fishery-dependent vessel logbook records and fishery-independent archival tags. Vessel logbook data were obtained from U.S. pole-and-line and troll fisheries, which target juvenile albacore throughout the NEP (Muhling et

al. 2019; Figure 1). The logbook program has been in place since the early 1970s, providing daily, set-level catch information for albacore within the spatial extent of the fishery (Frawley et al. 2020). To account for varying degrees of accuracy in occurrence locations reported, data was filtered to remove duplicates, points on land, points outside the NEP, and locations reported in whole degrees, assuming that these were approximations (Muhling et al. 2019). To align with the temporal extent at which environmental data were available, vessel logbook records were filtered to retain records between 1995 - 2019. While the proportion of active fishing vessels participating in the logbook program has varied over time, the composition of the fleet and the distribution of effort has remained relatively consistent since the 1990s, which falls within the temporal extent of this study (Frawley et al. 2020).

Fishery-independent data consisted of archival tags deployed on 25 individual juvenile albacore across the NEP from 2003 to 2016 (Figure 1). This dataset was generated by the Albacore Archival Tagging Program, which is a collaborative effort between the National Marine Fisheries Service and the American Fishermen’s Research Foundation to tag albacore in the NEP (Childers et al. 2011, Snyder et al. 2017). Albacore were fitted with one of three models of archival tags (Lotek LTD2310, LotekLAT2810, and Wildlife Computers MK9). To construct the most probable tracks from archival tagged albacore, we used a hidden Markov model (*HMMoce* R package; Braun et al. 2018), that compares tag-based observations against oceanographic measurements to provide daily location estimates and the associated uncertainty for each tagged individual (see additional details in Arostegui et al. 2023). To reduce the autocorrelation structure, both datasets were independently filtered to remove records with duplicate environmental conditions for each month (Varela et al. 2014). Lastly, data were filtered to include the spatial extent of 180°W - 100°W and 10°N- 57°N to focus the analysis on the NEP, as this is where the majority of logbook and tagging data were located (Figure 1) and where MHW intensities have been greatest (Welch et al. 2023).

Species Distribution Models

Albacore habitat suitability was modeled in relation to environmental variables using three distinct binomial generalized additive models (GAMs), each differing in their methods to combine data and treatment of spatial dependence (Table 1): a data pooled habitat-envelope model, a data pooled Gaussian field model, and a joint-likelihood Gaussian field model. All models used a logit link and were fitted with the Integrated Nested Laplace Approximation (INLA) framework (Rue et al. 2009), which offers a computationally efficient alternative to other methods of Bayesian inference (i.e., Markov chain Monte Carlo) while also enabling smoothing approaches akin to frequentist GAMs (e.g., as implemented in the *mgcv* R package; Lezama-Ochoa et al. 2020). Each model included three environmental covariates: sea surface temperature (SST), mixed layer depth (MLD), and bathymetry, which previously have shown to be important drivers of habitat use for juvenile albacore tuna (Muhling et al. 2019, Farchadi et al. 2024). Here, we outline the design of each SDM with further details on model parameterization and structure provided in the Supporting Information.

The first model employed a spatially implicit approach, often referred to as a “habitat-envelope” model (hereafter HE; Brodie et al. 2020), which relies on species-environmental relationships to explain the variation in species distributions without considering the spatial arrangement of habitats and species occurrences. This approach is consistent with many traditional applications of SDMs and has been widely adopted to model highly migratory marine species including albacore tuna (Muhling et al. 2019). To combine the albacore logbook and tag data in this model, we applied data-pooling methods to combine the two datasets into a single aggregated dataset for modeling. These methods have been shown to enhance model performance in similarly designed HE SDMs by mitigating biases inherent in individual datasets, offering a robust framework for applications in species distribution modeling (Braun et al. 2023b).

Building upon the HE model, the second model introduced Gaussian fields (GF) to account for spatial dependence while retaining the data-pooling approach. Unlike the inherent spatially implicit nature of the HE model, this second model (hereafter termed “GF”) used a geostatistical framework that explicitly incorporates spatial information through random spatial fields, which capture unmeasured spatial processes across the study domain (Stock et al. 2020). In INLA, random spatial fields are approximated as discrete Gaussian Markov random fields (GMRFs) using the stochastic partial differential equation approach with

a Matérn covariance structure (Lindgren et al. 2011), which serves as a smoother based on the assumption that nearby locations are more similar than distant ones (Krainski et al. 2018). To account for temporally varying spatial autocorrelation in the training dataset, the GF model was fitted with season-specific GMRFs, formulated as a cyclic first-order autoregressive spatiotemporal structure, where neighboring seasons (e.g., winter and fall) being more closely correlated than those farther apart (e.g., winter and summer).

The third model extended the GF model by employing joint-likelihood methods to explicitly integrate the two disparate data sources within a single iSDM framework. This model used two separate linear predictors, with each data source directly informing albacore habitat suitability through shared parameters in a jointly estimated likelihood. Both sub-models incorporated shared effects for three environmental covariates and the random spatial fields (Table 1). However, unlike the data pooled GF model, the iSDM included two sets of random spatial fields: (A) seasonal random spatial fields describing the spatiotemporal autocorrelation for the tag data and shared with the logbook linear predictor (Barber et al. 2021), and (B) a climatological spatial field, informed only by the logbook data, to account for any residual autocorrelation not explained by either the shared seasonal spatial fields or environmental covariates (Simmonds et al. 2020). The decision to share the archival tag-estimated spatial fields across the linear predictors was informed by prior studies that used iSDMs to investigate predator-prey interactions (Barber et al. 2021), akin to fisheries systems where prey spatial dynamics (i.e. albacore tuna) influence predator distributions (i.e. the fishery). With this structure, we assume that the spatial patterns influencing albacore tuna distributions, as indicated by fishery-independent archival tag data, directly correspond to the patterns explaining albacore catch in the fishery-dependent dataset. The second spatial field was modeled without a temporal component (i.e., climatology) as the distribution of U.S. pole-and-line and troll fishery varies minimally during the fishing season (May – November; Figure S2).

Since the data sources only include positive observations of occurrence, models were constructed following dynamic SDM techniques that use simulated data to represent where individuals were likely absent (i.e. “pseudo-absences”) as described in Farchadi et al. (*in revision*). These methods have been shown to capture dynamic habitat use at daily temporal scales (Hazen et al. 2018). Briefly, background sampling of pseudo-absences was generated from the monthly spatial extent of each dataset at a 1:1 ratio for the two datasets (Barbet-Massin et al. 2012) as has been shown effective for other pelagic species (Hazen et al. 2021, Braun et al. 2023b). Model outputs from each modeling approach describe albacore “habitat suitability” as continuous values ranging from 0 (low habitat suitability) to 1 (high habitat suitability).

Model Performance and Environmental Novelty Analysis

We evaluated each model’s forecasting ability during a period of multiple MHWs in the NEP by training each model on the full datasets from 1995 - 2013 and testing their performance at monthly time steps on the held-out data from 2014 - 2019 (Figure 2). Model performance was assessed across two different dimensions: *predictive skill* and *ecological realism*. *Predictive skill* denotes the model’s ability to accurately classify locations where species were present from those where a species was absent on independent occurrence data. We quantified predictive skill using two metrics: the Area Under the receiver-operating Curve (AUC) and Mean Absolute Error (MAE). Using AUC and MAE has been recommended for assessing SDMs, as they provide complementary insights on model performance while addressing shortcomings inherent in each metric’s assumptions (Konowalik and Nosol 2021). In addition to predictive skill, we evaluated *ecological realism*, which considers a model’s capacity to estimate biologically plausible species-environment relationships and predict spatiotemporal patterns consistent with observed ecological processes. This was assessed qualitatively by 1) comparing spatial predictions for a forecasted month to the known distribution of albacore during a MHW and 2) analyzing partial response curves to determine whether they aligned with observed environmental covariate distributions during the training (1995–2013) and forecasting (2014–2019) periods.

Beyond assessing overall model performance, we evaluated how effectively each model type handled environmental novelty using Hellinger Distance (Legendre and Legendre 2012, Johnson and Watson 2021, Karp et al. 2023), which measures the difference between two probability distributions (see Karp et al. 2023 for formulas). We calculated Hellinger Distance for both dynamic environmental covariates (SST and MLD) of

each month-year in the test data relative to the climatological conditions of the same month in the training data. Hellinger Distance quantifies the extent of extrapolation required by the fitted SDM when making predictions and ranges from 0 to 1, where a value of 0 indicates that the two distributions share the same information (e.g., complete data overlap), while values of >0.5 indicate greater dissimilarity than similarity between the two distributions (Johnson and Watson 2021). Finally, we assessed the impact of environmental novelty on forecast skill by comparing the relationship between AUC and MAE with Hellinger Distance across the different models.

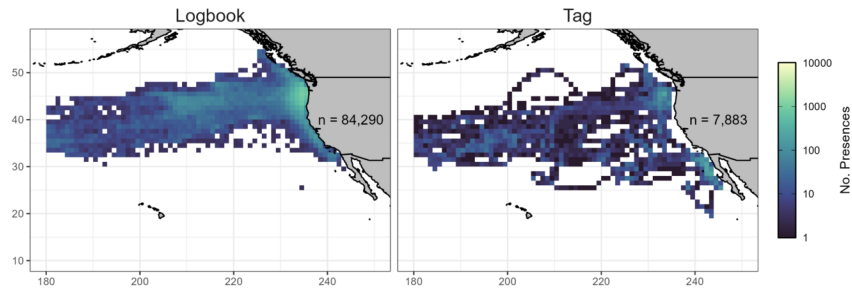


Figure 1. Presence locations of albacore tuna from (a) the U.S. pole-and-line and troll fishery logbook program (1995 - 2019) and (b) fishery-independent electronic archival tags (2003 - 2016). Note that to protect confidentiality, grid cells for the fishery observer data that contained < 3 vessels were removed.

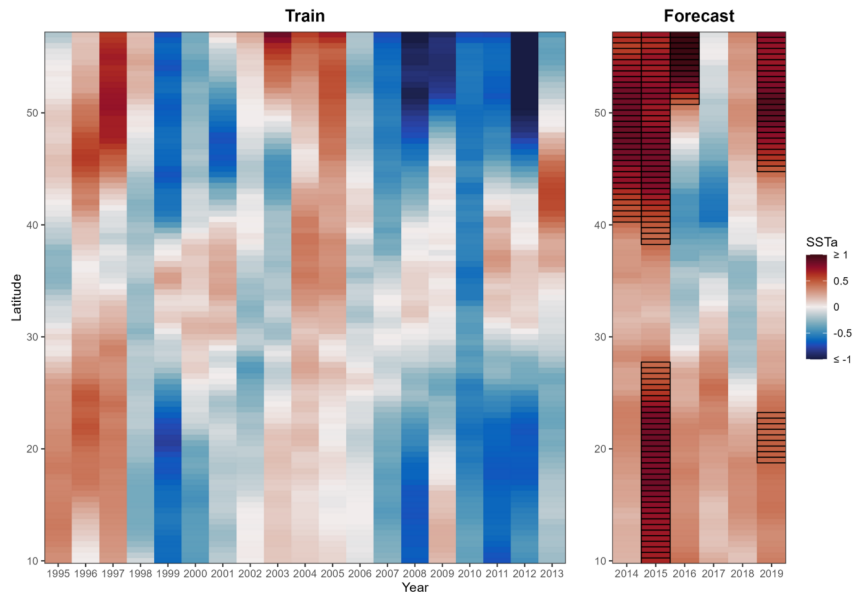


Figure 2. Yearly average sea surface temperature anomaly (SSTa) by latitude across the NEP throughout the training (1995 - 2013) and forecasting (2014 - 2019) periods. Latitudes with novel conditions in the forecasting period, SSTa exceeding the 90th percentile of the training period, are highlighted with black borders.

Model	Data Combination Approach	Environmental Covariates	Spatial Fields
HE	Data Pooling	SST + MLD + Bathymetry	NA
GF	Data Pooling	SST + MLD + Bathymetry	Seasonal
iSDM	Joint likelihood	SST + MLD + Bathymetry	Seasonal + climatological

Table 1. Details on forecasting models used in this study, including their approach to combine data, what environmental covariates were used, and inclusion of spatial fields. Model acronyms refer to habitat envelope (HE), Gaussian field (GF), integration species distribution model (iSDM). See section *Species Distribution Models* in the methods for more detail on model design.

not-yet-known not-yet-known

not-yet-known

unknown

Results

Forecasting Trends

Predictive skill varied among the three models across the forecasting period. The majority of the data (~97%) during this period consisted of logbook records (Figure 3), reflecting the seasonality of the albacore fishery in the California Current, which operates primarily between May – November (Xu et al. 2017). Among the models, predictive skill varied primarily based on spatial dependence treatments (i.e., spatially implicit or explicit). GF and iSDM exhibited similar trends, performing best on average in 2014 and 2019, with their poorest performance in 2016 (Figure 3a,b). HE followed similar patterns, but consistently showed lower performance, with its poorest performance in the beginning of the forecasting period (Figure 3a,b). Furthermore, the degree of novelty for each variable was correlated with the patterns of AUC ($r = -0.62$ and -0.58 for MLD and SST, respectively) and MAE ($r = 0.7$ and 0.55 for MLD and SST, respectively), equating to poorer predictive skill as conditions became increasingly novel relative to the training period (Figure 3c). For example, months experiencing the highest degree of novelty in MLD and/or SST (e.g., May 2018, April 2016, and January 2016) exhibited the poorest model performance, particularly for the HE model (Figure 3). Trends in novelty for MLD and SST were similar across all years, with small differences in Hellinger Distance between MLD and SST (Figure 3c), suggesting both variables exhibited comparable levels of novelty and variability during the forecasting period relative to the training period.

Predictive Skill and Environmental Novelty

All three models demonstrated high predictive skill under the forecasting period, accurately predicting albacore distributions most months (AUC > 0.8, MAE < 0.3; Figures 3, 4). However, predictive skill for all models declined as environmental novelty increased for both MLD and SST (Figure 4). Between the two environmental variables, greater SST novelty led to more pronounced declines in performance for all models, particularly for HE (Table S1). Despite all modeling approaches demonstrating similar relationships between predictive skill and environmental novelty, the iSDM consistently outperformed the other models as novelty increased (Figure 4), with higher average predictive skill under highly novel conditions (AUC = 0.69, MAE = 0.391 for novelty [?] 0.3). Notably, the HE model showed the greatest decline in predictive skill with increasing novelty (mean AUC 0.47, MAE 0.46) and demonstrated the least predictive skill overall under these conditions.

Ecological Realism

Similar to their predictive skill, all models’ ability to generate ecologically realistic environmental relationships and spatial predictions varied primarily by spatial dependence treatments. Response curves indicated that each model captured similar relationships between albacore presence observations and the environmental variables. However, spatially explicit models (i.e., GF and iSDM) demonstrated a broader relationship

with MLD compared to the HE model. For example, the HE model response curves suggested albacore suitability was highest at shallow MLDs ($\sim < 10$ meters; Figure 5). This relationship closely resembled the underlying MLD distributions of the logbook data (Figure S1), which suggested significantly deeper MLDs relative to the archival tag data (mean MLD: 32.7 ± 21.9 and 13 ± 4.03 for archival tag and logbook data, respectively). In contrast, the GF and iSDM models suggested high albacore habitat suitability for shallow MLDs to ~ 100 meters before declining with depth (Figure 5). Additionally, all models showed that response curves (i.e., from the training period) fully covered the conditions during the forecasting period, though the distributions for each environmental variable narrowed during this time (Figure 5). Despite this coverage, the distributions of environmental values differed between the training and forecasting periods. For example, SST was warmer, bathymetry shallower, and MLD nearer to the surface during the forecasting period, indicating that albacore inhabited warmer, shallower waters during MHW conditions (Figure 5).

Spatial predictions were also assessed for ecological realism. During the forecast period under MHW conditions, the models generally exhibited similar spatial patterns in predicted habitat suitability, though regional differences were apparent (Figure 6). All models identified coastal waters—particularly off the coasts of Washington, Oregon, and northern Baja California—and the North Pacific Transition Zone as highly suitable habitat. However, the HE model produced the least ecologically realistic predictions, as it forecasted higher habitat suitability across the study area compared to the spatially explicit models. Notably, the HE model predicted extensive areas of suitable habitat for albacore tuna in areas characterized by warm (positive) SST anomalies offshore of southern California, whereas the GF and iSDM models demonstrated a discernible discontinuity in suitability within this highly anomalous region (Figure 6). This overestimation in the HE model is further reflected in the distribution of predicted suitability values, where it overpredicted habitat suitability at pseudo-absence locations. In contrast, the GF and iSDM model predictions more accurately differentiated between presences and pseudoabsences, resulting in a more balanced, and likely realistic, distribution of suitability values (Figure 6). The primary differences between the spatially explicit models were in the iSDM predictions being more closely aligned with albacore occurrences in coastal Canada and absences off central California, whereas these regions were connected by a coastal band of apparent high suitability in the GF predictions. In addition, while both GF and iSDMs identified the waters off Baja California as suitable, the degree of predicted suitability was significantly higher for the GF model in this region.

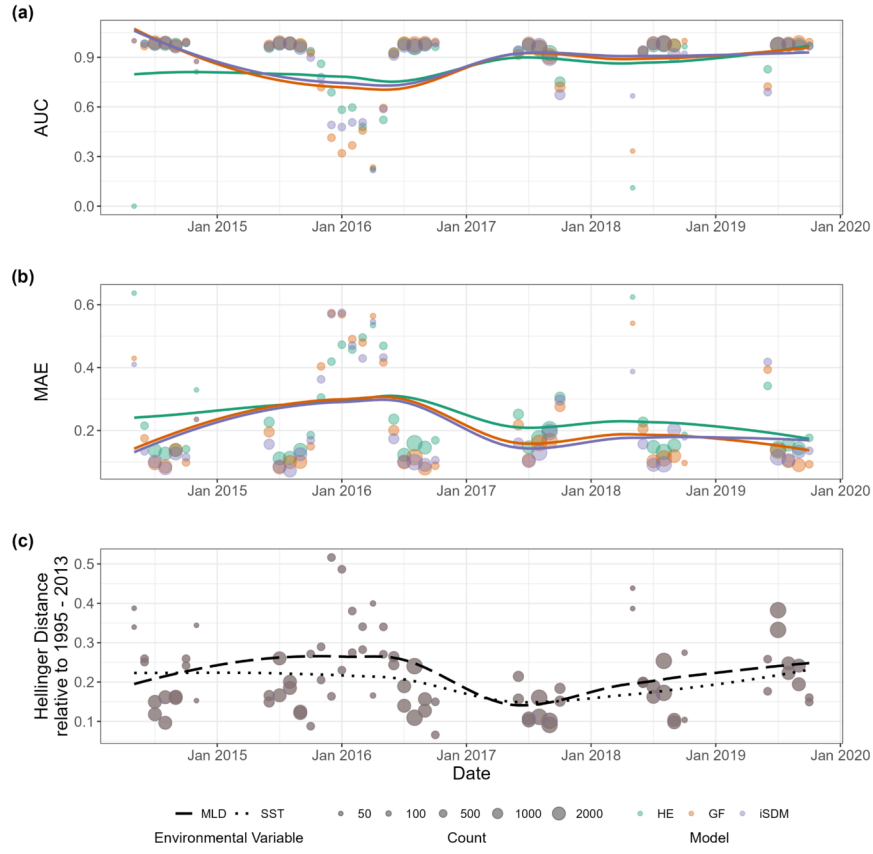


Figure 3. Time series of model performance metrics (a, b) and environmental novelty (c) during the forecasting period (2014 - 2019). Panels show (a) AUC, (b) MAE, and (c) Hellinger Distance relative to the training period (1995 - 2013). In (a) and (b), circles and lines are colored by model type, with lines representing smoothed monthly averages for each metric. In (c), line types differentiate between MLD and SST novelty. Model acronyms denote habitat envelope (HE), Gaussian field (GF), integrated species distribution model (iSDM). Circle sizes represent the count of data predicted by the models for each month.

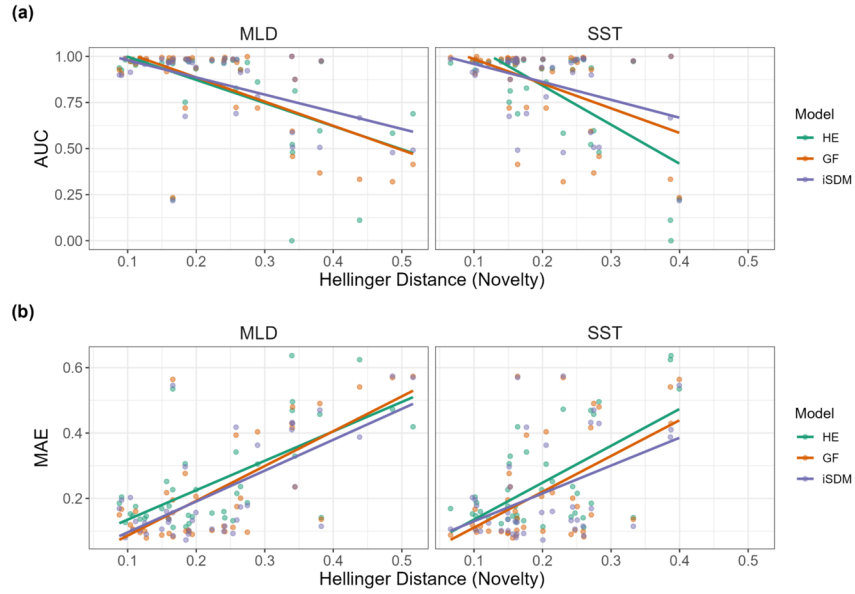


Figure 4. Relationship between MLD and SST environmental novelty, as measured by Hellinger Distance, and model predictive skill metrics: (a) AUC and (b) MAE. Points and lines represent monthly forecasts and linear relationships between model performance metrics and Hellinger Distance, respectively.

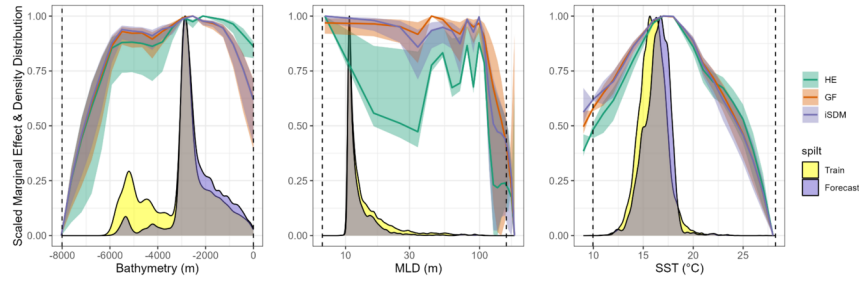


Figure 5. Relationships between estimated response curves and observed environmental covariate distributions between the training (1995 - 2013) and forecasting (2014 - 2019) periods for each model. Shading represents the scaled 95% credible interval bounds. Dashed vertical lines indicate the range of values within the forecasting period.

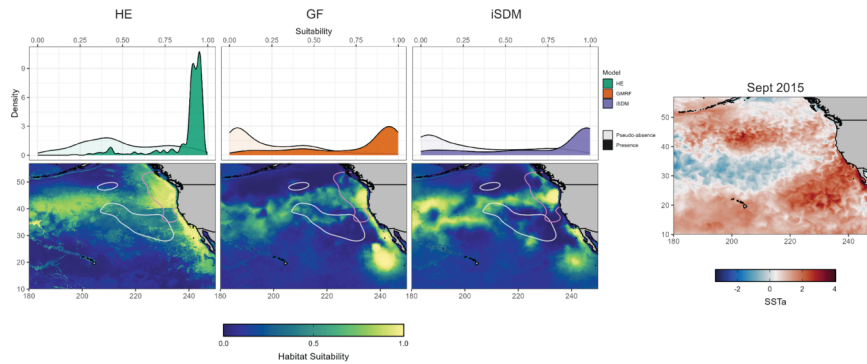


Figure 6. Forecasted habitat suitability (from 0 = low [in blue] to 1 = high [in yellow]) for each model during an example month when the NEP experienced a MHW (September 2015). Pink and white contours are the 90th percentile kernel densities for albacore presences and pseudo-absences, respectively, during the month across the two datasets. Density plots show the distribution of predicted suitability values at presences and pseudo-absences from each model. Color scale for mapped sea surface temperature anomaly (SSTa; °C) represents warmer (red) or colder (blue) than the climatological average (SST; 1993 - 2019).

Discussion

Approaches for leveraging diverse data in SDMs have advanced over the last decade, showing great potential to enhance our understanding of species distributions and improving the accuracy of predictive models (Fletcher et al. 2019, Isaac et al. 2020, Braun et al. 2023b). Digital and technological advancements have greatly expanded data availability which has increased efforts to mobilize more diverse data types, opening new opportunities to leverage multiple data sources for developing robust SDMs (Isaac et al. 2020). Our exploration of modelling approaches builds on these advances by considering how to maintain skillful SDM predictions under novel environmental conditions, pointing to promising paths to characterize and predict the impact of changing ocean ecosystems. Our findings affirm previous research that demonstrates that SDM performance declines as environmental novelty increases (Muhling et al. 2020, Brodie et al. 2022, Allyn et al. 2024). However, our results also highlight how spatially explicit joint likelihood approaches maintained greater predictive skill and ecological realism under novel environmental conditions than traditional spatially implicit data pooling models. These results emphasize the importance of model-based data integration as a tool to leverage multiple data sources to make robust predictions under novel conditions. The approaches can support marine conservation and management applications under uncertain and variable future conditions.

The Power of Integrated Models

Leveraging multiple data types, whether through pooling or explicit integration such as via joint likelihood approaches, has been shown to generally improve SDM performance by estimating more precise and accurate environmental relationships (Fletcher et al. 2019, Paradinas et al. 2023, Braun et al. 2023b). Although recent research has highlighted the application of combining various data for SDMs (Bedriñana-Romano et al. 2018, Rufener et al. 2021, Paradinas et al. 2023, Braun et al. 2023b), few studies have demonstrated their capacity to forecast and project potential distributional shifts under novel environmental conditions (Chevalier et al. 2021). Our study suggests that while all model approaches used here perform well during periods of normal environmental conditions, joint likelihood approaches that explicitly account for the biases in each data source (i.e., iSDMs) maintain robust and ecologically realistic forecasts as environmental conditions become increasingly novel. We demonstrate that iSDMs effectively mitigate issues that are broadly attributed to a model’s forecast skill. Our findings confirm that explicit integration of diverse datasets represents a promising approach to overcome the potential biases inherent in a single data source, as it enables harnessing the strength of various data types to facilitate more accurate inferences about a species’ distribution (Isaac et al. 2020). The models we tested all exhibited high predictive skill (average AUC > 0.83, MAE < 0.25) and strong ecological realism. This can be particularly beneficial for highly migratory pelagic species, such as albacore, as using a single data source may only capture a portion of their range, such as that represented by a fishery, which could lead to mischaracterizing a species’ realized niche (Paradinas et al. 2023, Braun et al. 2023b). However, our results also suggest that predictive skill may be higher for fishery-dependent data compared to fishery-independent sources, as seen in the deviations observed in early 2016 (Figure 3). This aligns with previous findings (Braun et al. 2023b; Farchadi et al. *in revision*), where models were more effective at predicting the fishery’s interaction with a species rather than broader habitat suitability. These differences underscore the need to carefully consider the representativeness of each data source when interpreting forecasted distributions.

The improved predictive performance of iSDMs under increasing environmental novelty may stem from differences in the fitted species-environmental response curves (Thuiller et al. 2004) and their ability to account for spatiotemporal variation (Muhling et al. 2019, Simmonds et al. 2020). Previous studies evaluating SDM forecasting performance, whether in the near-term (Muhling et al. 2020, Barnes et al. 2022) or long-

term (Thuiller et al. 2004, Karp et al. 2023), have emphasized that biased or limited species-environmental response curves can lead to erroneous predictions. This limitation is often an inherent bias in training data, such as in fishery catch data that only captures a portion of the species’ preferred habitat conditions due to sampling bias (e.g., clustering, gear selectivity, limited spatial and/or temporal coverage), resulting in truncated species-environmental response curves (Chevalier et al. 2021, Barnes et al. 2022, Paradinas et al. 2023). Our results indicate that leveraging diverse data types can help capture the full range of environmental conditions a species occupies, but the species response curves depend on how the model framework combines data types. For example, more generalized species-environmental relationships were estimated for both spatially explicit models (i.e. GF, iSDM) which performed better than the spatially implicit model. This is likely due, at least in part, to HE response curves that exhibited greater overfitting and were heavily biased towards distributions of the more data-rich vessel logbook records, particularly for MLD (Figure 5). Notably, the GF and iSDM response curves for MLD closely matched the known diving behavior of juvenile albacore tuna, which regularly dive to approximately 100 meters (Frawley et al. 2024) but are often vertically-limited by colder temperatures below the mixed layer (Graham and Dickson 1981). In contrast, the HE model suggested albacore suitability declined with deeper MLDs, particularly > 10 meters, a pattern that mirrors the environmental conditions targeted by the pole-and-line and troll fisheries along the U.S. West Coast (Figure S1). This demonstrates that the inclusion of GMRFs in the spatially explicit models helped account for unmeasured variation in albacore distribution. By modeling the spatial structure separately, these models provided more reliable estimates of environmental relationships, reducing the risk of response curves being artifacts of sampling biases in the fishery data.

Our results also highlight how approaches to spatial dependence and combining disparate data sources can influence an SDM’s capacity to accurately forecast species distributions under novel environmental conditions. Consistent with previous studies, we found that habitat envelope models produce narrower response curves than spatially explicit frameworks, likely due to their inability to capture residual variability (Thorson 2018, Simmonds et al. 2020). Consequently, tightly fit response curves may fail to account for non-stationary species-environment relationships under novel conditions. In contrast, the broader, more generalized response curves generated by iSDMs better capture these dynamics over time (Yates et al. 2018, Muhling et al. 2020; Figure 5). Additionally, the strong performance of spatially explicit models may stem from their ability to incorporate variation across multiple temporal scales. Consistent with prior findings, our analysis suggests that including GMRFs—analogueous to seasonal or climatological covariates—enhances forecast skill, particularly in the near term (Barnes et al. 2022). Furthermore, differences between the two spatially explicit models, GF and iSDM, highlight the influence of data integration methods. While the GF model pools data sources, potentially masking differences in sampling design (Fletcher et al. 2019), iSDMs estimate data-specific spatial fields, allowing for improved handling of spatiotemporal variation and biases while also balancing disproportionate sample sizes). This, in turn, can lead to more accurate representation of the underlying ecology of the species. Given the challenges of identifying and addressing bias in different data sources, ongoing evaluation of integration methods remains essential for optimizing predictive performance in species distribution modeling.

Implications for Conservation & Management

Accurate predictions of species distributions across multiple time scales, i.e. nowcasts to long term projections, are vital to support climate-ready and -resilient conservation and resource management (Lindgren et al. 2011, Crear et al. 2021). Prolonged MHWs in the NEP have been linked to widespread ecosystem changes that have exacerbated human-wildlife conflicts (e.g. whale entanglements and sea turtle bycatch; Santora et al. 2020) and intensified socio-economic stress on fishing communities (e.g., decreased catch or shifting fishing grounds; (Fisher et al. 2020, Smith et al. 2021, Free et al. 2023, Farchadi et al. 2024). With increased uncertainty about how future, extreme climate events will affect the displacement of species and fisheries, the ability to quickly adapt to such novel conditions poses considerable challenges for marine conservation and management (Fisher et al. 2020, Samhoury et al. 2021). Therefore, there is a critical need for skillful ecological forecasts that provide advanced warnings on relevant timescales for decision-making, enabling a more proactive management framework capable of keeping pace with MHWs (Brodie et al. 2023). For example, in

the case of transboundary fisheries like albacore tuna, which have exhibited cross-jurisdictional shifts under MHWs (Welch et al. 2023), the ability to leverage data across geographical and political regions can yield more accurate predictions of how albacore may redistribute during future extreme climate events. Here, we demonstrate the utility of model-based data integration in ecological forecasting and offer insights on best practices for integrating diverse data sources when predicting into uncertain and variable future conditions. Although extremely novel environmental conditions may always pose challenges (Pinsky and Mantua 2014, Pinsky et al. 2021), iSDMs are well-positioned to readily integrate disparate sources in a way that retains the strengths of each and can better inform potential ecological impacts of extreme events (Isaac et al. 2020, Chevalier et al. 2021).

Our study adds to the growing body of literature that indicates the utility of iSDMs (Isaac et al. 2020) and echoes calls to continue exploring their performance under different applications through retrospective skill testing (Thorson 2018, Barnes et al. 2022). For example, operational forecasts of SST in the California Current, when configured for specific management applications, have demonstrated skillful predictions up to 12 months in advance (Brodie et al. 2023). Incorporating such forecasting tools into an iSDM framework could enhance near-term seasonal forecasts of species distributions, though further studies are needed to evaluate their contribution and determine at what lead times do forecasts remain skillful (Thorson 2018, Brodie et al. 2023). Furthermore, while our study demonstrated that broader species-environment response curves may help buffer prediction skill against environmental novelty, previous studies have suggested that non-stationarity could impact model performance (Yates et al. 2018, Ward et al. 2022) – highlighting the need for additional research to understand how non-stationarity in environmental relationships can be accounted for when forecasting (Yates et al. 2018). As our social-ecological systems face increasingly novel conditions under climate change, enhancing our capacity to leverage growing, diverse datasets will be essential for developing robust models that support conservation and management decisions

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